GENETIC STUDIES ON QUANTITATIVE CHARACTERS IN SOYBEAN

VI. Gene number and gene effects for certain agronomic characters

FU-Sheng THSENG and Sadaji HOSOKAWA

(Laboratory of Industrial Crops, Faculty of Agriculture, Hokkaido University, Sapporo, Japan)

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As mentioned in our previous paper (THSENG and HOSOKAWA 1972 c) soybean varieties can be classified into three types according to growth habit: determinate, semi-indeterminate and indeterminate types. In general, the varieties of the latter two types have favorable characters. They have a higher productivity than varieties of the determinate types and are widely grown in soybean-growing countries, but have not been cultivated in Japan.

Introduction of indeterminate type characters into the determinate variety for breeding of "semi-indeterminate type" would be of value to soybean breeding in Japan. To facilitate the breeding program it was decided to study the inheritance of agronomic characters from the above two type varieties. The results of certain of these studies are reported in this paper.

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Materials and Methods

Two soybean varieties, Sangowase (P_1) (Japanese variety, determinate) and Harosoy (P_2) (U. S. A. variety, indeterminate), were used in this study. The cross was made in the summer of 1969 and thirty F_1 plants were grown to produce the F_2 generations, and sixty F_1 plants were used to develop backcross generations (F_1 to Sangowase and F_1 to Harosoy) in the next year.

On May 22, 1971, the P_1, P_2, F_1, F_2, P_1B_1 and P_2B_1 plants were planted in the farm of the Tokachi Agricultural Experiment Station, Hokkaido. The experimental design followed a modified randomized complete block with 12 replications. Every block contained each one plot of the P_1, P_2, F_1, P_1B_1 and P_2B_1, and three plots of the F_2 plants. Each plot contained 20 plants, 15 of them being used for study. Planting was made individually with a spacing 60×20 cm.

The following characters were measured for each plant in every population:

1) plant height, 2) number of branches, 3) number of nodes on stem, 4) number of nodes on branches, 5) number of nodes/plant, 6) number of pods on stem, 7) number of pods on branches, 8) number of pods/plant, 9) number of seeds/plant and 10) seed weight/plant.

The data were analysed and interpreted on the basis of the biometrical techniques developed by POWERS (1942, 1950, 1951, 1955), POWERS, *et al.* (1950), JINKS, *et al.* (1957) and HAYMAN (1958, 1960).

Results

1. Plant height

a. Magnitude of character difference and dominance

As shown in Table 1, Harosoy (P_2) plants averaged 72.30 and Sangowase (P_1) plants 21.37, or 50.93 low. The genetic variance for the F_2 population is greater than that for either backcross, and the genetic variance for P_2B_1 is greater than that for P_1B_1. The mean of the F_1 (48.50) lies somewhat closer to the mean of Harosoy than to that of Sangowase, the mean of P_1B_1 (35.31) closer to that of F_1 than to that of P_1, and the mean of P_2B_1 (60.73) lies somewhat closer to that of the Harosoy (P_2) than to that of

TABLE 1. Means ($\bar{x}$), standard errors ($\sigma_{\bar{x}}$), and phenotypic (σ_P) and genotypic (σ^2_G) variances of different populations for plant height

Population	$\bar{x}$	$\sigma_{\bar{x}}$	σ^2_P	σ^2_G	No. of plants
P_1	21.37	0.2169	8.2792		177
P_1B_1	35.31	0.6550	75.8780	57.2068	226
F_1	48.50	0.3814	22.1063		150
F_2	47.47	0.5366	150.0230	131.3518	522
P_2B_1	60.73	0.6054	96.5364	77.8652	208
P_2	72.30	0.4147	25.6268		153

F_1. These findings show that phenotypic dominance was partial for tall plants and indicate that genic dominance was also partial.

b. Number of gene pairs differentiating the parents

The assumption is made that the parents are differentiated by three gene pairs. Examination of the frequency distributions for plant height (Table 2) reveals that 25.2% of P_1B_1 plants fell into 30-class and 20-class. Of that P_2B_1 population, 8.6% of the plants fell into 70 or more class. The following genes have been assumed for high and low plant height:

TABLE 2. Frequency distribution (expressed in percentage) for plant height in each population

Population	Upper limit of class							
	20	30	40	50	60	70	80	90
P_1	29.4	70.6						
P_1B_1	5.3	19.9	48.7	19.0	6.2	0.9		
F_1			6.0	56.7	37.3			
F_2	1.9	5.4	23.6	26.1	29.7	11.5	1.5	0.4
P_2B_1			1.4	12.0	46.6	31.3	6.7	1.9
P_2						30.1	64.1	5.8

AA dominant genes for high plant *vs. aa* recessive gene for low plant.
BB dominant genes for high plant *vs. bb* recessive gene for low plant.
cc recessive gene for high plant *vs. CC* dominant genes for low plant.
Thus, the P_1 parent is symbolized as *aabbCC* and P_2 as *AABBcc*.

The means of the P_1 (21.37), P_2 (72.30) and F_1 (48.5) given in Table 1 were used to obtain a rough estimate of the effects of genes in the genotypes of the F_2 and backcross populations (POWERS, *et al.* 1950). The differences in the means of plant height are: between P_1 and F_1, 27.13 (48.50–21.37); between F_1 and P_2, 23.8 (72.3–48.5); between P_1 and P_2, 50.93 (72.3–21.37). The values 27.13 and 23.8 are 53.27 (27.13/50.93) and 46.73 (23.8/50.93) percent, respectively, of 50.93. With these percentage figures available, the effect of the substitution of a gene tending to produce higher plants can be roughly estimated for F_2 population. The percentage effects added in going from *aabbCC* (P_1) to *AaBbCc* (F_1) are $53.27(A)+53.27(B)+46.73(c)$, or a total of 153.27. On this basis, *A* or *B* adds 0.347 (53.27/153.27), and *c* adds 0.304 (46.73/153.27). Therefore, in the genotypes of P_1B_1 substitution of *A* or *B* results in an increase of 9.41 (0.347×27.13) and substitution of *c* results in an increase of 8.24 (0.304×27.13). In the genotypes of P_2B_1, substitution of *A* or *B* results in a 53.27% gain and

TABLE 3. Expected mean ($\bar{x}$), standard error (σ), and frequency distribution of plant height for each genotype in segregating population

Population and genotype	$\bar{x}$	σ	Upper limit of class 20	30	40	50	60	70	80	90	Expected percentage in
aabbCC	21.37	3.1591	33.0	66.7							1.5625
aabbCc	29.61	3.5440	0.4	54.6	43.9						3.1250
aaBbCC	30.78	3.6658		27.1	71.2	1.7					3.1250
AabbCC											3.1250
aabbcc	37.85	3.8915		2.6	71.0	26.4					1.5625
aaBbCc	39.02	4.0023		0.5	52.3	46.4	0.8				6.2500
AabbCc											6.2500
aaBBCC	40.19	4.0872		0.1	70.4	26.7	2.8				1.5625
AAbbCC											1.5625
AaBbCC	40.36	4.1106		0.1	76.9	18.4	4.6				6.2500
aaBbcc	47.26	4.3130			2.6	61.8	35.2	0.4			3.1250
Aabbcc											3.1250
AaBBCC	47.53	4.3300			2.1	58.5	38.9	0.5			3.1250
AABbCC											3.1250
aaBBCc	48.50	4.4133			0.6	59.7	37.5	2.2			3.1250
AAbbCc											3.1250
AaBbCc											12.5000
AABBCC	55.04	4.5679				11.5	72.4	16.1			1.5625
AaBBCc	56.10	4.6470				4.7	63.7	31.2	0.4		6.2500
AABbCc											6.2500
aaBBcc	56.50	4.6969				3.4	66.5	30.1			1.5625
AAbbcc											1.5625
AaBbcc	57.17	4.7246				1.7	48.7	47.9	1.7		6.2500
AABBCc	64.67	4.8694				0.2	81.4	5.9	2.5		3.1250
AaBBcc	64.73	4.9436					8.9	66.0	24.8	0.3	3.1250
AABbcc											3.1250
AABBcc	72.30	5.1533					0.5	73.4	16.4	9.7	1.5625
P_1B_1			4.2	22.1	46.1	21.8	5.5	0.3			
F_2			1.5	4.3	21.0	28.0	31.6	12.4	1.4	0.2	
P_2B_1					0.2	8.9	48.2	33.0	6.1	1.3	

substitution of *c* in a 46.73% gain. Therefore, the difference between plants of F_1 (*AaBbCc*) and P_2 (*AABBcc*) genotypes is 146.73 (46.73+46.73+53.27), *A* and *B* contribute 7.57 ((46.73/146.73)×23.8) and *c* contributes 8.63 ((53.27/146.73)×23.8).

The expected means of the genotypes for the backcross and F_2 populations (Table 3) were calculated from these estimates of effects of genes substitution.

Table 1 showed that the means and the variances of nonsegregating populations were positively correlated. Assuming that their relationship is linear, the variances and standard errors (single determination) of plants of each genotype in the F_2 population, can be estimated using the formula $y=mx+b$ (POWERS 1942). The results of this computation of standard errors are given in Table 3.

With these means and standard errors, the expected percentage frequency distributions for the each genotype and segregating populations were estimated by the method described by POWERS, *et al.* (1950) and are listed in Table 3.

The expected and observed frequency distributions for three segregating populations, χ^2 values for testing goodness of fit, and P-values are given in Table 4. These results indicated a good fit and supported the hypothesis that the two parents were differentiated by three gene pairs with respect to the plant height.

TABLE 4. Expected and observed frequency distribution, χ^2 value for testing goodness of fit, degree of freedom, and P-value for plant height

Population	Upper limit of class 20	30	40	50	60	70	80	90	χ^2	d.f.	P-values
P_1B_1											
Expected	9	50	104	49	12	2			2.8654	4	0.60–0.50
Observed	12	45	110	43	14	2					
F_2											
Expected	8	22	110	146	165	65	7	1	5.8481	6	0.50–0.40
Observed	10	28	123	136	155	60	8	2			
P_2B_1											
Expected			2	21	100	69	13	3	1.6534	3	0.70–0.60
Observed			3	25	97	65	14	4			

2. Number of Branches

a. Magnitude of character difference and dominance

The mean values of number of branches (Table 5) show that Sangowase (P_1) has a mean of 3.12 and Harosoy (P_2) of 8.78. The magnitude of the difference between the two parents is 5.66.

The mean of F_1 (8.45) equals the mean of P_2B_1 (8.46). The mean of the P_2 (8.78) is slightly greater than the mean for either F_1 or P_2B_1, but the difference is not significant. This indicates almost complete phenotypic dominance of more branches over fewer branches.

The genetic variance of P_2B_1 is very small (Table 5). This indicates that probably the genetic dominance is also complete.

TABLE 5. Means ($\bar{x}$), standard errors ($\sigma_{\bar{x}}$), and phenotypic (σ^2_P) and genotypic (σ^2_G) variances of different populations for number of branches

Population	$\bar{x}$	$\sigma_{\bar{x}}$	σ^2_P	σ^2_G	No. of plants
P_1	3.12	0.0581	0.5938		177
P_1B_1	5.64	0.1357	4.1421	2.9816	226
F_1	8.45	0.1068	1.6992		150
F_2	7.03	0.0998	5.1875	4.0272	522
P_2B_1	8.46	0.0939	1.8240	0.6635	208
P_2	8.78	0.1094	1.1887		153

b. Number of gene pairs differentiating the parents

The assumption is made that the two parents are differentiated by two gene pairs. The indication that two gene pairs are involved is obtained by F_2/P_1 (POWERS 1955) which gives a percentage value from 7.1 to 16.8 in

TABLE 6. Frequency distributions (expressed in percentage) of different populations for number of branches

Population	Upper limit of class										
	1	2	3	4	5	6	7	8	9	10	11
P_1	2.8	12.4	58.2	23.2	3.4						
P_1B_1	0.9	4.4	12.0	15.9	12.8	18.6	13.3	12.8	9.3		
F_1						6.0	20.0	24.0	29.3	14.0	6.7
F_2	0.2	1.1	4.0	10.9	7.3	14.5	16.5	17.4	17.6	6.3	4.0
P_2B_1						6.7	19.7	24.0	28.4	12.5	8.7
P_2						2.6	18.3	20.9	27.5	18.3	12.4

the first three estimates (F_2/P_1 is calculated in each class 1, 2 ,3 and 4, *cf* Table 6). On a two-gene-pairs basis, 6.25% is expected. Accordingly, the genotypes of P_1 are symbolized as *aabb* and of P_2 as *AABB*.

The frequency distributions of P_1B_1 and P_2B_1 (Table 6) are partitioned into their component genotypes as in Table 7. Row number 1 gives the frequency distribution of P_1B_1 population. In the P_1B_1 populption, the *AaBb* (F_1) and *aabb* (P_1) constitute 50% of the population. The frequency distribution of F_1 and P_1 for each class is multiplied by its theoretical percent, divided by 100, and then summed. Thus, row 2 gives the frequency distribution of F_1+P_1 genotypes. The difference between row 1 and row 2 gives the frequency distribution of the remaining two genotypes (*Aabb*, *aaBb*) of the P_1B_1 population as listed in row 3. This frequency distribution is then weighted on 100% basis and is given in row 4. Similarly, the P_2B_1 population is partitioned into its component genotype. The frequency distribution of genotypes (*AaBB*, *AABb*) of P_2B_1 population is obtained and given in row 8. On the basis of the frequency distribution for different genotypes of the P_1B_1 and P_2B_1 populations, the expected frequency distributions for F_2 genotypes are obtained. The only genotypes which do not occur in either of the backcross populations are *AAbb* and *aaBB*. Table 5 indicated complete genic dominance of more branches over fewer branches. Thus, for calculating the frequency distribution of the *AAbb*+*aaBB* genotypes, the frequency distribution of the *Aabb*+*aaBb* genotypes has been used (Table 8).

TABLE 7. Partitioning the frequency distributions of backcrosses into their component genotypes for number of branches

Population and genotype	Rew no.	Upper limit of class 1	2	3	4	5	6	7	8	9	10	11	Expected percentage
P_1B_1	1	0.9	4.4	12.0	15.9	12.8	18.6	13.3	12.8	9.3			100.00
P_1+F_1 (*aabb*+*AaBb*)	2	0.7	3.1	14.5	5.8	0.9	1.5	5.0	6.0	7.3	3.5	1.7	50.00
Row 1-2	3	0.2	1.3	−2.5	10.1	11.9	17.1	8.3	6.8	2.0	−3.5	−1.7	50.00
Row 3 (%)	4				18.2	23.8	34.2	16.6	7.2				100.00
P_2B_1	5						6.7	19.7	24.0	28.4	12.5	8.7	100.00
P_2+F_1 (*AABB*+*AaBb*)	6						2.2	9.6	11.2	14.2	8.1	4.8	50.00
Row 5-6	7						4.5	10.1	12.8	14.2	4.4	3.9	50.00
Row 7 (%)	8						9.0	20.2	25.6	28.4	8.8	7.8	100.00

TABLE 8. Expected frequency distribution (expressed in percentage) of number of branches for each genotype in F_2 population

Population and genotype	Upper limit of class											Expected percentage
	1	2	3	4	5	6	7	8	9	10	11	
AABB						2.6	18.3	20.9	27.5	18.3	12.4	6.25
AaBB						9.0	20.2	25.6	28.4	8.8	7.8	25.00
AABb												
AaBb						6.0	20.0	24.0	29.3	14.0	6.7	25.00
AAbb				18.2	23.8	34.2	16.6	7.2				12.50
aaBB												
Aabb				18.2	23.8	34.2	16.6	7.2				25.00
aaBb												
aabb	2.8	12.4	58.2	23.2	3.4							6.25
F_2	0.2	0.8	3.6	8.4	9.2	16.9	17.5	16.4	15.9	6.8	4.3	

The expected frequency distribution (Table 8) for the F_2 is obtained by taking the expected percentage of the distributions, then adding the results for each class (POWERS, *et al.* 1950).

The test for goodness of fit between observed and expected F_2 distributions gives a χ^2 value of 10.9774, and the P-value is between 0.3 and 0.2 (Table 9). This supports the hypothesis that the two parents are differentiated by two gene pairs.

TABLE 9. χ^2 value for testing goodness of fit between expected and observed frequency distribution in F_2 population for number of branches

Population	Upper limit of class											No. of plants
	1	2	3	4	5	6	7	8	9	10	11	
	expressed in percentage											
Expected	0.2	0.8	3.6	8.4	9.2	16.9	17.5	16.4	15.9	6.8	4.3	522
Observed	0.2	1.1	4.0	10.9	7.3	14.5	16.5	17.4	17.6	6.3	4.0	522
	expressed in number											
Expected	1	4	19	44	48	88	91	86	83	35	22	522
Observed	1	6	21	57	38	76	86	91	92	33	21	522

$\chi^2 = 10.9774$
d.f. = 9
P = 0.30–0.20

3. Node Number on Stem

a. Magnitude of character difference and dominance

The mean values of the node number on stem for the various generations are given in Table 10. It can be seen that the mid-parental mean (16.65) is slightly lower than the mean of F_1 (17.67), indicating the slight phenotypic dominance exhibited in greater node number. On the other hand, the mean of P_1B_1 (13.50) approximates the average of the mean of P_1 and F_1 (13.52=(9.37+17.67/2), and the mean of P_2B_1 (20.50) appoximates the average of P_2 and F_1 (19.97=(17.67+23.94/2). These results indicate that the genic dominance is intermediate and there is no interaction of genes.

TABLE 10. Means ($\bar{x}$), standard errors ($\sigma_{\bar{x}}$), and phenotypic (σ^2_P) and genotypic (σ^2_G) variances of different populations for node number on stem

Population	$\bar{x}$	$\sigma_{\bar{x}}$	σ^2_P	σ^2_G	No. of plants
P_1	9.37	0.0477	0.3452		177
P_1B_1	13.50	0.2132	10.2251	9.5596	226
F_1	17.67	0.0543	0.5193		150
F_2	17.30	0.1715	15.3230	14.6575	522
P_2B_1	20.50	0.1836	6.9743	6.3088	208
P_2	23.94	0.0872	1.1322		153

b. Number of gene pairs differentiating the parents

Table 11 reveals that 22.1% of the plants of the P_1B_1 population fall in the upper limit of 10-class. Thus, (22.1/100)×100 or 22.1% of the plants of P_1B_1 show the same characteristics as the plants of P_1 with respect to

TABLE 11. Frequency distributions (expressed in percentage) of different populations for node number on stem

Population	Upper limit of class									
	8	10	12	14	16	18	20	22	24	26
P_1	13.0	87.0								
P_1B_1		22.1	7.5	29.7	14.2	16.4	10.2			
F_1					12.0	68.0	20.0			
F_2		5.9	2.9	16.7	10.3	23.2	15.9	16.1	6.3	2.7
P_2B_1					1.0	16.8	24.0	29.8	18.3	10.1
P_2								4.6	85.6	9.8

the upper limit of 10-class and lower classes (theoretically, when parents are differentiated by two gene pairs, as they are here, the expected value is 25%). By studying the genetic variance in P_1B_1 and P_2B_1 populations (Table 10), it is obvious that the genetic variance of P_2B_1 is lower than the P_1B_1, which indicates that genic dominance is involved in P_2. Accordingly, the hypothesis of the genotype of P_1 is symbolized as *aabb* and of P_2 as *AABB*.

The means of P_1 and P_2 are 9.37 and 23.94, respectively. Thus, the total effect of these two gene pairs on the mean is 14.57 (23.94−9.37), and the effect of any one of the genes is 14.57/4, or 3.64. However, a slightly phenotypic dominance for small node number is observed, and the degree of dominance is determined as 17.67−(23.94+9.37)/2, or 1.02 node. The effect of *Aa* gene tending to produce small node was 1.02 node greater than that of *aa* gene. By using the effect of each gene as estimated above, the expected means of 9 genotypes of the F_2 population could be obtained. They are recorded in Table 12.

Table 10 shows that the means and the variances of nonsegregating populations were positively correlated. Assuming that their relationship is linear, the variances and standard errors (single determination) of plants of each genotype in the F_2 population, can be estimated using the formula $y=mx+b$. These results are given in Table 12.

TABLE 12. Expected means ($\bar{x}$), standard errors (σ), and frequency distributions of genotypes in segregating populations for node number on stem

Population and genotype	$\bar{x}$	σ	Upper limit of class 8	10	12	14	16	18	20	22	24	26	28	Expected percentage in B_1	F_2
AABB[1)]	23.94	1.0291								2.9	49.5	45.3	2.3	25.00	6.25
AaBB[1)]	21.39	0.9598							7.4	66.5	25.8	0.3		25.00	12.50
AABb[1)]	20.30	0.9286						0.7	36.7	59.2	3.4			25.00	12.50
AaBb[1,2)]	17.75	0.8512					2.0	59.4	38.2	0.4				25.00	25.00
AAbb} *aaBB*}	16.66	0.8158				0.1	20.8	74.0	5.1						12.50
Aabb[2)]	14.11	0.7264			0.2	43.8	55.5	0.5						25.00	12.50
aaBb[2)]	13.02	0.6847			6.8	85.6	7.6							25.00	12.50
aabb[2)]	9.38	0.5216	0.4	87.9	11.7									25.00	6.25
P_1B_1			0.1	21.9	4.7	32.4	16.3	14.9	9.6	0.1					
F_2				5.5	1.6	16.2	11.0	24.3	15.7	15.9	6.8	2.9			
P_2B_1							0.5	15.0	20.6	32.3	19.7	11.4	0.5		

1) and 2) occurring in P_1B_1 and P_2B_1 population, respectively.

With these means and standard errors, the expected percentage frequency distributions for 9 genotypes and P_1B_1, P_2B_1 and F_2 populations were estimated and are listed in Table 12.

The expected and observed frequency distributions for three segregating populations, χ^2 values for testing goodness of fit, and P-values are given in Table 13. These results indicated a good fit and supported the hypothesis that the two parents were differentiated by two gene pairs.

TABLE 13. Expected and observed frequency distributions, χ^2 values for testing goodness of fit, degrees of freedom, and P-values for node number on main stem

Population	Upper limit of class 10	12	14	16	18	20	22	24	26	χ^2	d. f.	P-values
P_1B_1												
Expected	49	11	73	37	34	21				4.9169	5	0.50–0.40
Observed	50	17	67	32	37	23						
F_2												
Expected	29	8	85	57	127	82	83	35	15	6.9560	8	0.60–0.50
Observed	31	15	87	54	121	83	84	33	14			
P_2B_1												
Expected				1	31	43	67	41	24	2.1151	4	0.60–0.50
Observed				2	35	50	62	38	21			

4. Node Number on Branches

a. Magnitude of character difference and dominance

The mean values for node number on branches (Table 14) show that the P_1 gave a mean value of 9.5, and the P_2, 36.65. The magnitude of the difference between the two parents is 26.15.

TABLE 14. Means ($\bar{x}$), standard errors ($\sigma_{\bar{x}}$), and phenotypic (σ^2_P) and genotypic (σ^2_G) variances of different populations for node number on branches

Population	$\bar{x}$	$\sigma_{\bar{x}}$	σ^2_P	σ^2_G	No. of plants
P_1	9.50	0.1711	5.1491		177
P_1B_1	17.03	0.5312	113.4968	50.2031	226
F_1	22.21	0.7253	78.3723		150
F_2	23.57	0.5022	131.3825	68.0888	522
P_2B_1	30.14	0.7339	111.4829	48.1892	208
P_2	36.65	0.8365	106.3599		153

If phenotypic dominance is intermediate and gene effects are additive, the F_1 mean should equal the average of the means of the two parents. The average of the means of the two parents is 23.07 ((36.65+9.5)/2), which is slightly higher than the mean of F_1 (22.21) but not significantly so. The mean of the P_1B_1 (17.03) approximates the average of the mean of P_1 and F_1 (15.86=(22.21+9.50)/2), and the mean P_2B_1 (30.14) approximates the average of P_2 and F_1 (29.43=(22.21+36.65)/2). These values are those expected if gene effects are additive and there is no genic dominance.

b. Number of gene pairs differentiating the parents

The hypothesis is proposed that the two parents are differentiated by two gene pairs. The indication that two gene pairs are involved is obtained by dividing 1.5 (upper limit of 56-class of P_2B_1) by 5.9 (upper limit of class from 56 to 64 classes of P_2) (refer to Table 15), which gives a value of 25.4%, whereas on a two-gene-pairs basis 25.0% is expected. By studying the genetic variance in P_1B_1 and P_2B_1 populations (Table 14), it can be seen that the genetic variance of P_1B_1 was lower than the P_2B_1 population which indicated genic dominance is involved in P_1. Thus, the genotypes of P_1 are symbolized as *AABB* and of the P_2 as *aabb*.

The means of P_1 and P_2 are 9.5 and 36.65, respectively. Thus the total effects of these two gene pairs on the mean was 36.65−9.50, or 27.15, and the effect of any one of the genes was 27.15/4, or 6.79. However, a slightly phenotypic dominance for small node was observed, and the degree of dominance is determined as 22.21−(36.65+9.5)/2, or −1 node. The effect of *Bb* gene tending to produce small node was 1 node greater than that of *BB* gene. By using the effect of each gene as above, the expected means of 9 genotypes of the F_2 population could be obtained (Table 16).

Table 14 showed that the means and the variances of nonsegregating populations were positively correlated. Assuming that their relationship is linear, the variances and standard errors (single determination) of plants of each genotype in the F_2 population, can be estimated using the formula $y=mx+b$, the results of which can be found in Table 16.

With these means and standard errors, the expected percentage frequency distributions for 9 genotypes and P_1B_1, P_2B_1 and F_2 populations were estimated and are listed in Table 16.

The expected and observed frequency distributions for three segregating populations, χ^2 values for testing goodness of fit, and P-values are given in Table 17. These results indicated a good fit and supported the hypothesis that the two parents were differentiated by two gene pairs.

TABLE 15. Frequency distributions (expressed in percentage) of different populations for node number on branches

Population	Upper limit of class															
	4	8	12	16	20	24	28	32	36	40	44	48	52	56	60	64
P_1	5.6	17.0	63.8	13.6												
P_1B_1	1.8	10.2	19.9	22.1	17.7	12.8	5.3	5.3	2.7	1.3	0.9					
F_1				10.7	18.0	25.3	13.3	12.0	6.7							
F_2	2.1	5.4	10.5	12.6	14.2	13.0	11.5	9.2	7.7	5.0	3.6	2.3	2.1	0.6		
P_2B_1		1.4	1.9	5.8	9.6	10.6	17.8	13.9	12.5	10.1	6.7	5.8	2.4	1.5		
P_2				0.7	3.9	7.8	11.1	13.7	20.9	13.1	11.1	7.2	5.2	2.6	2.0	1.3

TABLE 16. Expected means ($\bar{x}$), standard errors (σ), and frequency distributions of node number on branches for each genotype in segregating populations

Population and genotype	$\bar{x}$	σ	Upper limit of class														Expected percentage in	
			4	8	12	16	20	24	28	32	36	40	44	48	52	56	B_1	F_2
AABB[1)]	36.65	10.6729		0.4	0.6	1.7	3.2	5.8	9.2	12.1	14.6	14.6	13.3	10.0	7.0	7.5	25.0	6.25
AaBB[1)]	29.86	9.4619		1.0	1.8	4.0	7.4	11.6	15.5	16.6	15.3	12.1	7.6	4.2	2.9		25.0	12.50
AABb[1)]	28.86	9.2628		1.1	2.1	4.6	8.6	12.7	16.1	17.0	14.8	11.1	6.5	3.3	2.1		25.0	12.50
AAbb *aaBB*	23.07	7.9550	0.8	2.1	5.3	10.5	16.1	20.0	18.4	13.7	7.9	3.5	1.7				25.0	25.00
AaBb[1,2)]	22.07	7.8393	0.9	2.2	5.8	11.1	17.1	20.0	18.4	13.0	7.1	3.1	1.3					12.50
Aabb[2)]	16.28	6.0887	2.4	6.9	16.2	24.1	24.6	16.3	7.0	2.5							25.0	12.50
aaBb[2)]	15.28	5.7744	2.8	8.3	18.7	26.9	23.8	13.4	4.8	1.3							25.0	12.50
aabb[2)]	9.50	3.5622	6.2	27.5	42.1	20.9	3.3										25.0	6.25
P_1B_1			3.1	11.2	20.6	20.6	16.9	12.4	7.6	4.4	2.0	0.9	0.4					
F_2			1.4	4.7	9.6	12.9	14.6	14.6	12.9	10.5	7.5	5.1	3.2	1.6	1.1	0.4		
P_2B_1			0.2	1.2	2.5	5.2	8.8	12.5	14.8	14.8	13.2	10.3	7.3	4.4	3.0	1.9		

1) and 2) occurring in P_1B_1 and P_2B_1 population, respectively.

TABLE 17. Observed and expected frequency distributions, χ^2 values for testing goodness of fit, degrees of freedom, and P-values for node number on branches

Population	Upper limit of class 4	8	12	16	20	24	28	32	36	40	44	48	52	56	d.f.	χ^2	P
P_1B_1																	
obs.	4	23	45	50	40	29	12	12	6	3	2				7	3.657	.9–.8
exp.	7	25	47	47	38	28	17	10	4	2	1						
F_2																	
obs.	11	28	55	66	74	68	60	48	40	26	19	12	11	3	12	10.650	.6–.5
exp.	7	25	50	67	76	76	67	55	39	27	17	8	6	3			
P_2B_1																	
obs.		3	4	12	20	22	37	29	26	21	14	12	5	2	10	4.322	.9–.8
exp.		2	5	11	18	26	31	31	28	21	15	9	6	4			

5. Node Number/plant

a. Magnitude of character difference and dominance

From the mean values listed in Table 18, it can be seen that node number/plant of P_1 is 19.86, and the P_2 is 59.60. Thus, there is a difference of 39.74 between the two parents. If phenotypic dominance is intermediate, the mean of F_1 approximates the average of the means of the two parents (39.73). As shown in Table 18, the close similarity of these two values shows that phenotypic dominance was intermediate. If genic dominance was also intermediate and there was no interaction of the genes, that is. if the effects wers additive, then it would be expected that the mean of P_1B_1 would equal the average of the means of P_1 and F_1, the mean of the F_2 would equal that of the F_1, and the mean of P_2B_1 would equal the

TABLE 18. Means $\bar{x}$, standard errors ($\sigma_{\bar{x}}$), and phenotypic (σ^2_P) and genotypic (σ^2_G) variances of different populations for node number

Population	$\bar{x}$	$\sigma_{\bar{x}}$	σ^2_P	σ^2_G	No. of plants
P_1	19.86	0.1937	6.6065		177
P_1B_1	25.02	0.5138	67.4020	2.5749	226
F_1	39.29	0.7612	86.3429		150
F_2	34.25	0.5896	181.0875	116.2604	522
P_2B_1	49.34	0.8706	156.8866	92.0595	208
P_2	59.60	0.8173	101.5321		153

average of the means of the F_1 and P_2. The average of the means of the P_1 and F_1 is 29.58, and the P_2 and F_1 is 49.45. By comparing these figures with those in Table 18, it can be seen that the magnitude of the mean of P_2B_1 is that expected, but the means of the F_2 and P_1B_1 are lower than expected compared to the mean of F_1 and the average of the means of F_1 and P_1, respectively. For this reason, and since the mean of the F_1 is intermediate between the means of the two parents, multiple-factor inheritance must have been involved and both intra- and interallelic interactions must have operated to produce the results noted. The inter-allelic interactions were supposed to diminish the effect of the genes tending to produce such a high node number as genes tending to produce a low node number increased in the genotype.

b. Number of gene pairs differentiating the parents

As mentioned above, an examination of the values given in Table 18 shows that the mean of F_1 (39.29) is not significantly different from the average of the means of the two parents (39.73) and that the mean of P_2B_1 is not significantly different from the average of means of F_1 and P_2. This indicates that the effects of genes were additive both within and between gene pairs. However, the mean of P_1B_1 is lesser than the average of means of F_1 and P_1. This indicates that effects of genes were not the same throughout all genotypes, but that genes tending to increase node number had a greater effect in genotypes of P_2B_1 than in genotypes of P_1B_1. These results suggest that effects of the genes were additive in all genotypes having at least one dominant gene in each of the gene pairs, and that dominant gene had a greater effect in these genotypes than they did in genotypes having at least one recessive gene pair.

Since number of nodes on stem and on branches were conditioned by two gene pairs respectively, number of nodes per plant should be differentiated by four gene pairs (refer to Table 19). Thus, the genotypes of P_1 are symbolized as *aabbccdd* and of P_2 as *AABBCCDD*.

In order to partition the backcross and F_2 population into their genotypes, it was necessary to have an estimate of the effect that a gene contributes. Results already stated show that the dominant genes had a greater effect in the genotypes having at least one gene present in each gene pair. The effects of a single gene in those genotypes were determined from the P_2 and F_1 population mean by the following procedure (POWERS, *et al.* 1950).

From Table 18 it can be seen that the mean of P_2 is 59.60 and the mean of F_1 is 39.29. These two populations differ by four dominant genes.

TABLE 19. Frequency distributions (expressed in percentage) of different populations for node number

Population	Upper limit of class								
	20	30	40	50	60	70	80	90	100
P_1	59.9	40.1							
P_1B_1	25.2	54.0	17.3	3.1	0.4				
F_1	2.7	21.3	34.7	30.7	10.7				
F_2	10.9	35.6	25.3	15.3	8.4	2.9	1.5		
P_2B_1		4.8	19.2	31.3	26.4	13.9	3.9	0.5	
P_2			0.7	18.3	41.8	26.1	9.8	2.6	0.7

Therefore, the total effect of these four genes on the mean was 20.31 (59.60−39.29). When the gene designated as *A* is assumed to have the same effect as the total effect of the other three genes, the effect is 10.16 (20.31/2). Thus, the effect of each of the other three genes is 3.39 (10.16/3).

The effect of the dominant genes in those genotypes having both genes in at least one of the four recessive gene pairs was estimated from the means of the F_1, P_1B_1 and P_1 populations. The procedure was as follows:

The P_1B_1 population possessed one genotype (*AaBbCcDd*) that had a dominant gene in each gene pair. This is the genotype of the F_1, and in estimating the effect of a single dominant gene, its effects had to be subtracted. From Table 18 it can be seen that the mean of P_1B_1 population is 25.02. The least number of individuals necessary for a population having all genotypes of the backcross is 16. Since the average of such a population is 25.02, the estimated total is 400.32 (25.02×16). The percentage contributed by the *AaBbCcDd* and *aabbccdd* genotypes to this total is 59.19 (19.86 (P_1) + 39.29 (F_1)). Subtracting this contribution from the total of the theoretical P_1B_1 population gives the value 341.13 (400.32−59.19). This is the theoretical total for the remaining 14 genotypes of the theoretical P_1B_1 population, and the mean is 24.37 (341.13/14). The difference between this mean and the mean of P_1 is 4.51 (24.37−19.86). Since these 14 genotypes differ from the genotype of P_1, on an average, by two dominant genes, the effect of the four genes is twice this sum, or 9.02. Since the effect of the *A* gene equals the effect of the other genes combined, it is 4.51 and the effect of *B*, *C*, or *D* is 1.5 (4.51/3).

The expected means given in Table 20 were obtained by starting with 19.86 for the genotype *aabbccdd* (P_1), adding 4.51 for each *A* gene and 1.5 for each *B*, *C* or *D* gene until the genotype, whose mean was under consideration, had at least one dominant gene in each of the four pairs, and

TABLE 20. Expected means ($\bar{x}$), standard errors (σ), and frequency distributions of genotypes in segregating populations for node number

Population and genotype	$\bar{x}$	σ	Upper limit of class										Expected percentage in	
			10	20	30	40	50	60	70	80	90	100	B_1	F_2
AABBCCDD[1]	59.62	10.6388			0.3	3.0	15.1	33.2	32.0	13.7	2.5	0.2	6.25	0.390625
AABBCCDd[1]	56.23	10.2471			0.5	5.2	21.4	37.3	27.1	7.5	1.0		18.75	2.343750
AABBCcDd[1]	52.84	9.8398			1.0	8.7	28.9	38.1	19.2	3.8	0.3		18.75	4.687500
AABbCcDd } [1] *AaBBCCDD* }	49.45	9.4149		0.1	1.8	14.0	36.5	34.5	11.6	1.5			12.50	3.906250
AaBBCCDd[1]	46.07	8.9712		0.2	3.4	21.2	42.2	26.9	5.7	0.4			18.75	4.687500
AaBBCcDd[1]	42.68	8.5030		0.4	6.4	30.6	43.1	17.4	2.0	0.1			18.75	9.375000
AaBbCcDd[1,2]	39.29	8.0074		0.8	11.5	41.3	37.4	8.5	0.5				6.25	6.250000
AABBCCdd	34.86	7.3094		2.1	23.4	50.3	22.3	1.9						1.171875
AABbccDD	33.36	7.0574		2.9	28.7	51.0	16.5	0.9						4.687500
AABBccdd	31.86	6.7961	0.1	3.9	35.4	49.1	11.1	0.4						5.859375
AABbccdd } *AaBBCCdd* }	30.36	6.5244	0.1	5.5	42.0	45.5	6.9							4.687500
AaBbccDD } *AAbbccdd* }	28.86	6.2408	0.1	7.7	49.3	39.2	3.7							10.156250
AaBbCcdd } [2] *aaBBCcDD* }	27.36	5.9436	0.2	10.5	56.3	31.3	1.7						18.75	14.062500
AaBbccdd } [2] *aaBBCCdd* }	25.86	5.6309	0.2	14.7	62.1	22.4	0.6						18.75	10.546875
Aabbccdd } [2] *aaBBCcdd* }	24.36	5.2997	0.3	20.3	64.9	14.3	0.2						12.50	8.593750
aaBbCcdd[2]	22.86	4.9464	0.5	27.6	64.4	7.5							18.75	5.859375
aaBbccdd[2]	21.36	4.5658	0.6	37.6	58.9	2.9							18.75	2.343750
aabbccdd[2]	19.86	4.1504	0.7	48.1	50.5	0.7							6.25	0.390625
P_1B_1			0.4	22.6	57.3	16.4	2.8	0.5						
F_2			0.1	9.0	37.7	28.0	14.4	7.6	2.6	0.5	0.1			
P_2B_1				0.2	3.1	16.8	33.3	29.4	13.6	3.3	0.4			

1) and 2) occurring in P_2B_1 and P_1B_1 population, respectively.

thereafter adding 10.16 for each *A* gene and 3.39 for each *B*, *C*, or *D* gene. The means of 81 different genotypes of the F_2 and 16 genotypes of each of the backcross populations form an array of 18 different values (Table 20). Using the formula $y=mx+b$, the variances and standard errors (single determination) of plants of each genotype in the F_2 population can be estimated, and are listed in Table 20.

With those means and standard errors, the expected percentage frequency distributions for the genotypes and F_2, P_1B_1 and P_2B_1 populations were estimated and are listed in Table 20.

The expected and observed frequency distributions for three segregating population, χ^2 values for testing goodness of fit, and P-values are given in Table 21. The results indicated a good fit and supported the hypothesis that the two parents were differentiated by four gene paris.

TABLE 21. Expected and observed frequency distributions, χ^2 values for testing goodness of fit, degrees of freedom, and P-values for number of nodes

Population	Upper limit of class 10	20	30	40	50	60	70	80	90	χ^2	d.f.	P-value
P_1B_1												
Expected	1	51	129	37	6	1				1.1114	3	0.80–0.70
Observed		57	122	39	7	1						
F_2												
Expected	1	46	197	146	75	39	14	3		7.1761	5	0.30–0.20
Observed		57	186	132	80	44	15	8				
P_2B_1												
Expected			6	35	69	61	28	6		5.7384	5	0.40–0.30
Observed			10	40	65	55	29	8	1			

c. Interactions of genes

The interactions of the genes were such that any given gene did not have the same degree of effect in all genotypes. Those genes tending to increase the node number had a greater effect in genotypes having at least one such gene present in each of the four gene pairs. This shows that the effects of the genes were cumulative but not strictly additive throughout the range of genotypes. The effects of genes were not equal, because the *AA* genes had an effect as great as the combined effects of the three other gene pairs.

To manifest clearly the nature of gene interactions, the epistasis is

calculated by HAYMAN's method (1958) and given in Table 22. The values for m, d, and h are determined in terms of a three-parameter non-epistatic model. The χ^2 value is found to be significant, showing that epistasis is present. The values for m, d, h, i, j and l were then calculated in terms of a six-parameter epistatic model. It was found that epistasis is mainly due to additive x additvie and additive x dominance interactions. The upper half of Table 22 shows the observation along with the differences between them and expectations on the three-parameter model. These indicate that epistasis suppresses the negative dominance in F_1 and enhances it in the F_2 and backcross generations.

TABLE 22. Mean, constant, additivity, dominance, and three kinds of epistasis for number of nodes

	Observation	Difference(1)
P_1	19.86±0.1937	1.23±0.5391
P_2	59.60±0.8173	0.18±0.5829
F_1	39.29±0.7612	3.21±0.6033
F_2	34.25±0.5896	−3.30±0.5186
P_1B_1	25.02±0.5138	−2.34±0.3964
P_2B_1	49.34±0.8706	1.59±0.8069
	3-parameter model	6-parameter model
m(2)	37.55±0.2805	34.25±0.5896
d	−20.39±0.3358	−24.32±1.0110
h	− 2.94±0.7397	11.28±3.2258
i		11.72±3.1064
j		− 4.45±1.0947
l		− 2.40±4.9937
$\chi^2=71.860$		
$P<0.01$		

(1) Differences were estimated by subtracting expected values of P_1, P_2, F_1, F_2, P_1B_1 and P_2B_1 (as obtained under 3-parameter model) from their respective observed values. Expected values were estimated as follows:

$P_1=m+d-\frac{1}{2}h$; $P_2=m-d-\frac{1}{2}h$; $F_1=m+\frac{1}{2}h$; $F_2=m$; $P_1B_1=m+\frac{1}{2}d$;

and $P_2B_1=m-\frac{1}{2}d$.

(2) Gene effects: m=mean; d=additive; h=dominance; i=additive×additive; j=additive×dominance; l=dominance×dominance.

6. Pod Number on Stem

a. Magnitude of character difference and dominance

The mean values of the pod number on stem for various populations are given in Table 23. It can be seen that the average of the mean 18.53 ((11.25+25.81)/2) of these two parents approximates the mean of F_1 (18.98). The mean of P_1B_1 (15.74) approximates the average of the mean of P_1 and F_1 (15.12=(11.25+18.98)/2), the mean of P_2B_1 (23.31) approximates the average of the P_2 and F_1 (22.40=(18.98+25.81)/2). Furthermore, the mean of F_2 (19.21) is approximate to the mean of F_1. From all of these results two facts are evident: (1) genic dominance was intermediate (2) there were no interaction of genes.

TABLE 23. Means ($\bar{x}$), standard errors ($\sigma_{\bar{x}}$), and phenotypic (σ^2_P) and genotypic (σ^2_G) variances of different populations for pod number on stem

Population	$\bar{x}$	$\sigma_{\bar{x}}$	σ^2_P	σ^2_G	No. of plants
P_1	11.25	0.2768	13.4861		177
P_1B_1	15.74	0.4123	35.1820	15.7391	226
F_1	18.98	0.3465	17.8855		150
F_2	19.21	0.2631	36.0558	16.6129	522
P_2B_1	23.31	0.4123	29.0492	9.6063	208
P_2	25.81	0.4211	26.9573		153

b. Number of gene pairs differentiating the parents

On the basis of the segregating generations, the assumption is made that the two parents are differentiated by two gene pairs. The indication that the two gene pairs are involved is verified by the fact that 9.9% (F_2/P_1=0.9/9.6) of the individuals in the F_2 population fell in the upper limit of 5-class (Table 24), whereas on a two-gene-pairs basis, 6.25% would be expected. The indication is further supported by a value of 19.3% which was obtained by dividing 1.8 (5-class of P_1B_1) by 9.6 (5-class of P_1), because this value is approximate to a ratio of 25% expected on the basis of two gene pairs. By studying the genetic variance in P_1B_1 and P_2B_1 populations, it is obvious that the genetic variance of P_2B_1 was lower than that of P_1B_1, which indicated genetic dominance is involved in P_2. Thus, the genotypes of P_1 are symbolized as *aabb* and of P_2 as *AABB*.

The means of P_1 and P_2 are 11.25 and 25.81 respectively (Table 23). Thus, the total effects of these two gene pairs on the mean was 14.56

TABLE 24. Frequency distributions (expressed in percentage) of different populations for pod number on stem

Population	Upper limit of class							
	5	10	15	20	25	30	35	40
P_1	9.6	25.4	55.9					
P_1B_1	1.8	14.6	35.8	27.4	17.7	2.7		
F_1		2.7	13.3	52.7	24.7	6.7		
F_2	0.9	5.2	22.0	29.1	29.9	10.0	2.9	
P_2B_1			9.1	18.3	41.4	22.1	9.2	
P_2				11.8	42.5	26.1	13.7	5.9

TABLE 25. Expected means ($\bar{x}$), standard errors (σ), and frequency distributions of pod number on main stem for each genotype in segregating populations

Population and genotype	$\bar{x}$	σ	Upper limit of class									Expected percentage in	
			5	10	15	20	25	30	35	40	45	B_1	F_2
AABB[1]	25.81	5.1138		0.1	1.6	11.0	30.9	35.8	17.0	3.3	0.3	25.00	6.25
AaBB[1]	22.62	4.8144		0.5	5.2	23.8	39.3	24.9	5.8	0.5		25.00	12.50
AABb[1]	22.17	4.7672		0.5	6.2	25.6	39.9	22.7	4.7	0.4		25.00	12.50
AaBb[1,2]	18.98	4.4413	0.1	2.1	16.2	22.5	50.4	8.0	0.7			25.00	25.00
AAbb, *aaBB*	18.53	4.3934	0.1	2.5	18.6	41.7	30.0	6.6	0.5				12.50
Aabb[2]	15.34	4.0374	0.5	8.8	37.5	40.7	11.7	0.8				25.00	12.50
aaBb[2]	14.89	3.9845	0.7	10.2	40.3	38.8	9.4	0.6				25.00	12.50
aabb[2]	11.25	3.5288	4.8	31.5	49.2	13.8	0.7					25.00	6.25
P_1B_1			1.5	13.2	35.8	29.0	18.1	2.4	0.1				
F_2			0.7	5.3	20.4	28.5	30.7	11.2	3.0	0.3			
P_2B_1				0.8	7.3	20.7	40.1	22.9	7.1	1.1			

1) and 2) occurring in P_1B_1 and P_2B_1 population, respectively.

(25.81−11.25), and the effect of any one of the genes was 3.64 (14.56/4). However, a very slightly phenotypic dominance for more pod number was observed, and the degree of dominance was determined as 18.98−(25.8+11.25)/2, or 0.45. The effect of *Aa* gene tending to produce high pod number was 0.45 greater than that of *aa* gene. By using the effect of each gene as estimated above, the expected means of 9 genotypes of the F_2 population could be obtained (POWERS, *et al.* 1950). They are recorded in Table 25.

Table 23 shows that the means and variances of nonsegregating population were positively correlated. The variances and standard errors (single determination) (Table 25) of plants of each genotype in the F_2 population, can be estimated using the formula $y=mx+b$.

With these means and standard errors, the expected percentage frequency distributions for 9 genotypes and segregating populations P_1B_1, F_2, P_2B_1 were estimated and are listed in Table 25.

The expected and observed frequency distributions for three segregating populations, χ^2 values for testing goodness of fit, and P-values are given in Table 26. The results indicated a good fit and supported the hypothesis that the two parents were differentiated by two gene pairs

TABLE 26. Expected and observed frequency distributions, χ^2 values for testing goodness of fit, degrees of freedom, and P-values for pod number on stem

Population	Upper limit of class 5	10	15	20	25	30	35	40	χ^2	d. f.	P-values
P_1B_1											
Expected	3	30	81	66	41	5			0.9515	4	0.95–0.90
Observed	4	33	81	62	40	6					
F_2											
Expected	4	28	106	149	160	58	15	2	1.7803	5	0.90–0.80
Observed	5	27	115	152	156	52	11	4			
P_2B_1											
Expected		2	15	43	83	48	15	2	4.0928	4	0.40–0.30
Observed		5	19	38	86	43	12	5			

7. Pod Number on Branches

a. Magnitude of character difference and dominance

The mean values of the node number on branches for the P_1, P_2 and their F_1 are 12.15, 41.32 and 47.57, respectively (Table 27). The mean of F_1 is greater than the mean of the higher parent P_2. This indicated that F_1 showed heterosis.

The gene effect of heterosis make the data too complex to estimate gene number conditioning this trait.

b. Gene interactions and components of heterosis

The nature of gene interactions is calculated which is given in Table 27. The values for m, d and h were determined in terms of a three-parameter non-epistatic model. Significant χ^2 value (63.588) indicated the presence of

TABLE 27. Mean, constant, additivity, dominance, and three kinds of epistasis for pod number on branches

	Observation	Difference(1)
P_1	12.15±0.2943	1.61±0.7596
P_2	41.32±1.1065	0.44±0.7488
F_1	47.57±1.0541	4.65±0.8193
F_2	31.39±0.8519	−2.92±0.7457
P_1B_1	20.90±0.9788	−5.82±0.8558
P_2B_1	42.18±1.2820	0.28±1.1907
	3-parameter model	6-parameter model
m(2)	34.31±0.412Q	31.39±0.8519
d	−15.17±0.4731	−21.28±1.6129
h	17.21±1.0394	21.44±4.8432
i		0.60±4.6923
j		−6.70±1.7115
l		21.85±7.6806
$\chi^2=63.588$		
$P<0.01$		

(1), (2): Symbols are the same as in Table 22.

epistasis. In the presence of epistasis the six-parameter provides an exact fit to the generation mean. The values calculated for m, d, h, i, j and l in terms of the six-parameter epistatic model are shown in Table 27. Epistasis was due to additive x dominance and dominance x dominance effects. The differences between the observed and their expected values bases between the observed and their expected values based on the three-parameter model, indicated that epistasis has enhanced positive dominance in F_1 and suppressed it in the F_2 and backcross generations.

From Table 27, heterosis can be expressed in terms of four of the components of the generation means (JINKS, *et al.* 1957; HAYMAN 1960). The estimated components of heterosis are as follows:

Component: $h-i+d-1/2\,j=$ heterosis

Estimate: $21.44-0.60-21.28+3.35=2.91$.

Clearly, heterosis results are due to dominance (h) and additive x dominance (j) effects opposed to a large extent by the additive (d) effect.

8. Pod Number/plant

a. Magnitude of character difference and dominance

The means for pod number/plant (Table 28) show that P_1 has a mean of 23.21 and P_2 of 66.65. The magnitude of the difference between the two parents is 43.44.

The mean of P_2 is very close to the mean of F_1 (66.48). The mean of P_2B_1 (65.67) is lower than the mean of P_2, but the difference is not significant. These indicate almost complete phenotypic dominance of larger pod number over fewer ones.

TABLE 28. Means ($\bar{x}$), standard errors ($\sigma_{\bar{x}}$), and phenotypic (σ^2_P) and genotypic (σ^2_G) variances of different populations for pod number

Population	$\bar{x}$	$\sigma_{\bar{x}}$	σ^2_P	σ^2_G	No. of plants
P_1	23.21	0.3720	24.3595		177
P_1B_1	36.37	0.9630	208.6512	81.1830	226
F_1	66.48	1.1338	191.5391		150
F_2	50.82	0.9189	439.9241	312.4559	522
P_2B_1	65.67	0.9187	174.5062	47.2263	208
P_2	66.65	1.0460	166.5062		153

b. Number of gene pairs differentiating the parents

On the basis of the segregating generations, the assumption is made that the two parents are differentiated by three gene pairs. The indication is supported by dividing 5.0 (upper limit of classes 10 and 20 of P_1B_1) by 30.0 (upper limit of classes 10 and 20 of P_1) (see Table 29) which gives a value of 16.66%. On a three-gene-pairs basis, a ratio of 12.5% can be expected. The genotypic variance of P_2B_1 is lower than the genotypic variance of P_1B_1. The genotypes of P_1 are symbolized as *aabbcc* and of P_2 as *AABBCC*.

The P_1B_1 and P_2B_1 frequency distributions are partitioned into their component genotypes (Table 30). Row 1 gives the frequency distribution of P_1B_1 population. In the P_1B_1 population, the *AaBbCc* (F_1) and *aabbcc* (P_1) constitute 25.0% of the population. The distribution of the P_1 and F_1 for each class is multiplied by its expected percentage, divided by 100, and then summed. Thus row 2 gives the frequency distribution of F_1+P_1 genotypes. The difference between row 1 and row 2 gives the frequency distribution of the remaining six genotypes of the P_1B_1 population as listed

TABLE 29. Frequency distributions (expressed in percentage) of different population for pod number

Population	Upper limit of class									
	10	20	30	40	50	60	70	80	90	100
P_1	0.6	29.4	64.4	5.7						
P_1B_1	0.5	4.5	32.6	29.2	19.9	8.0	2.2	1.8	0.9	0.4
F_1			1.3	2.0	5.3	19.3	45.3	12.0	8.0	6.7
F_2	0.6	7.3	13.4	13.2	13.8	14.8	20.7	8.4	4.2	3.6
P_2B_1			0.5	2.9	7.2	17.8	41.8	16.8	7.2	5.8
P_2				2.6	6.5	19.6	41.8	16.3	7.2	5.9

TABLE 30. Partitioning the frequency distributions of backcrosses into their component genotypes for number of pods

Population and genotype	Row no.	Upper limit of class										Expected percentage
		10	20	30	40	50	60	70	80	90	100	
P_1B_1	1	0.5	4.5	32.6	29.2	19.9	8.0	2.2	1.8	0.9	0.4	100.00
P_1+F_1 (*aabbcc*+*AaBbCc*)	2	0.1	3.7	8.3	1.0	0.7	2.4	5.7	1.5	1.0	0.8	25.00
1−2	3	0.4	0.8	24.3	28.2	19.2	5.6	−3.5	0.3	−0.1	−0.4	75.00
Row 3 (%)	4	0.6	1.3	34.0	37.6	25.6	7.5	−4.7	0.4	−0.1	−0.5	100.00
P_2B_1	5			0.5	2.9	7.2	17.8	41.8	16.8	7.2	5.8	100.00
P_2+F_1 (*AaBbCc*+*AABBCC*)	6			0.2	0.6	1.5	4.9	10.9	3.5	1.9	1.5	25.00
5−6	7			0.3	2.3	5.7	12.9	30.9	13.3	5.3	4.3	75.00
Row 7 (%)	8			0.4	3.1	7.6	17.2	41.2	17.7	7.1	5.7	100.00

in row 3. This frequency distribution is weighted on 100 per cent basis and is given in row 4. Similarly, the P_2B_1 population is partitioned into its component genotypes. On the basis of the frequency distributions of the different genotypes of the backcross populations, an expected frequency

TABLE 31. Expected frequency distribution (expressed percentage) of number of pods for each genotype in F_2 population

Population and genotype	Upper limit of class										Expected percentage
	10	20	30	40	50	60	70	80	90	100	
AABBCC				2.6	6.5	19.6	41.8	16.3	7.2	5.9	1.5625
AABBCc			0.4	3.1	7.6	17.2	41.2	17.7	7.1	5.7	28.1250
AABbCC											
AABbCc											
AaBBCc											
AaBbCC											
AaBBCC											
AaBbCc			1.3	2.0	5.3	19.3	45.3	12.0	8.0	6.7	12.5000
AabbCc	0.6	1.3	37.0	37.6	25.6	7.5	−4.7	0.4	0.1	−0.5	28.1250
AaBbcc											
Aabbcc											
aabbCc											
aaBbcc											
aaBbCc											
AaBBcc	0.2	9.8	21.5	3.6	4.3	13.1	27.9	10.9	4.8	3.9	23.4375
AAbbCC											
AAbbCc											
AABBcc											
AABbcc											
aaBBCC											
aaBBCc											
aaBbCC											
AabbCC											
aabbCC	0.4	19.6	43.0	4.7	2.2	6.6	14.0	5.5	2.4	2.0	4.6875
aaBBcc											
AAbbcc											
aabbcc	0.6	29.4	64.4	5.7							1.5625
F_2	0.1	6.4	15.0	12.7	11.2	14.1	23.6	9.7	4.5	3.9	

distribution for the F_2 genotype is obtained (Table 31). The distribution for the *AABBCC*, *aabbcc* and *AaBbCc* genotypes is that of P_2, P_1 and F_1 respectively. The distribution of the following genotypes is obtained from the indicated backcross populations and is given in Table 30, row 4 and 8, respectively.

P_1B_1	P_2B_1
AabbCc	*AABBCC*
AaBbcc	*AABbCC*
Aabbcc	*AaBBCC*
aaBbCc	*AABBCc*
aabbCc	*AaBbCC*
aaBbcc	*AaBBCc*

The following genotypes of the F_2 do not occur in either of the backcross populations:

Group I	Group II
AaBBcc	*aabbCC*
AAbbCC	*aaBBcc*
AAbbCc	*AAbbcc*
AabbCC	
AABBcc	
AaBbcc	
AaBBCC	
aaBbcc	
aaBBCc	

As already mentioned, there is complete genic and phenotypic dominance. If all the genes have the same effect and the gene action is additive between loci, then all the genotypes in Group I should have the same frequency distribution. Similarly the genotypes of Group II will be alike in their distribution. The frequency distribution of each genotype in Group I can thus be roughly calculated by taking 66.67 percent of the P_2 distribution and 33.3 percent of the P_1 distribution. The frequency distribution of each genotype in Group II will thus lie between the frequency distribution of Group I and P_1 genotypes. Table 31 gives the expected frequency distributions calculated on the above assumption.

From preceding distributions of the F_2 genotypes, the expected frequency distribution for the F_2 population is obtained. The test for goodness of fit between expected and observed frequency distributions gives a χ^2 value of 9.0479, and the P-value lies between 0.5 and 0.4 (Table 32).

This result supports the hypothesis that the two parents are differentiated by three gene pairs.

TABLE 32. χ^2 for testing goodness of fit between expected and observed frequency distribution in F_2 population for number of pods

Population	Upper limit of class										No. of plants
	10	20	30	40	50	60	70	80	90	100	
	expressed in percentage										
Expected	0.1	6.4	15.0	12.7	11.2	14.1	23.6	9.7	4.5	3.9	522
Observed	0.6	7.3	13.4	13.2	13.8	14.8	20.7	8.4	4.2	3.6	522
	expressed in number										
Expected	1	34	76	66	59	68	123	51	24	20	522
Observed	3	38	70	69	72	77	108	44	22	19	522

$\chi^2 = 9.0479$ d. f. = 8 P = 0.50–0.40

TABLE 33. Mean, constant, additivity, dominance, and three kinds of epistasis for seed number

	Observation	Difference(1)
P^1	38.70 ± 0.6794	1.26 ± 1.5313
P_2	113.26 ± 1.9274	−0.18 ± 0.9531
F_1	132.07 ± 2.2250	3.15 ± 1.7171
F_2	102.84 ± 2.1312	0.66 ± 1.9211
P_1B_1	71.39 ± 2.4528	−11.79 ± 2.2268
P_2B_1	122.27 ± 3.0468	1.09 ± 2.8689
	3-parameter model	6-parameter model
m(2)	102.18 ± 0.9228	102.84 ± 2.1312
d	−38.00 ± 0.8968	−50.88 ± 3.9108
h	53.48 ± 2.1455	32.05 ± 11.8256
i		−24.04 ± 11.5693
j		−13.60 ± 4.0421
l		52.82 ± 18.4760
χ^2=21.601		
P<0.01		

(1), (2): Symbols are the same as in Table 22.

9. Seed Number/plant

From the mean values listed in Table 33 it can be found that the mean of P_1, P_2 and F_1 is 38.70, 113.26 and 132,07, respectively. Thus, there is a heterosis in F_1.

b. Gene interactions and components of heterosis

The χ^2 value calculated from the three-parameter of non-epistasis is 21.601 (Table 33) indicating that the epistasis is present in this character. Thus, the values for *m*, *d*, *h*, *i*, *j* and *l* were calculated in terms of a six-parameter epistatic model. It was found that epistasis was due to additive x dominance and dominance x dominance effects. The differences between observed and expected values based on the three-parameter model indicated that the epistasis appeared to have increased the positive dominance in F_1.

The components of heterosis were calculated as follows:

Component: $h-i+d-1/2\,j=$ heterosis
Estimate: $32.05-50.88+24.04+6.80=12.01$

Clearly, additive (*d*) and epistasis (*j*) dominance (*h*) components are major factors in the heterosis, and are opposed by the epistasis (*i*) component.

10. Seed Weight/plant

a. Magnitude of character difference and dominance

P_1 plants averaged 6.76 and P_2 plants 19.22, or 12.46 more (Table 34). The mean for the F_1 (23.96) is greater than the mean for either parent. Clearly, the F_1 showed heterosis for seed weight/plant.

b. Gene interactions and components of heterosis

As shown in Table 34, the χ^2 value calculated from the three-parameter of non-epistasis is 57.939, indicating that the epistasis is present in this character. The values for *m*, *d*, *h*, *i*, *j* and *l* were then calculated in terms of a six-parameter epistatic model. It was found that epistasis was due to additive x dominance effect. The differences between the observed values and their expections based on the three-parameter model indicated that the epistasis appeared to have increased the positive dominance in F_1, whereas, it seems to have suppressed it in F_2 and backcross generations.

From the Table 34, the heterosis can be expressed as follows:

Component: $h-i+d-1/2\,j=$ heterosis
Estimate: $12.59-1.62-8.31+1.04=3.70$

Clearly, epistasis (*j*) and dominance (*h*) are major factors in heterosis and are opposed by the additive (*d*) and epistasis (*i*) components.

TABLE 34. Mean, constant, additivity, dominance, and three kinds of epistasis for seed weight

	Observation	Difference(1)
P_1	6.76±0.1348	0.50±0.2665
P_2	19.22±0.3644	0.19±0.2161
F_1	23.96±0.3630	1.46±0.2729
F_2	16.14±0.3532	−1.43±0.3186
P_1B_1	12.39±0.3881	−1.99±0.3467
P_2B_1	20.70±0.4867	−0.06±0.4543
	3-parameter model	6-parameter model
m(1)	17.57±0.1546	16.14±0.3532
d	−6.39±0.1697	−8.31±0.6225
h	9.85±0.3691	12.59±1.9276
i		1.62±1.8831
j		−2.08±0.6521
l		6.10±2.9789
$\chi^2=57.939$		
$P<0.01$		

(1), (2): Symbols are the same as in Table 22.

Discussion

The estimation of the number of genes for quantitative characters offers us means for examining the inherent potential variability of the characters studied.

Numerous methods of genetic analysis for determining the number of genes controlling the expression of quantitative characters have been developed by many workers (CASTLE 1921; MATHER 1949 a, b; MATHER and VINES 1952; POWERS 1942, 1950, 1951, 1955, 1963; POWERS, LOCKE and GARRETT 1950; LEONARD, MANN and POWERS 1957; *etc*). POWERS, LOCKE and GARRETT (1950) suggested and described a method (partitioning method) for estimating the number of genes controlling quantitative characters. Recently, experiments have been performed in some crop plants for estimation of gene number by using the partitioning method (OKA and MURAOKA 1957; YASUDA 1958; MOHAMED 1959; MOHAMED and HANNA 1964, 1965; THSENG and HOSOKAWA 1970, 1972 a, b; HECKER, *et al.* 1970; *etc*).

In the application of this method, its limitations should be recognized.

When the number of individuals in a population is small, the validity of chi square test is reduced, disturbing the conclusion. There should be a fairly large number of individuals for all populations and an extensive genetic design in order to arrive at a final conclusion. In this experiment, the available data (*i. e.* parents, their F_1, F_2 and backcrosses) contain a large number of individuals in all populations, so that the genetic analysis on the mode of inheritance might be adequately ascertained.

The two parental lines were found to be differentiated by two gene pairs in regard to branch number, node number on stem, node number on branches and pod number on stem, by three gene pairs in regard to plant height and pod number/plant, by four gene pairs in regard to node number/plant. The characters of pod number on branches, seed number/plant and seed weight/plant exhibit a great degree of heterosis. It appears that the parents are most probably differentiated by five or more gene pairs but some complex intra- and interallelic interactions make it difficult to analyze the data. To obtain very conclusive proof for the exact number of genes involved, it will be necessary to grow the progenies of the backcross and F_2.

For the sake of simplification, gene pairs have been designated by conventional symbols that differentiated the genes within characters. But, it is not appropriate for the consideration of two or more characters together. Thus, different symbols are now assigned to those genes found to have differentiated the parents. The new symbols, in which the subcripts 1, 2, 3 and 4 correspond to the former symbols of A, B, C and D respectively, are as follows :

Character :	gene symbols
Plant height	$H_1h_1H_2h_2H_3h_3$
Branch number	$B_1b_1B_2b_2$
Node number on stem	$Nm_1nm_1Nm_2nm_2$
Node number on branches	$Nb_1nb_1Nb_2nb_2$
Node number/plant	$N_1p_1N_2p_2N_3p_3N_4p_4$
Pod number on stem	$Pm_1pm_1Pm_2pm_2$
Pod number/plant	$P_1p_1P_2p_2P_3p_3$

In studying the phenomenon of dominance, it is necessary to recognize both phenotypic and genic dominance. Phenotypic dominance can be determined by comparing the means of the two parents with the mean of the F_1 generation. Genic dominance is determined from a study of the means, variance and phenotypes of the different genotypes. It must also be realized that genic dominance is dependent upon the genotypic variance.

Data on F_1 and parent performance in soybean have been reported by a number of workers (WENTZ and STEWORT 1924; VEATCH 1930, WOODWORTH 1933; WEISS, *et al.* 1947; KALTION 1948; LEFFEL and WEISS 1958; LEFFEL and HANSON 1961; CHANG, *et al.* 1961; *etc*). Among them, CHANG, *et al.* (1961), based on 12 F_1 populations from a diallel cross among 4 determinate type varieties, reported that the partial dominance was observed in plant height, branch number and yield. LEFFEL and WEISS (1958) also studied the F_1's from diallel crosses among indeterminate type varieties and obtained the results indicating complete dominance or over-dominance for yield and plant height. In this study, the following results were found: 1) no phenotypic and genic dominance for pod number and node number on stem, and node number on branches, 2) complete phenotypic and genic dominance for branch number and pod number/plant, 3) partial phenotypic and genic dominance for plant height and node number/plant and 4) great degree of heterosis in F_1 (not complete genic dominance, but can not be determined whether any of these have partial genic dominance) for pod number on branches, seed number/plant and seed weight/plant.

The nature of gene interactions will be considered here. The nature of gene action has been found to be nearly additive for pod number and node number on stem, and node number on branches. The intra- and interallelic interactions were found in the node number/plant, pod number on branches, pod number/plant, seed number/plant and seed weight/plant. The epistasis due to additive × additive and additive × dominance effects were found for node number/plant, those due to additive × dominance and dominance × dominance effects for pod number on branches, seed number/plant and seed weight/plant. The dominance and epistasis (additive × dominance) effects were major factors in heterosis, which show in the pod number on branches, seed number/plant and seed weight/plant.

Small gene number and epistasis observed in the plant height indicated that selection breeding may be successful and give quick achievement. The high additive effect suggests significant potential for improving the pod number on stem, node number on stem and node number on branches through selection. On the other hand, the high degree of heterosis indicated that individual selection in early hybrid generations may be easy, but showed slow achievement in breeding work for pod number on branches, seed number/plant and seed weight/plant.

Summary

Estimation of the gene number and the gene effects for the inheritance of certain agronomic characters in soybean were studied using a cross between determinate type and indeterminate type varieties.

Each of the following characters was differentiated by two gene pairs: branch number, node number on stem, node number on branches and pod number on stem.

The plant height and pod number/plant are differentiated by three gene pairs; node number/plant, by four.

Both phenotypic and genic dominance were intermediate for pod number on stem, node number on stem and node number on branches.

There is complete phenotypic and genic dominance for the branch number and pod number/plant. There is partial phenotypic dominance and genic dominance for plant height and node number/plant. The seed number, seed weight and pod number on branches show a great degree of heterosis in F_1.

The epistasis due to additive × additive and additive × dominance effects were found for node number/plant, due to additive × dominance and dominance × dominance effects for pod number/plant, pod number on branches, seed number/plant, and due to additive × dominance effect for seed weight/plant.

The dominance and epistasis, additive × dominance effect which were major factors in heterosis, were found in the pod number on branches, seed number/plant and seed weight/plant.

Literature cited

CASTLE, W. E. 1921. On a method of estimating the number of genetic factors concerned in cases of blending inheritance. Science 54: 93–96.

CHANG, C. M. and W. T. TANG 1962. Diallel cross in soybean. 台湾省雜糧作物試驗簡報第十輯

HAYMAN, B. I. 1958. The separation of epistatic from additive and dominance variation in generation means. Heredity 12: 371–390.

———— 1960. *Ditto* II. Genetica 31: 133–146.

HECKER, R. J., G. W. MAAG and M. G. PAYNE 1970. Inheritance of 3-hydroxytyramine in sugarbeet; a phenolic compound associated with *Cercospora* leaf spot resistance. J. Amer. Soc. Sugar Beet Tech. 16: 52–63.

JINKS, J. L. and R. M. JONES 1958. Estimation of components of heterosis. Genetics 43: 223–234.

KALTON, R. R. 1948. Breeding behavior at successive generations following hybridization in soybeans. Iowa Agr. Exp. Sta. Res. Bul. 358: 669–732.

LEFFEL, R. C. and M. G. WEISS 1958. Analyses of diallel crosses among ten varieties of soybeans. Agron. Jour. 50: 528–534.

LEFFEL, R. C. and W. D. HANSON 1961. Early generation testing of diallel crosses of soybeans. Crop sci. 1: 169–174.

LEONARD, W. H., H. O. MANN and L. POWERS 1957. Partitioning method of genetic analysis applied to plant height inheritance in barley. Colorado Agr. Exp. Sta. Tech. Bull. No. 60.

MATHER, K. 1949 a. Biometrical genetics. Methuen, London.

———— 1949 b. The genetical theory of continuous variation. Proc. 8th Intern. Congr. Genet. (Hereditas Suppl. Vol.): 376–401.

MATHER, K. and VINES, A. 1952. The inheritance of plant height and flowering time in a cross of *Nicotiana Rustica*. pp. 49–80. *Quantitative inheritance*. His Majesty's Stationery Office, London.

MOHAMED, A. H. 1959. Inheritance of quantitative charcters in *Zea Mays*. I. Estimation of the number of genes controlling the time of maturity. Genetics 44: 713–724.

MOHAMED, A. H. and A. HANNA 1964. Inheritance of quantitative characters in rice. I. Estimation of the number of effective factor pairs controlling plant height. Genetics 49: 81–93.

———— and ———— 1965. *Ditto*. II. Inheritance of panicle length. Can. J. Genet. Cytol. 7: 406–417.

OKA, M. and Y. MURAOKA 1957. Inheritance of photoperiodism (short-day) in a cross of tobacco varieties. I. Xanthi×Bright Yellow cross (in Japanese with English Summary) Jap. J. Breed. 7: 12–16.

PEARSON, E. S. and H. O. HARTLEY 1958. Biometrika Tables for statistician. Vol. 1: 104–110. Second edition, Cambridge Univ. Press.

POWERS, L., 1942. The nature of the series of environmental variance and the estimation of the genetic variances and the geometric means in a crosses involving species of *Lycopersicon*. Genetics 27: 561–575.

———— 1950. Gene analysis of weight per locule in tomato hybrids. Bot. Gaz. 112: 163–172.

———— 1951. Gene analysis by the partitioning method when interactions of gene are involved. Bot. Gaz. 113: 1–23.

———— 1955. Components of variance method and partitioning method of genetic analysis applied to weight per fruit of tomato hybrids and parental populations. U. S. Dept. Agr. Tech. Bull. 1131.

———— 1963. The partitioning method of genetic analysis and some aspects of its application to plant breeding. Natl. Acad. Sci. Natl. Res. Council. Publ. 982: 280–318.

POWERS, L., F. L. LOCKE and J. C. GARRETT 1950. Partitioning method of genetic analysis applied to quantitative characters of tomato crosses. U. S. Dept. Agr. Tech. Bull. No. 998.

THSENG, F. S. and S. HOSOKAWA 1970. Genetic studies on quantitative characters in soybean. I. Genetic analysis on first internode length by partitioning method.

Jour. Facul. Agr., Hokkaido Univ., Sapporo, Vol. 56, Pt. 3: 257–266.

THSENG, F. S. and S. HOSOKAWA 1972 a. Genetic studies on quantitative characters in soybean. IV. Gene effect controlling the size of primary leaves (in Japanese with English Summary). Japan J. Breed. 22: 217–222.

———— and ———— 1972 b. *Ditto.* V. Estimation of gene number and gene action for the date of flowering and maturity. Japan J. Breed. 22: 313–322.

———— and ———— 1972 c. Significance of growth habit in soybean breeding. I. Varietal differences in characteristics of growth habit. Japan J. Breed. 22: 261–268.

VEATHCH, C. 1930. Vigor in soybeans as affected by hybridity. Jour. Amer. Soc. Agron. 22: 289–310.

WEISS, M. C., C. R. WEBER and R. R. KALTON 1947. Early generation testing in soybeans. Jour. Amer. Soc. Agron. 39: 791–811.

WENTZ, J. B. and R. J. STEWART 1924. Hybrid vigor in soybeans. Jour. Amer. Soc. Agron. 16: 534–540.

YASUDA, S. 1958. Genetic analysis of the response to short photoperiod in a barley cross by means of the partitioning method (in Japanese). Nogaku Kenkyu. 46: 54–62.