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GENETIC STUDIES ON QUANTITATIVE CHARACTERS IN SOYBEAN

II. On the growth habit

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The majority of soybean varieties grown in Japan are determinate type. In China, United States and other soybean growing countries, indeterminate types are widely grown (NAGATA 1960 a). The determinate and the indeterminate types are known to differ in physiological and ecological characteristics (NAGATA 1960 a, b, c). Indeterminate varieties generally have higher productivity than determinate varieties, and their yield is relatively stable in varying environmental conditions (FUJIMORI 1964; SANBUICHI 1967).

Breeding for indeterminate and "*half-indeterminate type*" of soybean seems to be an important objective in Japan. For this, how to identify and select genes expressing indeterminate type is an important problem to be studied. From this viewpoint, the authors have made attempts to elucidate the mode of inheritance of the growth habit in soybean.

Materials and Methods

An indeterminate variety, Harosoy (from the U. S.), and two determinate varieties of Japanese origin, Tokachi-nagaha and Kitami-shiro, were used for experiments. Two crosses, Harosoy \times Tokachi-nagaha (6801) and Harosoy \times Kitami-shiro (6802), were made in 1968 and their F_2 seeds were obtained in a greenhouse in the winter of the same year. In 1969, the P_1 , P_2 , F_1 and F_2 plants were grown in the farm of Tokachi Agricultural Experiment Station, Hokkaido. The experimental design followed a complete randomized block with six replications. Each replication contained two plots of P_1 , P_2 and F_1 and ten plots of F_2 , except that the F_1 plots of Harosoy \times Kitami-shiro were only two in total because of shortage of the seed. Each plot consisted of 12 plants, 10 of them were used for taking records. All the plants were spaced at 60 cm \times 60 cm so as to reduce the effect of competition between plants.

Results

1. Characters related to growth habit

a) *Differences between parental varieties*: Varieties of determinate type usually stop to produce foliar buds when flower buds are formed. Indeterminate types continually produce foliar buds after flower bud formation, and they have both foliar and floral buds simultaneously (NAGATA 1960 a). For investigating the characteristics of the growth habit, plant height and node number in the main stem were observed at the time of the first flowering and at maturity. The results are given in Table 1 and in Fig. 1, which show that determinate types did not increase those characters so much after the first flowering. In contrast, the indeterminate variety (Harosoy) began to flower when the plant was on the way to full growth and increased height and node number even after flowering. It may be said that in determinate reproductive growth occurs after the completion of vegetative growth, while both phases of growth simultaneously proceed in indeterminate types.

b) *Differences between parental and F_1 plants*: As shown in Table 1 and Fig. 1, the F_1 plants showed heterosis in both plant height and node number. They showed almost the same grade of stem elongation after flowering as in the indeterminate parent, while the increase of nodes after flowering was intermediate between the indeterminate and the determinate parents.

c) *Variations in F_2 populations*: To measure the intergrades between determinate and indeterminate types, the increment of node number after first flowering in percent of the total node number, and the height increment after the first flowering in percent of the height at maturity, were obtained from each plant. The F_2 means of these percentages, and those of node number and height at first flowering and at maturity, are also given in Table 1. The F_2 means were generally greater than the parental values, while the increment percentages were close to the mid-parental values.

The genetic variances of F_2 populations were estimated by subtracting the mean variances for P_1 , P_2 and F_1 plants ($\frac{1}{4}V_{P_1} + \frac{1}{4}V_{P_2} + \frac{1}{2}V_{F_1}$) from phenotypic F_2 variances. The heritability values (broad sense) and the phenotypic as well as genetic correlations of respective characters are given in Table 2. All the characters showed high heritability values, possibly because of markedly different strains were crossed and the F_2 plant segregated in a wide range. As indicated in the table, the node number at the first flowering (a) was uncorrelated with its increment after first flowering (b) and with the increment percentage in plant height (h). Also the plant height at

TABLE 1. Means for growth habit and quantitative characters in parental, F₁ and F₂ populations

Population	a*	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p
Tn.	9.2	4.4	13.5	32.7	12.9	45.6	32.6	28.1	70.3	7.6	35.6	48.9	3.4	40.7	101.0	142.0
Hs.	9.5	12.9	18.8	21.3	61.9	83.2	69.1	74.4	62.5	9.1	50.9	70.3	4.4	46.9	122.0	168.0
Ks.	9.3	3.1	12.4	34.9	6.9	41.7	24.3	16.1	69.8	6.0	28.2	40.5	3.3	30.0	75.0	106.0
6801																
F ₁	10.8	9.1	20.1	40.9	60.0	101.1	45.9	59.5	76.6	8.0	69.6	89.6	5.1	48.8	166.7	218.8
H(%)	143.0	105.0	125.0	152.0	160.0	158.0	92.0	116.0	139.0	96.0	161.0	150.0	131.0	111.0	146.0	140.0
F ₂	9.9	7.7	27.5	35.7	42.9	78.2	42.2	50.5	75.4	7.7	55.1	72.1	4.4	39.0	133.5	172.5
6802																
F ₁	13.9	6.8	20.5	57.6	63.4	120.2	32.4	52.7	87.8	9.8	73.6	94.8	5.9	33.2	149.0	180.0
H(%)	183.0	85.0	131.0	205.0	184.0	192.0	69.0	116.0	183.0	130.0	186.0	171.0	153.0	86.0	151.0	131.0
F ₂	11.5	7.3	18.9	45.7	43.6	89.0	37.7	45.5	80.6	8.3	60.4	79.5	4.6	30.7	117.4	148.0

Note. a: Node number of main stem at first flowering. i: Period from seeding to first flowering.
 b: Node number of main stem increased after first flowering. j: Number of branches.
 c: Node number of main stem at maturity. k: Node number with branches.
 d: Plant height at first flowering. l: Node number per plant.
 e: Plant height increased after first flowering. m: Mean of internode length on main stem.
 f: Plant height at maturity. n: Pod number of main stem.
 g: Ratio calculated by $b/c \times 100$. o: Pod number of branches.
 h: Ratio calculated by $e/f \times 100$. p: Pod number per plant.
 H: $\bar{F}_1 / \frac{1}{2}(\bar{P}_1 + \bar{P}_2) \times 100$ to describe F₁ heterosis.

*: Node number calculated from the cotyledon node to the node of unfolding leaf.

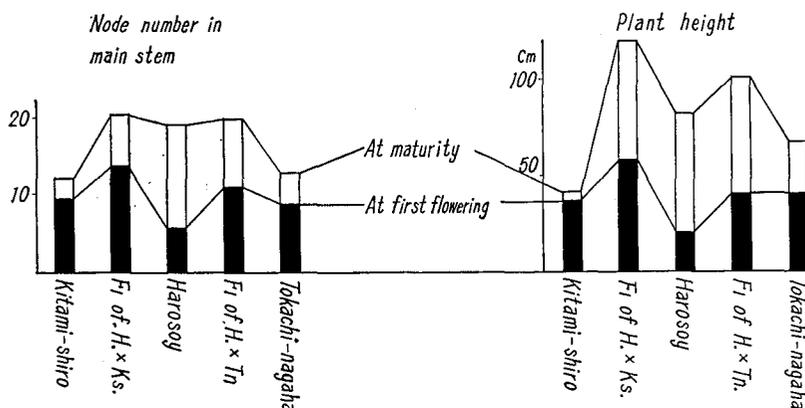


Fig. 1. Growth habit of three parental varieties and their F₁ hybrids.

TABLE 2. Phenotypic and genotypic correlation coefficients, and heritability value for growth habit characters in F₂ populations

Character	a	b	c	d	e	f	g	h
a	(90)	#-.015 -.028	.610** .633	.924** .954	.389** .418	.684** .667	-.279** -.247	.113 .142
b		(88)	.783** .797	.024 .034	.820** .833	.618** .659	.918** .945	.880** .860
c			(95)	.594** .609	.892** .923	.890** .910	.554** .575	.768** .810
d				(95)	.423** .450	.708** .719	-.233* -.255	.099 .131
e					(95)	.918** .923	.634** .634	.845** .860
f						(96)	.379** .410	.669** .694
g							(90)	.812** .847
h								(95)

Average figures for 6801 and 6802 population are shown.

Symbols are the same as Table 1.

#: Upper line: Phenotypic correlation coefficient.

Lower line: Genotypic correlation coefficient.

(): Heritability values (%)

** Significant at 1% level, * at 5% level.

first flowering (d) was uncorrelated with the node number increment after the first flowering (b) and the increment percentage in plant height. All other measurements were significantly correlated, indicating that the plants in F₂ population varied remarkably in vigor after the first flowering.

2. Relation among other quantitative characters

From the above mentioned data, it might be found that the determinate and the indeterminate type differ remarkably in developmental pattern. On this basis, attempts were made to analysis the genetic parameter and to estimate the expected gains.

Table 1 also shows that the mid-parental value and F₁ or F₂ population means did not differ significantly in branch number (j) and pod number in main stem (n), though significant difference were found in all other characters.

a) *Heritabilities and correlations on quantitative characters*: Table 3 showed that the heritability values were considerably high in all characters, except the node number of branches and pod number in main stem. The

TABLE 3. Phenotypic and genotypic correlation between growth habit characters and quantitative characters, and heritability value in F₂ population

Character	i	j	k	l	m	n	o	p
a	# .950**	.570**	.618**	.709**	.715**	-.343**	.709**	.415**
	.968	.613	.733	.733	.749	-.180	.729	.444
b	-.091	.250*	.206*	.354**	.414**	.378**	.382**	.431**
	-.107	.338	.280	.399	.450	.446	.432	.486
c	.544**	.624**	.616**	.801**	.855**	.060	.527**	.482**
	.560	.725	.757	.870	.906	.079	.574	.520
d	.899**	.672**	.613**	.715**	.717**	-.080	.290**	.177
	.920	.690	.729	.742	.744	-.090	.300	.172
e	.181	.801**	.367**	.622**	.652**	.228*	.411**	.381**
	.185	.841	.474	.652	.679	.232	.431	.397
f	.586**	.929**	.585**	.818**	.841**	.089	.436**	.355**
	.594	.962	.723	.829	.880	.098	.452	.362
g	-.499**	.052	-.049	.045	.095	.460**	.091	.303**
	-.527	.102	-.046	.040	.106	.548	.120	.358
h	-.137	.444**	.195	.369**	.408**	.347**	.405**	.444**
	-.140	.475	.253	.397	.433	.390	.422	.483
Heritability (%)	98	87	54	92	92	60	90	92

Average figures for 6801 and 6802 population are shown.

Symbols are the same as in Table 1.

** Significant at 1% level, * at 5% level.

#: Same as in Table 2.

phenotypic and genetic correlation coefficients between growth habit and quantitative characters are also given in Table 3. The table shows that the period to the first flowering (i) was uncorrelated with node number increment (b) and plant height after the first flowering (e), and with the increment percentage of plant height (h), also the pod number in main stem (n) was uncorrelated with node number at maturity (c), and with plant height at first flowering (d) and at maturity (f). Furthermore, the increment percentage in node number (g) was uncorrelated to all characters (j, k, l, m, o) except the period to the first flowering, and the pod number in main stem and of per plant. All other characters were significantly correlated.

b) Estimate of expected genetic gain: To obtain the expected genetic gain in five agronomic characters (c, p, f, i, m), the partitioning method (POWERS 1951, 1957) which are briefly described below and in Table 4, was applied to two F_2 populations derived from the crosses between the determinate and the indeterminate varieties.

The genetic gain was calculated as follow :

The formula for predicting the mean of sub-group frequency distributions is $y = z - s_a x'$ (POWERS 1951). In identifying genetically-superior individuals the z values given in Table 4 are obtained by the application of the formula $z = \bar{x} + s_a x'$. This formula is derived from the formula $y = z - s_a x'$, in which \bar{x} is substituted for y . In the application of these formulas the symbols used and those given in Table 4 have the following connotations.

y = predicted mean

\bar{x} = obtained mean of population

z = upper limit of any given class of frequency distribution

s_a = estimated standard error calculated from the environmental variance of parents and F_1 populations

$p = 1 - q$

$q = p(x)$ of PEARSON'S and HARTLEY'S (1958) tables

$x' = x$ of PEARSON'S and HARTLEY'S (1958) tables

The results obtained by these methods are also shown in Table 4. The expected genetic gain calculated from the sub-group at the two extremities of the frequency distribution for F_2 populations showed that those for internode length and node number were very low but those for other characters were higher. In order to select the individuals having the same expected genetic gain, the F_2 hybrid plants located outside of frequency distribution of both parent should be chosen. The number of plant were shown in Table 4, line IV.

TABLE 4. Estimated genetic gains in two F₂ populations⁽¹⁾

Population	Character	I*	II	III	IV	V	VI	VII	VIII	
6801	i ** (+)***	40.0	45.0	1.4885	4.2	1.73	36.0	42.4	6.4	
		(-) 32.0	25.0		12.9	1.13		26.7	9.3	
	f	(+) 95.5	100.0	5.2770	23.4	0.73	81.2	96.1	14.8	
		(-) 66.9	60.0		21.8	0.78		64.1	17.1	
	c	(+) 20.5	21.0	0.9651	2.0	2.81	17.9	18.3	0.4	
		(-) 15.3	12.0		5.6	1.56		13.5	6.4	
	m	(+) 5.2	5.5	0.2567	4.3	1.72	4.5	5.1	0.6	
		(-) 3.8	3.5		8.4	1.38		3.9	0.7	
	p	(+) 226.0	243.0	19.8129	5.9	1.56	172.5	203.1	30.6	
		(-) 119.0	108.0		9.3	1.32		138.9	33.6	
	6802	i	(+) 45.0	50.0	1.4024	8.8	1.36	41.0	48.1	7.1
			(-) 37.0	30.0		20.7	0.82		31.1	9.9
f		(+) 107.4	110.0	6.2384	21.2	0.80	90.6	105.0	14.4	
		(-) 73.8	65.0		19.8	0.85		70.3	20.3	
c		(+) 21.9	24.0	1.1105	0.2	3.49	18.9	21.1	2.2	
		(-) 15.9	12.0		5.6	1.56		13.7	6.2	
m		(+) 5.5	6.0	0.2891	6.9	1.49	4.7	5.7	0.8	
		(-) 3.9	3.0		3.1	1.86		3.6	1.2	
p		(+) 205.2	216.0	20.2200	6.0	1.52	150.6	185.3	34.7	
		(-) 96.4	90.0		8.5	1.37		117.7	32.9	

Note:

(1). The number of plants in 6801=595, in 6802=320.

* I: Value of z for $p=0.003$.

II: Value z used (class values of which beyond the values of I).

III: Standard error calculated from the environmental variance of parents and F₁.

IV: Superior individuals, estimated from the percentage listed under the extremities of individuals in frequency distributions of each characters falling beyond the values of z used.

V: Value of x' (value of x in PEARSON'S and HARTLEY'S (1958) tables for $\frac{1}{2}(1+a)$ equal I-IV).

VI: Observed mean.

VII: Superior individuals in predicted y (which was calculated by the formula $y = z - sa.x'$).

VIII: Genetic gains obtained from the VII column-VI column.

** i: Days to first flowering.

f: Plant height.

c: Node number in main stem.

m: Mean of internode length in main stem.

p: Pod number of individual plant.

*** (+): Increased genetic gains.

(-): Decreased genetic gains.

Discussion

The growth habits of soybean are generally classified into two types, the determinate and the indeterminate types, which are different in physiological and ecological characteristics. WOODWORTH (1932, 1933) reported that the developmental difference was controlled by a *Dt* gene.

Several reports have been published concerning agronomic characters of indeterminate type (NAGATA 1960 etc.). As shown by NAGATA (1967), the uniformity of beans is known to exist in the indeterminate types in their long flowering period. This results might be related to the node number increment after first flowering, because the indeterminate types begin to flower when the node number is still small and they produce more nodes after flowering. In the present study, the authors found that the node number at first flowering was uncorrelated with its increment after first flowering in F_2 populations (Fig. 2). The possibility of selection for "half-indeterminate type" whose node number increment after first flowering is fewer than and equal of the node number at first flowering, should be studied in the future.

In this study, the heritability values for growth habit characters were found to be very high. In addition, the increment of node number after flowering in percent of the total node number was strongly correlated with the pod number. This indicates that the percentage may be used as an

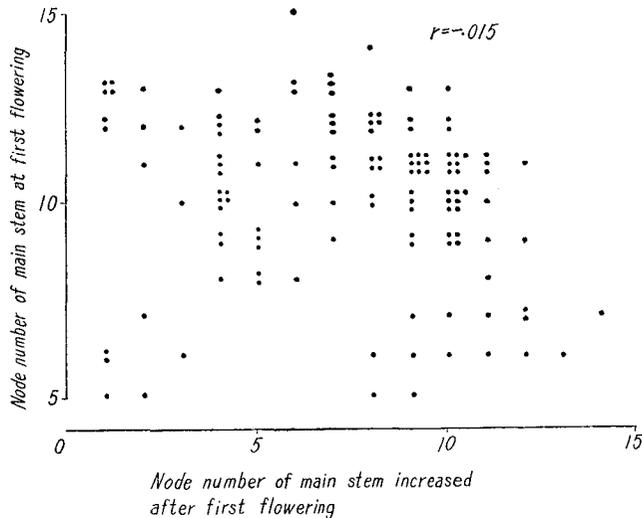


Fig. 2. Relationship between node number of main stem at first flowering and its increment after first flowering in F_2 population plants.

index for higher yield. Also the heritability values of agronomic characters obtained from the present study were generally high possibly because 1) variation due to competition between plants was reduced owing to wide spacing and 2) different gene recombinations occurred between the determinate and the indeterminate types.

To examine effectiveness of hybridization between determinate and indeterminate types for selection of the useful progenies, the partitioning method (POWERS 1951, 1957) was used in the present study. The results showed that expected genetic gains for the five characters, first flowering date, plant height, node number, internode length and pod number were extremely high. The high expected genetic gains observed in this experiment might represent transgressive segregation in F_2 . This may be of interest for making crosses between the indeterminate and the determinate varieties.

Summary

1. Three soybean varieties, Harosoy (indeterminate type), Tokachi-nagaha and Kitami-shiro (determinate type), and their F_1 and F_2 generations obtained from Harosoy \times Tokachi-nagaha and Harosoy \times Kitami-shiro were used for genetic analysis of growth habit characters.

2. The heterosis of F_1 plant was present in all growth habit and quantitative characters except ratio of node number and number of pods in main stem.

3. The increment of node number after first flowering in percent of total node number was positively correlated with pod number.

4. The node number at first flowering was uncorrelated with its increment after first flowering in F_2 populations.

5. Both the heritability values and expected genetic gains were high for quantitative characters and growth habit in F_2 populations.

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