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STUDIES WITH SOME AGRONOMIC
CHARACTERS IN NAVY BEANS

Thesis for the Degree of M. S.
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Salim Amin Makarem
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THESIS

This is to certify that the

thesis entitled

STUDIES WITH SOME AGRONOMIC CHARACTERS
IN NAVY BEANS

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Salim Amin Makarem

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of the requirements for

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E. E. Down

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STUDIES WITH SOME AGRONOMIC CHARACTERS

IN NAVY BEANS

By

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INTRODUCTION

The navy bean is one of Michigan's most important cash crops. Any effort made toward improving the production of this crop will help in adding to the prosperity of the farmer and the state. For this reason a breeding program has been set at Michigan Agricultural Experiment Station to develop varieties that are outstanding in yield and quality, resistant to the more important diseases, and in accordance with the requirements for economical production practices.

The Robust (13) white pea bean was selected by F. A. Spragg to meet some of these purposes. Compared with many of the commonly grown varieties of white navy bean, Robust develops much larger vines, ripens more uniformly, is resistant to common bean mosaic, is highly resistant, but not immune, to blight and anthracnose, is highly productive but has the tendency to mature a few days later than some of the other varieties; it lacks uniformity of size and shape, and does not look quite as chalky white in color as some of the other varieties.

To meet some of the desired qualities that are lacking in Robust, this station introduced the Michelite white pea bean in 1937, developed by E. E. Down (2) and J. W. Thayer, Jr. The Michelite has inherited the good qualities of its parent Robust, plus the uniformity in size and shape, and the clean white color of its other parent, Early Prolific. Furthermore, the Michelite is slightly more resistant to blight and wilt, and carries its pods off the ground higher than Robust, thus reducing the percentage of the cull material, "pick."

Although at the present time the Michelite bean is the best white pea bean for Michigan, breeding is in progress to add the important characters of resistance to virus 15 and anthracnose. It is thought also that if a bush bean could be developed, having the outstanding characteris of the Michelite and bearing the pods off the ground high enough to permit harvesting with a combine, and possessing resistance to the above-mentioned diseases, it would be very beneficial. This is because the type of growth of a bush bean helps to keep the pods off the ground, matures the pods in a shorter range of time, and permits the use of the combine much better than a vine bean.

In the present work an attempt has been made to study the behavior of the inheritance of virus 15 resistance, and the agronomic characters which are concerned with the height of the stem from the level of the soil to the first branching node.

REVIEW OF LITERATURE

Habit of Growth

Mendel (4) reported the results of crosses between tall and dwarf forms of beans. He found that tallness is dominant to dwarfness; the F_2 segregated in a ratio of three tall to one dwarf.

Von Tschermak (4) crossed tall and short varieties of bean. The F_1 plants were all tall. Of the F_2 generation, thirty-five were classified as short, two as intermediate, and eighteen as tall. As it is noticed from these results, Tschermak attacked the problem from a different angle than Mendel; instead of dealing with the determinate versus indeterminate habit of growth as a separate character, he dealt with the general character of tall versus short habit of growth.

Emerson (3, 4) showed that there are three factors involved in bean height:

(1) determinate versus indeterminate habit of growth;

(2) number of internodes (in pole beans this depends largely on environmental conditions);

(3) internode length.

Norton (10) interpreted his results by means of three factors governing height, A-a indeterminate versus determinate, L-l tall versus short, T-t twining versus nontwining.

Three-to-one segregation of tall to short has been observed by Doornhaot and others (18). Hilpert (8) found that indeterminate habit of growth behaved as a simple dominant to determinate.

Common Bean Mosaic

The common bean mosaic was observed, according to Nelson (10), by Groanowski in Russia in 1899.

At present, the common bean mosaic includes two types, bean virus 1, and its variant bean virus 15 which was first observed in New York State by Richards and Burkholder (15). Since then it has been observed in the principal bean growing regions of the United States.

The inheritance of common bean mosaic has been the subject of studies of several investigators. McRostie (9) studied the inheritance of resistance to bean virus 1 in crosses involving the resistant variety, Robust. He obtained data that suggested a two-factor ratio in which either factor in recessive form produces resistance. Pierce (13), from crosses involving three resistant varieties, Corbett Refugee, Robust, and Great Northern U. I. No. 1, and one susceptible variety, Refugee Green, found that Corbett Refugee carries the dominant type of resistance, whereas Robust and Great Northern U. I. No. 1 carry the recessive type. Parker (12) found in reciprocal crosses between the mosaic resistant Robust and the susceptible Stringless Green Refugee varieties, that the maternal parent determined to a large extent the reaction of the F_1 generation plants. In the F_1 generation all plants were susceptible when Robust was used as male and 82 percent of the plants were resistant when it was used as female. In the F_2 and F_3 generations this influence was less noticeable, but still evident. It was assumed that the cytoplasm or some extranuclear inclusion govern the immediate reaction of the plant to the virus. Wade and Andrus (19), crossing the tolerant variety, Black Valentine, with the resistant one, U. S. No. 5 Refugee, concluded that resistance to mosaic virus was dominant to tolerance by a single factor. A factorial scheme to explain the results obtained from crossing the susceptible variety, Stringless Green Refugee, and the three resistant varieties, U. S. No. 5 Refugee, Idaho Refugee, and

Robust, was presented by Ali (1). The inheritance of resistance to virus 1 is governed by two factor pairs exhibiting dominant and recessive epistasis. Varieties derived from Corbett Refugee have the dominant type of resistance; but when the virus was continuously supplied by the approach-graft inoculation, the resistant plants developed top necrosis and black root. The recessive type of resistance present in Robust prevented both the expression of mosaic symptoms and top necrosis.

Resistance to mosaic virus 15 has been investigated recently at Michigan State College and reported in two theses, by Ford (5) and Rhodes (16). From crosses between a susceptible variety of navy bean, Michelite, and a resistant one, Cornell 46-62, Ford obtained data in the F_2 generation indicating that resistance to virus 15 was controlled by a single factor that expressed itself at low temperature as three-to-one ratio, and at high temperature as one resistant to three susceptible. Rhodes carried an extensive work to study the inheritance of resistance to virus 15 in crosses involving the resistant varieties, Trag 279-1, Z-1 (Topcrop), Cornell 46-62, and the susceptible one, Rainy River. He concluded that inheritance to virus 15 resistance may be interpreted in terms of two factor pairs that exhibited dominant and recessive epistasis, respectively, and that the letters II and aa, that stand for rèsistance to virus 15, are the same symbols used by Ali for resistance to virus 1; resistance to both strains of common mosaic virus, virus 1 and virus 15, are controlled by genes that occupy the same loci. He deduced from his finding that the recessive genes for virus 15 resistance are members of a triple allele series: AA for susceptibility, a-15 a-15 for resistance to virus 1 but susceptibility to virus 15 as present in Michelite and Robust. Top necrosis has been observed on plants that carried both types of resistance. The necrosis that was present in the recessive type of resistance appeared to be controlled by a second pair of recessive factors that were expressed only in susceptible plants infected with virus 15.

Internode Length

The only study the author is aware of being related to the inheritance of the height of the stem from the level of the soil to the branching node in beans, is the one that was carried on by Emerson (4). From the comparisons of bush and pole bean varieties within themselves, with each other, and with the

F_2 generations, Emerson pointed out that the potential internode lengths of bush beans can be determined roughly from measurements of the first five internodes. The length of the first fifteen internodes is thought to give a fair approximation to the mean internode length of pole beans. In order that pole and bush beans may be directly compared, it is necessary to limit consideration to a definite number of internodes common to both types, and the comparison must relate to the first five or six internodes. He also pointed out that growth is fairly rapid at the start but soon slackens materially as the food stored in the cotyledons becomes exhausted, and then becomes increasingly more rapid as the young plant becomes well established. In general, the hypocotyl is longer than the epicotyl, which, in turn, is longer than the second internode.

Crossing varieties of bush beans with different internode lengths is shown to result in an intermediate condition in F_1 and F_2 and a wider range of variation in the latter. The same is true between pole beans of different mean internode lengths; in the F_2 generation the mean lengths of the first five internodes were intermediate and exhibited more variability than the pole and bush parents, which was evidence for segregation in the F_2 generation of factors for length of the first five internodes. Emerson thought that, where there is distinct segregation in the F_2, it should be possible to isolate types of both pole and bush beans of different internode lengths from a single cross of pole and bush races. He thought that a multiple-factor hypothesis afforded a simple and direct interpretation of the known facts of inheritance derived from selection experiments as well as those obtained from cross-breeding.

branches runs on the ground; the internodes are shorter than the preceding one; the seeds are as large, approximately, as the Michelite bean seeds. Seeds of both strains lack the white chalky color of Michelite.

The bush bean type is selection No. 7149 from a second generation of backcrossing to the Michelite variety of a bush type of bean. The original bush used in the cross was a selection from a progeny developed by Clarence F. Genter at Michigan State College from seeds of the Michelite variety treated with X rays in the year of 1939. Then, in 1945, this original bush line was crossed with Michelite to incorporate in it some of the desired characteristics of the latter. In the fall of 1946 the F_1 was backcrossed to Michelite. During the winter, the backcross was again backcrossed to Michelite. Reselections were carried on until a true breeding bush bean, Selection No. 7149, was obtained.

MATERIALS

In the investigations described in this thesis, two strains of the vine bean type and one strain of the bush bean type were used. The two vine bean strains were selections from the fourth generation of a cross between Michelite and Trag varieties. The latter is a Mexican introduction with black seed coat. The United States Department of Agriculture carried the breeding until the F_2 generation. Then, in 1949, the Section of Vegetable Crops of the above-mentioned Department sent the F_2 generation to Michigan Agricultural Experiment Station, who carried their breeding to the F_4 generation, when two selections, No. 1031 and No. 0987, were made in 1950. Both strains are of the white pea bean type. Selection No. 1031 has a spreading habit of growth; the lateral branches are long and running; the internodes are rather long; the seeds are a little larger than the seeds of the Michelite. Selection No. 0987 has a conical upright type of growth; the lateral branches are rather short and stocky; the main axis is stocky too, but although longer than the lateral branches, it is still considered medium short; the whole body of the plant stands upright and none of the

METHODS

The present investigations started in the fall of the year 1950 in the greenhouse. Seeds of the two vine bean strains were planted in three pots each, on the same day. Seeds of the bush bean were planted twice, at four-day intervals, starting three days after the vine beans were planted. This arrangement was to provide coincidence in the time of flowering between the bush and the vine beans.

The bush, used as female, was crossed with the two vine bean strains. The reason for using the bush as female was to be able later to detect the hybrid progenies. The flowers were emasculated before the banner petal began to open. The bud was carefully opened with a pair of small forceps; the banner petal was folded back; the spiral keel was then slit and opened, leaving anthers and stigma exposed; the anthers were carefully pinched off so as to prevent any injury to the pistil or any contact with it. Then pollination followed. A mature flower which opened the night before was taken from the male parent vine plant. The stigma was forced out by folding back the banner petal, and with most of the pollen adhering to it, was then brought in contact with the female bush parent pistil and the pollen rubbed off upon it. The banner petal was then folded back over the pistil. In twenty-four to forty-eight hours after crossing, a check was made to detect successful crossing.

The crosses were identified during these operations. Each parent plant was given a number. When a cross was made, these numbers and the date of crossing were recorded on a small tag which was fastened to the flower stalk of the female parent. Self-polinated flowers on the mother parent plants were removed daily. Approximately six pods were left on each plant. Some shriveling had been observed, even after the pods were around three inches long. This was probably due to nutritional disorders or pathological ones. The number of crosses was as many as it was felt necessary to produce sufficient F_1 plants to give the amount of seeds desired for the F_2 generation. It was aimed to get a large number of seeds, due to the complexity of some of the characters involved.

When mature, the beans were shelled out. The ones that were developed from the crosses of one individual male parent plant with the bush were grouped and placed in one envelope and allowed to dry for several days before planting.

During winter the grouped F_1 seeds and the ones from the individual male parents were planted in the greenhouse. The reason for planting the male parent seeds was to check upon their homozygosity, especially for virus 15 resistance. Two successive plantings of the bush variety seeds were made for the purpose of backcrossing.

All the F_1 plants and the male parent progenies were inoculated with a culture of virus 15. The inoculation was carried on as follows. The leaves of the diseased plants were macerated in a Waring Blender, and the virus 15 infected juice was separated by filtration through a fine mesh cheesecloth. The extract was then diluted in a proportion of nine water to one juice, though it was demonstrated later that one part of the infected juice to ninety-nine parts of water was more than enough. The infectious plant extract, with a teaspoonful of carborundum powder added to one hundred centiliters, was sprayed on the primary leaves with a suction feed glass atomizer at a pressure of approximately forty pounds. A strip across the middle of the leaf was traced with the spray. This strip darkened at once and turned partly dry after a few days from the time of the spraying. After ten days to two weeks, the time required for the appearance of the infection symptoms, the results were recorded. This technique of inoculation proved to be one hundred percent accurate when it was checked on several susceptible plants of the bush strain. All affected plants were discarded. Most of the resistant hybrids were used as males in the backcrossing to the bush parent. Enough pods were left on these hybrid plants for the production of the F_2 seeds. The mature seeds of the hybrids, backcrosses, male parents, and female parents were shelled out, identified on a progeny basis, and placed in separate envelopes to dry out. After this they were ready to be planted in the field.

On June 18, 1951, these seeds were planted on a progeny basis. Six successive rows of the segregating progenies and two rows of the vine and bush parent progenies were planted in lines. Planting was done with a V-Belt drill which spread and covered seeds evenly. The percentage of germination was low and differing from one progeny to the other. It was found that the bean maggot was chiefly responsible for that damage. At the time the primary leaves developed, all the segregating progenies and vine parents were inoculated with virus 15, using a concentration of 10 percent of the diseased leaf extract and 90 percent water. A row six feet long of the susceptible bush plants was inoculated as a check. Along with these inoculations, a demonstration on the effect of a lower concentration of the inoculum, and a 24 hour keeping possibility was carried out. A portion of an inoculum made of 1 percent virus 15 infected extract to 99 percent water was applied directly after preparation to the susceptible plants. Another portion was kept 24 hours in a shady place and then sprayed on susceptible plants. Three weeks later, data on the reaction to virus 15 and habit of growth began to be taken.

When mature, the individual plants were put in paper bags with several small holes to allow aeration. The plants of a plot were put into a burlap bag and hung in the barn. Measurement of the stem height from the level of the soil to the first branching node was taken in quarters of an inch. The level of the soil could be determined by the trace of dirt that covered the underground portion of the stem and the subsequent change in color and morphology.

EXPERIMENTAL RESULTS

Habit of Growth

Habit of growth, as referred to in this part of the thesis, involves the determinate (bush) and the indeterminate (vine) types of plant.

Crosses between the bush bean, used as female, and the spreading and the upright vine, used as males, were made. The resulting F_1 generation was backcrossed to the bush strain. The F_1 plants were of the vine type, indicating a Mendelian type of inheritance with the vine character being dominant.

In the first generation backcross to the bush variety, segregation into pole and bush types occurred. Examination of Table 1 shows that from a total of 321 progenies involving spreading vine, 152 are vine and 169 are bush; and of Table 2, shows that from a total of 236 progenies involving upright vine, 126 are vine and 110 are bush. A X^2 of 0.152 for the former and 1.724 for the latter indicates a good fit to the ratio 1 vine to 1 bush.

In the F_2 generation, from a total of 531 progenies from the cross bush by spreading vine, shown in Table 3, 440 are vine

TABLE 1

INHERITANCE OF HABIT OF GROWTH AND RESISTANCE TO VIRUS 15 IN THE FIRST GENERATION BACKCROSS OF THE F_1 OF BUSH BY SPREADING VINE ONTO BUSH

Progeny No.	Habit of Growth Not Considered				Vine			Bush		
	Healthy	Top Necrotic	Mosaic	Sum	Res.	Susc.	Sum	Res.	Susc.	Sum
13322	21	4	13	30	14	8	22	11	5	16
23	10	0	10	20	6	3	9	4	7	11
24	12	1	10	23	7	5	12	6	5	11
25	12	2	10	24	7	5	12	7	5	12
26	12	4	21	37	8	14	22	8	7	15
27	20	3	15	38	12	8	20	16	7	23
30	12	2	17	31	6	7	13	8	10	18
31	11	3	11	25	5	1	6	9	10	19
32	17	4	16	37	8	8	16	13	8	21
33	12	2	17	31	9	8	17	5	9	14
34	8	0	9	17	4	4	8	4	5	9
Grand	147	25								
Total	172		149	321	86	71	152	86	78	169
Ratio	1	:	1		1 :	1		1 :	1	
Chi-square	1.646				1.432			0.390		

Chi-square of independence of the reaction to virus 15 from habit of growth is 0.174.

TABLE 2

INHERITANCE OF HABIT OF GROWTH AND RESISTANCE TO VIRUS 15 IN THE FIRST GENERATION BACKCROSS OF THE F_1 OF BUSH BY UPRIGHT VINE ONTO BUSH

Progeny No.	Habit of Growth Not Considered				Vine			Bush		
	Healthy	Top Ne-crotic	Mosaic	Sum	Res.	Susc.	Sum	Res.	Susc.	Sum
13335	15	1	17	33	7	9	16	9	8	17
38	16	1	17	34	10	8	18	7	9	16
39	1	2	6	9	1	3	4	2	3	5
40	15	2	12	29	8	10	18	9	2	11
41	8	2	17	27	4	8	12	6	9	15
42	9	-	11	20	5	6	11	4	5	9
43	14	-	15	29	9	8	17	5	7	12
52	30	3	22	55	19	11	30	14	11	25
Total	108	11								
	119		117	236	63	63	126	56	54	110
Ratio	1	:	1		1 : 1			1 : 1		
Chi-square	0.016				0.000			0.036		

Chi-square of independence of the reaction to virus 15 from habit of growth is 0.016.

TABLE 3

INHERITANCE OF HABIT OF GROWTH AND RESISTANCE TO VIRUS 15 IN THE F_2 OF CROSSES BETWEEN BUSH AND SPREADING VINE

Progeny No.	Habit of Growth Not Considered				Vine			Bush		
	Healthy	Top Ne-crotic	Mosaic	Sum	Res.	Susc.	Sum	Res.	Susc.	Sum
13353	28	2	6	36	27	6	33	10	0	10
54	32	4	10	46	30	9	39	6	1	7
55	29	2	12	43	23	7	30	8	5	13
56	27	2	4	33	19	4	23	7	0	7
57	27	1	11	39	20	7	27	8	4	12
60	30	4	8	42	27	7	34	7	1	8
61	24	4	12	40	22	8	30	6	4	10
62	27	0	10	37	19	9	28	8	1	9
63	26	3	8	37	16	4	20	13	4	17
64	28	2	5	35	22	4	26	7	1	8
65	26	3	6	35	20	5	25	6	1	7
68	32	2	11	55	27	8	35	7	3	10

TABLE 3 (Continued)

Progeny No.	Habit of Growth Not Considered				Vine			Bush		
	Healthy	Top Ne-crotic	Mosaic	Sum	Res.	Susc.	Sum	Res.	Susc.	Sum
13369	32	3	13	48	27	10	37	8	3	11
70	30	4	9	43	23	7	30	11	2	13
71	18	4	10	32	17	6	23	5	4	9
Total	416	40					440			151
	456		135	591	339	101		117	34	
Ratio	3	:	1		3 :	1		3 :	1	
Chi-square		1.466			0.981			0.496		

Chi-square of independence of the reaction to virus 15 from the habit of growth is 0.0106.

and 151 are bush. Table 4 shows that from a total of 698 progenies from the cross bush by upright vine 539 are vine and 159 are bush. A X^2 of 0.094 for the former and 1.334 for the latter indicates a good fit to the ratio 3 vine to 1 bush.

These ratios in the backcrosses and in the F_2 generations indicate that indeterminate habit of growth is governed by a single dominant gene in this material.

Virus 15 Resistance

The demonstration that was carried on the concentration of the inoculum and duration of effectiveness showed that 1 percent of the virus 15 extract in water is satisfactorily effective. Keeping the inoculum twenty-four hours in the shade did not hinder its effectiveness. The progenies from the spreading and upright vine strains and their crosses with the bush strain were tested in the greenhouse for resistance to virus 15. Although it was hoped that these two vine strains were homozygous when inoculated with the virus 15 infected juice, it was found that they were still segregating for this characteristic, and the F_1 generation plants, accordingly, were not all resistant. Examination of Table 5 shows that progenies from

TABLE 4

INHERITANCE OF HABIT OF GROWTH AND RESISTANCE TO VIRUS 15 IN THE F_2 OF CROSSES BETWEEN BUSH AND UPRIGHT VINE

Progeny No.	Habit of Growth Not Considered				Vine			Bush		
	Healthy	Top Ne-crotic	Mosaic	Sum	Res.	Susc.	Sum	Res.	Susc.	Sum
13372	30	4	11	45	24	7	31	10	4	14
73	32	4	13	49	29	8	37	7	5	12
82	28	1	10	39	26	8	34	3	2	5
83	30	1	12	43	22	10	32	9	2	11
84	17	0	7	24	15	5	20	2	2	4
85	22	4	6	32	20	6	26	6	0	6
86	25	4	13	42	21	10	31	8	3	11
87	24	2	8	34	18	6	24	8	2	10
90	27	0	12	39	23	10	33	4	2	6
91	29	0	7	36	22	6	28	7	1	8
92	29	2	13	44	23	10	33	8	3	11
93	25	1	7	33	22	6	28	4	1	5

TABLE 4 (Continued)

Progeny No.	Habit of Growth Not Considered				Vine			Bush		
	Healthy	Top Ne-crotic	Mosaic	Sum	Res.	Susc.	Sum	Res.	Susc.	Sum
13394	19	4	6	29	16	5	21	7	1	8
95	15	1	5	21	9	4	13	7	1	8
98	17	2	4	23	15	4	19	4	0	4
99	13	4	7	24	13	6	19	4	1	5
400	31	0	11	42	27	9	36	4	2	6
401	17	3	6	26	16	4	20	4	2	6
402	7	1	4	12	7	3	10	1	1	2
403	21	0	7	28	16	5	21	5	2	7
404	24	2	7	33	18	5	23	8	2	10
Total	482	40					539			159
	522		176	698	402	137		120	39	
Ratio	3	:	1		3 :	1		3 :	1	
Chi-square		0.016			0.050			0.018		

Chi-square of independence of the reaction to virus 15 from the habit of growth is 0.051.

TABLE 5

VIRUS 15 REACTIONS FROM TESTING PROGENIES OF SPREADING AND UPRIGHT VINE MALE PARENTAL LINES AND THE F_1's OF THESE LINES WITH BUSH

Progeny No.	Healthy	Top Necrotic	Mosaic Virus 15
Spreading vine			
02244	11	-	4
45	0	-	11
46	10	-	0
47	10	-	0
Upright vine			
02248	12	-	0
49	5	1	0
50	7	-	0
51	10	-	6
F_1 of Spreading x Bush			
02244 x 02107	4	-	4
45 x "	0	-	13
46 x "	3	-	11
47 x "	11	1	0
F_1 of Upright x Bush			
02248 x 02107	6	2	-
49 x "	3	-	3
50 x "	11	-	-
51 x "	6	-	4

the spreading and upright strains reacted differently. Two of them showed that the parent plants were heterozygous; another was apparently homozygous for susceptibility; the other five, apparently, were homozygous for resistance. The F_1 progenies reacted accordingly. The ones that originated from the heterozygous individuals segregated into resistant and susceptible individuals, while those which resulted from the homozygous susceptible parent were all susceptible. The progenies that had their spreading and upright parent plants homozygous for resistance were resistant. The progeny of 02246 x 02107 segregated to resistant and susceptible plants, indicating that the vine parent was not as homozygous as it was demonstrated by its progeny, the number of which probably was not large enough to show the susceptible ones.

Whatever was the case, these results did not affect the latter inheritance studies concerning virus 15 resistance. Since all the susceptible F_1 plants were discarded, only heterozygous resistant plants were left, as expected when vine parents were all homozygous for resistance.

Crosses between the bush strain used as female and the spreading and upright vine strains used as males were made.

The F_1 generation was backcrossed with the bush. The F_1 hybrids that resulted from homozygous resistant vine parents were all resistant, indicating a Mendelian type of inheritance with resistance being dominant.

The backcross and F_2 generations exhibited three types of reaction following inoculation with virus 15: (a) healthy; (b) top necrotic; (c) mosaic. Most necrotic plants died within about two weeks, the others, soon after. None of them lived long enough to develop and mature pods. Most of these plants grew enough so as to be distinguished concerning the type of growth. Others did not grow to that extent.

In the first generation backcross to the bush strain, the segregation as shown in Tables 1 and 2 occurred as follows. From a total of 321 plants involving spreading vine, 147 were healthy, 25 top necrotic, and 149 mosaic. From a total of 236 plants involving upright vine, 108 were healthy, 11 top necrotic, and 117 mosaic. When the top necrotic plants were added to the healthy ones and considered as resistant plants, the distribution then showed a good fit to the ratio 1 resistant to 1 susceptible, as it has been proven by the X^2 tests with values of 1.646 for the former and 0.016 for the latter. When habit of growth was taken into consideration, the vine and bush types of the progenies segregated, respectively (Table 1), into 86 resistant plants and 71 susceptible, and 86 resistant plants and 78 susceptible, when the spreading vine was involved in the crosses. There were (Table 2) 63 resistant and 63 susceptible, and 56 resistant and 54 susceptible, respectively, when the upright vine entered the crosses. The X^2 values of 1.432, 0.392, 0.000, and 0.036, respectively, demonstrated good fits to the ratio 1 resistant to 1 susceptible.

In the F_2 generation of the cross bush by spreading vine (Table 3) from a total of 591 plants, 416 were healthy, 40 top necrotic, and 135 mosaic. In the F_2 of the cross bush by upright vine, Table 4 shows that from a total of 698 plants, 482 were healthy, 40 top necrotic, and 176 mosaic. When the necrotic plants are added to the healthy ones and considered as resistant, a X^2 of 1.466 for the former distribution and 0.016 for the latter one indicated a good fit to the ratio 3 resistant to 1 susceptible. When habit of growth was taken into consideration, the vine and bush types segregated, respectively, as shown in Table 3, 339 resistant to 101 susceptible, and 117 resistant to 34 susceptible. Table 4 shows a segregation of 402 resistant and

137 susceptible in the vine type, and 120 resistant and 39 susceptible in the bush type. The distribution of the F_2 plants suggests a ratio of 3 resistant to 1 susceptible. This is confirmed by the values of X^2 of 0.981, 0.426, and 0.050 and 0.018, respectively, which prove a good fit.

Height of the Stem From the Level of the Soil to the First Branching Node

The same cultures of strains of beans used in the studies of habit of growth and virus 15 resistance were used in this study. Some of the peculiarities of growth of these strains have been considered in some detail in the previous discussion of materials and methods. The virus 15 infected plants were not used in this study, so as to reduce the causes of variability due to disease reaction. The characteristic with which this study is concerned is especially subject to wide variability due to the sensitivity of the branching habit of growth to differences in the environment and due to modifications of the level of the soil. The stem heights of the F_1 generation were not measured because of the small number of individuals and the different environmental conditions that prevailed in the greenhouse, where the F_1

generation was raised, as compared with those of the field, where the F_2 and backcrosses were raised.

In Table 6 are presented the data obtained from the bush and spreading vine strains and their crosses with respect to the heights of the stem from the level of the soil to the first branching node. As thus determined, the mean height of the bush strain was 4.56 quarters of an inch and that of the spreading vine was 8.26. Although there was an overlapping in the distribution of heights, the difference between the two means was significant. The F_2 generation of the cross between these two strains had a mean height of 6.32, which is between the mean heights of the parents. When habit of growth was taken into consideration, the vine type of the F_2 had a mean height of 6.40, while the bush type had a mean height of 5.92. Although the mean height of the F_2 vine progenies was closer to the average of the two parents than that of the bush type, this difference might have been due to other than hereditary factors. The mean height of the F_2 generation, which came almost midway between the mean heights of the parents, indicated that it is probably a nondominance type of inheritance. The first backcross generation had a mean height of 5.85 when the vine and bush types were considered together,

TABLE 6

FREQUENCY DISTRIBUTION OF HEIGHTS OF THE STEM FROM THE LEVEL OF THE SOIL TO FIRST BRANCHING NODE OF BUSH AND SPREADING VINE STRAINS OF BEAN AND THEIR CROSSES

	Habit of Growth	No. of Individuals	Mean	Standard Deviation	Coefficient of Variability
Parents:					
Bush	bush	140	4.56 ± 0.09	1.14 ± 0.06	25.00 ± 1.59
Spreading vine	vine	86	8.26 ± 0.13	1.27 ± 0.09	15.37 ± 1.33
Backcross:	bush	69	5.59 ± 0.18	1.62 ± 0.13	28.98 ± 2.67
	vine	64	6.14 ± 0.20	1.63 ± 0.14	26.54 ± 2.48
Total		133	5.85 ± 0.13	1.61 ± 0.09	27.52 ± 1.79
F_2:	bush	109	5.92 ± 0.14	1.47 ± 0.01	24.85 ± 1.78
	vine	290	6.40 ± 0.11	2.01 ± 0.08	31.40 ± 1.42
Total		399	6.32 ± 0.08	1.71 ± 0.06	27.05 ± 1.03

TABLE 6 (Continued)

Class Centers in Quarters of an Inch											
1	2	3	4	5	6	7	8	9	10	11	12
1	6	13	47	45	24	3	1				
					3	17	38	18	5	2	3
		4	8	25	21	6	2	1	-	-	2
		1	5	16	23	7	9	1	1	-	1
		5	13	41	44	13	11	2	1	-	3
		6	7	27	40	17	6	4	1	1	
	1	7	20	55	84	51	34	22	9	4	3
	1	13	27	82	124	68	40	26	10	5	3

whereas the vine and bush progenies averaged, respectively, 6.14 and 5.59. The general trend in the mean height of the backcross is toward the mean height of the bush parent, which is expected in such type of inheritance. The mean height of the backcross generation should fall in between the mean height of the F_2 and that of the bush, theoretically, at 5.44. A comparison between these means shows that the mean heights in the backcross were always higher than 5.44, especially when the vine progenies were taken into consideration; but in both cases these means were lower than the average height of the F_2 generation, as it was expected. These discrepancies may be due to other than hereditary factors.

In all but one case the standard deviations and the coefficients of variation of the F_2 generation and first backcross were higher than those of the parents, taken separately, and much higher than their averages. Even the coefficient of variation value of this one exception was higher than the average coefficient of variation of the parents. This increased variability in the F_2 and first backcross generations was considered to indicate that there was segregation of factors for stem height.

The fact that no distinct classes could be observed indicated that multiple factor inheritance was involved.

In Table 7 are shown the frequency distributions for the height of the stem, the mean heights, and the variabilities pertaining to these distributions for the bush and upright vine strains and their crosses. The significant difference between the mean height, 4.56, of the bush strain, as compared with the mean height, 6.02, of the upright vine strain, is narrower than that between the bush and the spreading vine. Still the difference between the stem heights of the bush and upright strains is significant. The F_2 generation of the crosses between these two strains exhibited a mean height of 5.36, which is very close to the average of the two parents. When habit of growth was taken into consideration, the vine type of the F_2 generation had a mean height of 5.41, and the bush type had a mean height of 5.21. Neither type differed much from the average of the two parents. Here, too, the independence of inheritance of height of the stem from the habit of growth is evident. The mean height of the F_2 generation being almost midway between the mean heights of the parents is another evidence, probably, of

TABLE 7

FREQUENCY DISTRIBUTION OF HEIGHTS OF THE STEM FROM THE LEVEL OF THE SOIL TO FIRST BRANCHING NODE OF BUSH AND UPRIGHT VINE STRAINS OF BEAN AND THEIR CROSSES

	Habit of Growth	No. of Individuals	Mean	Standard Deviation	Coefficient of Variability
Parents:					
Bush	bush	140	4.56 ± 0.09	1.14 ± 0.06	25.00 ± 1.59
Upright vine	vine	181	6.02 ± 0.10	1.37 ± 0.07	22.75 ± 1.19
Backcross:	bush	46	5.02 ± 0.24	1.67 ± 0.17	23.26 ± 2.54
	vine	53	5.53 ± 0.27	1.97 ± 0.19	35.44 ± 3.78
Total		99	5.33 ± 0.17	1.70 ± 0.12	31.89 ± 2.46
F_2:	bush	95	5.21 ± 0.16	1.59 ± 0.11	30.51 ± 2.37
	vine	338	5.41 ± 0.09	1.72 ± 0.04	31.79 ± 1.33
Total		433	5.36 ± 0.08	1.71 ± 0.05	31.9 ± 1.08

TABLE 7 (Continued)

Class Centers in Quarters of an Inch											
1	2	3	4	5	6	7	8	9	10	11	12
1	6	13	47	45	24	3	1				
		1	18	53	54	25	20	9	1		
	3	4	11	13	7	3	4	1			
	2	4	10	14	11	4	4	1	2	1	
	5	8	21	27	18	7	8	2	2	1	
1	2	11	13	35	16	6	7	4			
3	10	26	55	112	71	22	31	10	8		
4	12	37	68	147	87	28	38	14	8		

the nondominance type of inheritance that is concerned in the height of the stem.

In the first backcross generation of the bush x upright cross (Table 7), the mean height of the stem from the level of the soil to the branching node was 5.33; this is very close to 5.29, the average of the two parents, and 5.36, the average of the F_2 generation. On the basis of nondominance, the average height of the backcross should have been approximately 4.92. While the mean height of the bush type is close to it, that of the vine type is considerably higher. When the vine and bush mean heights were compared, no significant difference was found. Examination of Table 7 shows that the number of individuals in the backcross generation is small, and it looks as if the three individuals in the class centers ten and eleven had much to do in the discrepancies observed. The author thinks that, due to the great effect of the environment on the type of character he was studying, these discrepancies could be expected.

The F_2 and first backcross generations, which resulted from crosses between the bush and upright vine strains of beans, showed greater variablity in all but one case. In all cases, the standard deviation and coefficient of variation were greater than the parent average. This greater variability tends to indicate a segregation of factors. From the data shown in Table 7, there is no indication as to the number of factors concerned with height of the stem.

DISCUSSION

The main objects of the present studies were to find out the types of inheritance which are concerned with habit of growth, virus 15 resistance, and stem height, and to find the possibilities of recovering the bush type together with the resistance to virus 15 and the greater height of the stem of the vine parent.

The populations obtained from the bush x spreading vine and bush x upright vine crosses were large enough to give reliable results concerning the determinate versus the indeterminate habit of growth. A ratio of three vine to one bush was obtained in the F_2 generation, and one vine to one bush in the backcross. The vine and bush beans were shown to differ by a single character for habit of growth, which was governed by a single factor--dominant for indeterminate. Selection for the type of growth in this case does not present any difficulty, whether it is by direct segregation of the F_2 or by backcrossing.

Resistance to virus 15 in the above-mentioned crosses was found to be governed by a single dominant factor, when the necrotic plants were added to the healthy ones. Evidence that top necrotic plants should be classified as resistant is obtained from the following facts: (a) Among more than a hundred of inoculated bush plants susceptible to virus 15, not one was found to be top necrotic. (b) Rhodes (16) obtained seeds from a plant made necrotic as a result of inoculation with virus 15. When these seeds were planted and then inoculated with virus 15, he found that the necrotic parent behaved as if it were heterozygous for resistance. (c) Grogan and Walker (7) and Ali (1), working with virus 1, demonstrated that varieties carrying the dominant type of resistance must be regarded as field resistant because, when the inoculum escaped into the vascular tissues, top necrosis and black root would result. (d) Only by counting the necrotic plants as resistant could a hypothesis, common to all the crosses, be established. This hypothesis assumed that resistance was governed by a single dominant factor. The data in Tables 1, 2, 3, and 4 indicate that inheritance of virus 15 resistance was independent from habit of growth. These facts, single factors and independent type of inheritance, make selection for a bush type with resistance to virus 15 a simple one.

Height of the stem from the level of the soil to the first branching node is probably governed by a nondominant type of inheritance. Segregation of factors is considered to have occurred. A brief discussion is needed to clarify the problem as to whether one pair of factors or multiple pairs of factors are involved in this segregation. If inheritance of stem height is governed by a single pair of factors, segregation into distinct classes should occur in the F_2 and backcrosses, except when the difference between the means of the two parents is not large, and the overlapping of the frequency distributions is considerable. If inheritance of stem height is governed by many pairs of factors, there will be a larger number of classes. This larger number of classes, together with the usually expected variability in size within them, is likely to make it practically impossible to set them up distinctly as to height of the stem. Such was found to be the case with the bush x spreading vine crosses; the difference between the mean height was relatively considerable, and the overlapping of frequency distributions was slight. The segregation into three distinct classes in the F_2 and two distinct classes in the first backcross should have occurred, if only one pair of factors were involved. Examination of Table 6 does not reveal any distinct classes. This fact indicates that more than one pair of factors were involved in the inheritance of stem height in the bush by spreading vine crosses.

Table 7 shows that the difference between the means of the bush and upright vine is not large, and the overlapping in the frequency distributions is considerable. These facts prevent any conclusion concerning the number of factors involved in the inheritance of stem height in the bush by upright crosses. The only way to get a decision in this respect is to grow and study the succeeding generations. If homozygous progenies of intermediate stem heights are obtained, this would prove that multiple factors are involved. Otherwise stem height might be governed by one pair of factors.

If the inheritance for height were governed by a single pair of factors, the possibility of recovering the greater height of stem by backcrossing to the bush or direct segregation of the F_2 is fairly likely. The larger the number of factors involved, the less the chance of recovering the greater height of the vine parent. Comparatively, the chance of recovering it by direct segregation of the F_2 and succeeding generations is higher than by backcrossing method. For example, if one pair of factors is involved, there is 1/2 chance of recovering the gene responsible for the greater height by backcrossing, and 3/4 by direct segregation of the F_2. If two pairs of factors are involved, the chances of recovering the factors for greater height are 1/4 by backcrossing and 9/16 by direct segregation of the F_2. Thus, when several factors are involved, a large number of F_2 plants should be grown, if selection of a bush with the greater height is wanted, and many more plants will be needed, if the backcrossing method is practiced. It is evidently more practical to use the direct segregation method when multiple factor inheritance is involved. Both methods are practical when only one pair of factors are responsible.

Thus, in the cross of bush by spreading vine, in which the stem height is probably governed by multiple factors, a large number of F_2 plants should be grown. Selection for bush type, resistance to virus 15, greater height of the stem, and other desirable characteristics should then be possible. A smaller number of plants could be used if intermediate heights of stem are satisfactory. More information must be available before any decision can be reached as to height of stem in the cross of bush by upright vine.

SUMMARY

At the present time the Michelite vine bean is the best white pea bean for Michigan. It is thought that it would be very beneficial if a bush bean with the outstanding characters of Michelite, resistant to the more important diseases and bearing the pods off the ground high enough to permit the use of the combine.

In the present work an attempt has been made to study the inheritance of habit of growth, virus 15 resistance and stem height. One strain of bush bean, selection No. 7149, having most of the good seed characteristics of the Michelite; and two strains of vine bean selections, No. 0987 and No. 1031 of greater stem height but less desirable seed characteristics than the bush, were used.

Inheritance of habit of growth was limited, in the present work to determinate versus indeterminate types. Two crosses, bush x spreading vine and bush x upright vine segregated into one vine to one bush in the backcross, and three vine to one bush in the F_2, indicating that indeterminate habit of growth is governed by single dominant gene.

The bush x spreading vine and bush x upright vine crosses segregated into healthy, necrotic, and susceptible plants. Necrotic plants were considered as resistant. Both crosses segregated into a ratio of one resistant to one susceptible in the backcross, and three resistant to one susceptible in the F_2. Resistance to virus 15 was found to be governed by a single dominant factor. Inheritance of habit of growth was found to be independent of virus 15 resistance.

Inheritance of height of the stem from the level of the soil to the first branching node was found to be independent of habit of growth.

A nondominance type of inheritance was apparently involved in the inheritance of height of the stem.

The backcross and F_2 generations of the bush x spreading vine cross did not segregate into distinct classes and behaved as though they were governed by multiple factors.

Due to the fact that the difference between the mean heights of the bush and upright parents was not large, and the overlapping of the parental height frequency distributions was considerable, it was not possible to detect the type of inheritance that governed their height, although segregation of factors appeared evident.

A very large number of plants should be grown to recover the bush type and with it the greater stem height of the spreading vine. There is more chance of recovering it by the method of direct segregation than by the backcrossing method.

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APPENDIX

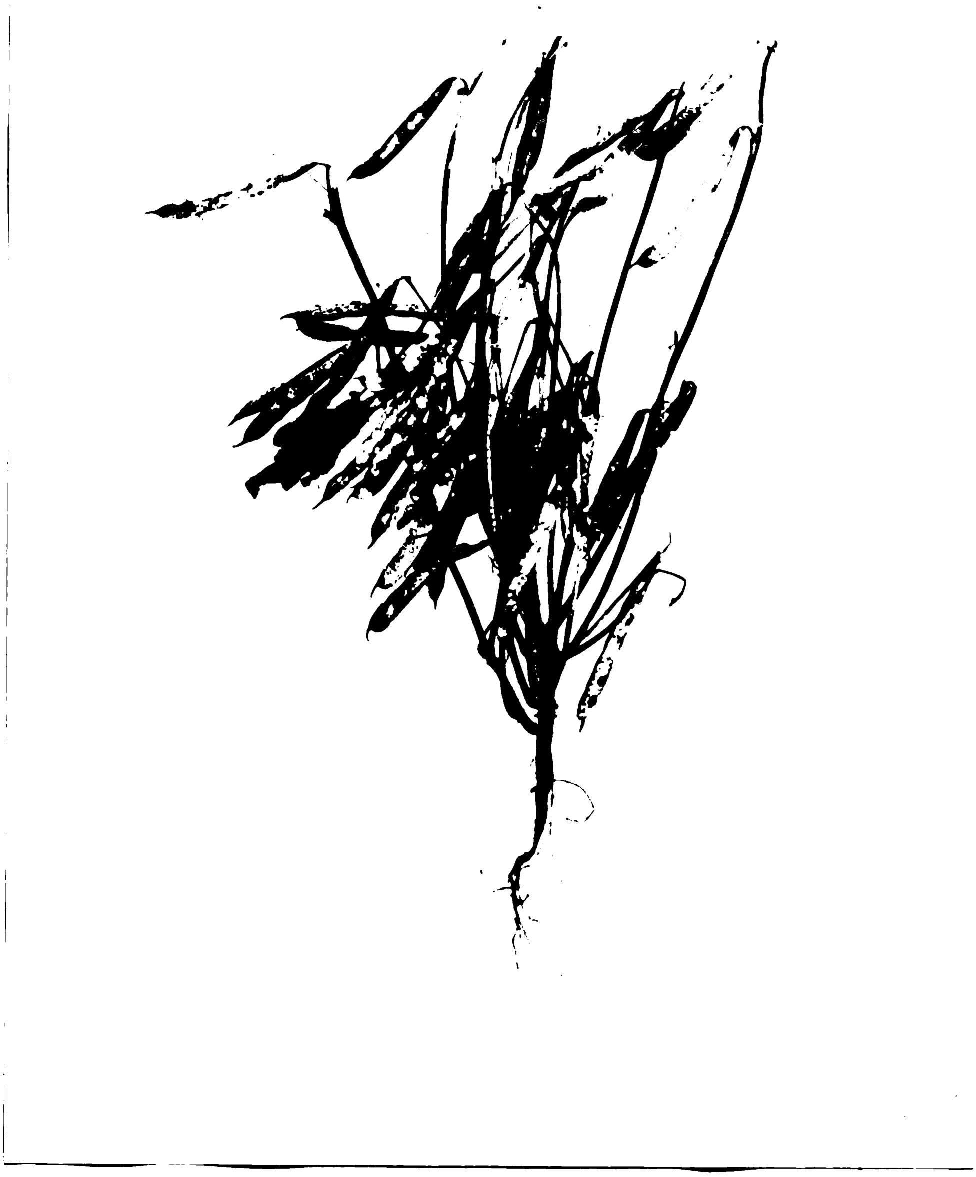

PLATE I

Field grown plant of the bush type, selection No. 7149.

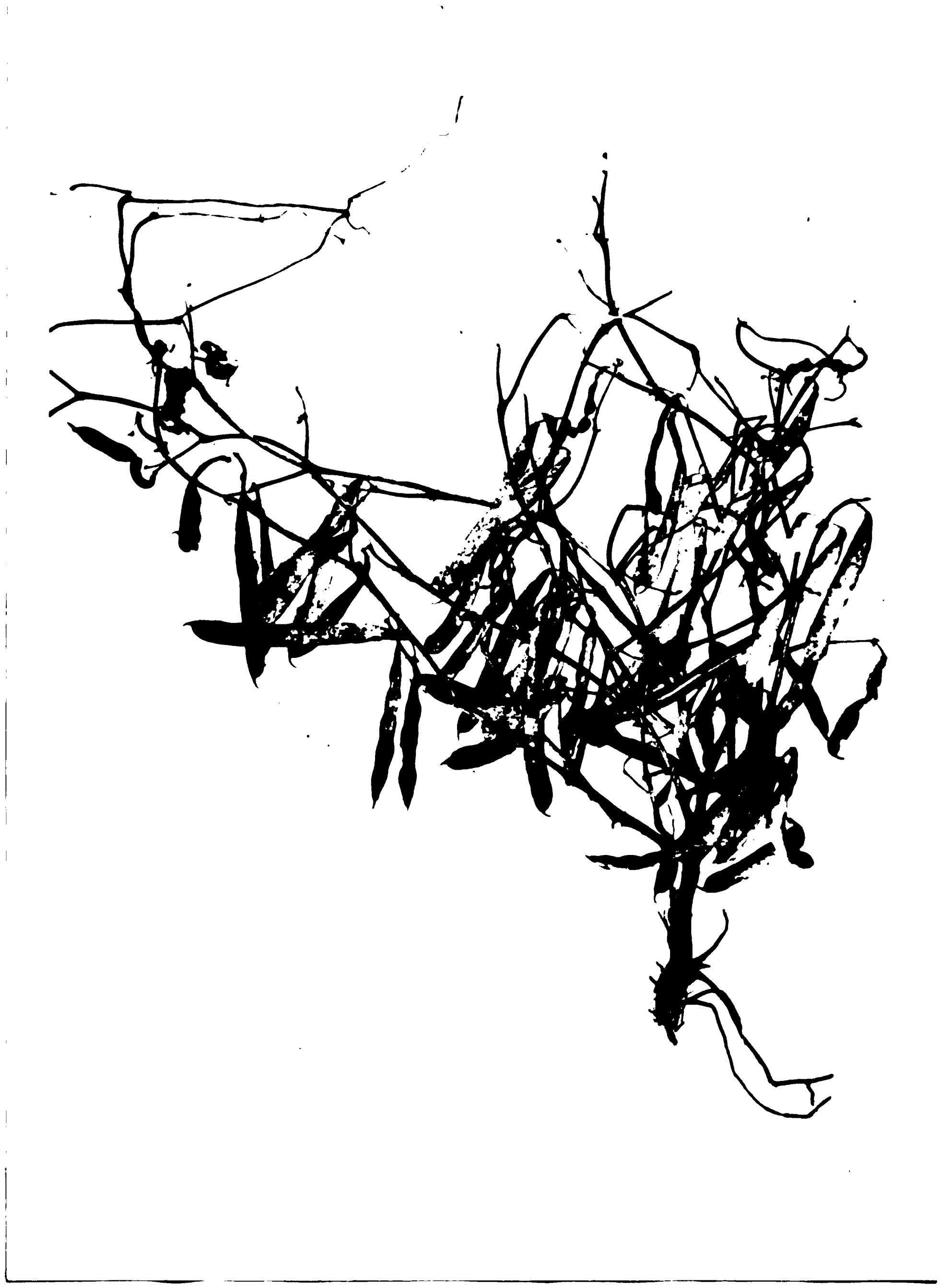

PLATE II

Field grown plant of the spreading vine type, selection No. 1031.

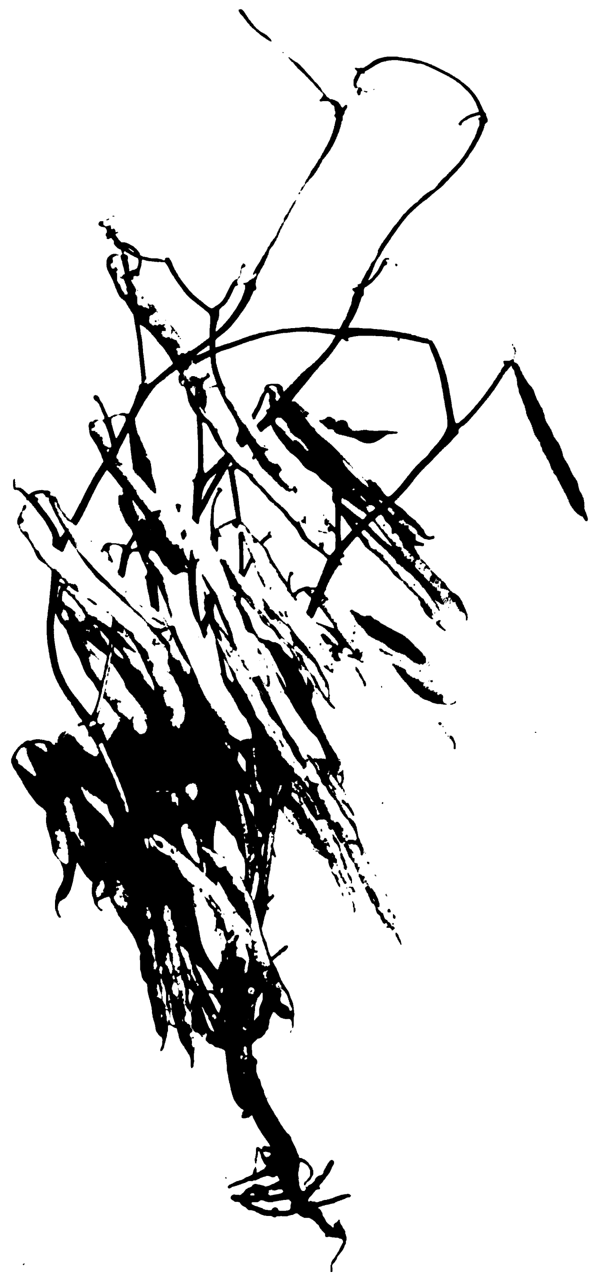

PLATE III

Field grown plant of the upright vine type, selection No. 0937.

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