THE DEVELOPMENT OF ANTHRACNOSE AND VIRUS 15 RESISTANT STRAINS OF RAINY RIVER NAVY BEANS BY BACKCROSSING

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INTRODUCTION

Michigan farmers raise over 90 per cent of the navy beans in the United States. In 1950 they produced about three million bags (100-pound) valued at approximately twenty million dollars.

The State's navy bean acreage is planted largely to two varieties, Michelite (11) and Robust (29). High quality seed of these varieties are maintained by a foundation seed program and a certified seed program controlled by the Michigan Foundation Seed Association and the Michigan Crop Improvement Association, respectively. There are, however, many older varieties grown in the state. Among these is the variety Rainy River which is early, has a desirable size and shape of seed (Plate I), and yields well, especially in some years. Its use is limited because of a high degree of susceptibility to the common bean diseases.

Rainy River is susceptible to the following bean diseases, all of which are seed-borne: (a) Common bacterial blight, caused by *Xanthomonas phaseoli* (E. F. Sm.) Dows; (b) fuscous blight, caused by *X. phaseoli* var. *fuscans* (Burk.) Starr and Burk; (c) bacterial wilt, caused by *Corynebacterium flaccumfaciens*

(Hedges) Dows; (d) the alpha race of anthracnose caused by *Colletotrichum lindemuthianum* (Sacc. and Magn.) Briosi and Cav.; and (e) common bean mosaic, caused by both virus 1 and its variant strain, hereafter referred to as virus 15 in this study. Michelite and Robust, in comparison, show a greater tolerance to the bacterial diseases and are resistant to virus 1 but not to virus 15.

The bacterial blights and anthracnose have been responsible for considerable losses to bean growers during wet growing seasons favorable for the development and spread of these pathogens (2, 20). As yet, virus 15 is not prevalent in the navy beans in Michigan, but there is a potential danger that the disease may be introduced through western grown garden bean seed.

Although the planting of disease free seed on non-infested soil is generally recommended for control of these diseases, the planting of disease resistant strains would be more satisfactory. Unfortunately, no common bean varieties (*Phaseolus vulgaris* L.) are known that possess a high degree of resistance to either common blight or fuscous blight; but several varieties are available that are resistant to either one or more of the races of the anthracnose fungus or to both strains of the common bean mosaic virus. With this in mind, the Michigan State College Agricultural Experiment Station, in cooperation with the Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture, initiated a bean breeding program in 1948. The objective was to develop new disease resistant varieties of navy beans of better type and quality than the present varieties. Rainy River was not included initially in this program, but since Michigan needs the quality and earliness of this variety, it was included in a similar breeding program.

The present investigation is a study of the inheritance of resistance to the alpha race of Colletotrichum lindemuthianum and bean virus 15 in conjunction with the preliminary development of disease resistant strains of Rainy River.

REVIEW OF THE LITERATURE

Bean Anthracnose

Anthracnose is an old disease in beans. According to Harter and Zaumeyer (15), the earliest satisfactory evidence of it dates back to 1843. Muncie (20) reported that the first authentic specimens of the disease in Michigan were collected by Dr. W. J. Beal in 1889. Since then several physiological races of the fungus have been reported. In 1911 Barrus (4) distinguished two different races by the differential response of several bean varieties. Later he inoculated a large number of bean varieties with cultures from fifteen different sources and classified the fungus into two races, alpha and beta (5). In 1923 Burkholder (10) isolated from the White Imperial Variety a third race, which he called gamma. Leach (17) distinguished eight races as a result of inoculating 14 varieties of beans with various isolates. In Germany Schrieber (27) isolated 34 races, which could be divided into three major groups corresponding to the alpha, beta, and gamma races of Barrus (5) and Burkholder (10).

Numerous studies have been made on the inheritance of resistance to *Colletotrichum lindemuthianum*. Burkholder (9) in

1918 crossed Well's Red Kidney, which is resistant to races alpha and beta, with White Marrow, which is resistant to alpha, and found that resistance to beta was controlled by a dominant pair of genes. In 1919 McRostie (18) used Well's Red Kidney in crosses with Michigan Robust, which is resistant to beta, and showed that a dominant pair of genes governed resistance to alpha. Later McRostie (19) in five intervarietal crosses involving six varieties, showed that resistance to races alpha and beta were controlled by different dominant genes. Burkholder (10) found, in crosses between resistant Robust and susceptible Well's Red Kidney, that resistance to gamma was controlled by still a third dominant gene. Schrieber (27, 28), using two intervarietal crosses involving three varieties, reported that resistance to a single race of *Colletotrichum lindemuthianum* was controlled by a single dominant factor; but at least three independent factors were responsible for resistance to 34 races consisting of three main groups, which corresponded to the alpha, beta, and gamma races. By inoculating the same crosses with a mixture of a number of other races of the pathogen, he concluded that at least eight genes were responsible for resistance. Andrus and Wade (3), in thirty intervarietal crosses involving 15 parent varieties and selections, proposed a system of ten genes in three allelomorphic series to satisfy their data concerning resistance to races beta and gamma.

Common Bean Mosaic

Common mosaic, like anthracnose, is not a new disease in beans. According to Nelson (21), common bean mosaic was observed by Iwanowski in Russia as early as 1899. Spragg and Down (29) believed it may have been present in Michigan by 1908.

At present, common bean mosaic virus may be classified into two groups, bean virus 1 and its variant strain virus 15. The latter was first observed in 1939 by Richards and Burkholder (24) in New York State. Since then it has been reported in the principal bean growing sections of the West and Mid-West.

Several investigators have studied the inheritance of resistance to bean virus 1. McRostie (19), in crosses involving the resistant variety Robust, obtained data that suggested a two factor ratio, in which either factor in the recessive state would produce resistance to the disease. Pierce (23) reported that Corbett Refugee, and varieties developed from it, showed a dominant type of resistance, whereas Robust and Great Northern U. I. No. 1 possessed a recessive type of resistance. Parker (22) made reciprocal crosses between Robust and Stringless Green Refugee, a susceptible variety, and found that the maternal parent determined to a large extent the reaction of the hybrid. This influence was more noticeable in the F_1 generation but was still evident in the F_3 generation. The convergence of results between reciprocal crosses in succeeding generations was interpreted as a delayed genetic action. In crosses between a tolerant variety Black Valentine and a resistant variety U. S. No. 5 Refugee, Wade and Andrus (31) showed that resistance was dominant to tolerant and governed by a single factor. In 1950 Ali (1) presented a factorial scheme that explained the inheritance of resistance to bean virus 1 in terms of two factor pairs exhibiting dominant and recessive epistasic, respectively. He pointed out that the dominant type of resistance, present in varieties derived from Corbett Refugee, prevented the expression of mosaic symptoms; but if the virus was continuously supplied by the approach graft method of inoculation, as used by Grogan and Walker (13), the resistant plants developed top necrosis and black root. The recessive type of resistance, present in Robust and possibly Michelite and Great Northern U. I. No. 1, prevented both the expression of mosaic symptoms and top necrosis.

The author is not aware of any publication on the inheritance of resistance to the variant strain, virus 15. Ford (12) made crosses between Michelite and Cornell 46-62, a resistant strain of navy beans developed by Dr. H. M. Munger (Cornell University). The F_2 data indicated that resistance to virus 15, as shown by Cornell 46-62, was controlled by a single factor that expressed itself at low temperatures as three resistant plants to one susceptible and at high temperatures as one resistant plant to three susceptible.

Backcrossing

The term backcross means to cross a hybrid between two varieties or strains back to either parent. In this study the hybrids produced with Rainy River were backcrossed to Rainy River. This method is of value especially where it is desirable to transfer a dominant character to another variety or strain. The characters of the recurrent parent are automatically recovered by crossing and the desired character of the non-recurrent parent are retained by selection. In 1922 Harlon and Pope (14) demonstrated its value in small grain breeding by transferring smooth awns to Manchuria barley. They suggested that in some breeding programs this method would be of more value than the usual method of selection within segregating generations after the desired crosses had been made. Briggs (6) described a backcross project in wheat in which bunt resistance of the Martin variety was transferred to Baart, a susceptible commercial variety. Later discussions by Briggs (7, 8) indicates the extensive use made of backcrossing by him and his co-workers. Sunneson, Riddle, and Briggs (30) conducted a backcross program in which there were no significant differences between the original and resistant varieties of wheat with respect to yield, plant height, date of heading, or resistance to other diseases. In work with corn, a cross pollinated crop, Johnson and Hayes (16) transferred Golden Bantam's tender pericarp to Crosby. Convergent improvement, suggested by Richey (26), is essentially a double backcross program for the improvement of inbred lines of corn that combine well in a single cross without changing the yielding ability of the single cross. In this case, the hybrid progenies were successively crossed back to both parent inbreds and selection was made after each backcross for desired characters of the non-recurrent inbreds, respectively.

MATERIALS AND METHODS

The bean hybridization and disease testing studies were carried out in a greenhouse maintained, as near as possible, within a temperature range of 65 to 77° F. The greenhouse was kept relatively free of insects by frequent fumigation. The plants were grown in pots or benches filled with sand and watered every day. Once a week they were given a nutrient solution of the following composition: one pound of $CaNO_3 \cdot H_2O$; one-half pound of KH_2PO_4; three-fourths pound of $MgSO_4 \cdot 7H_2O$ per hundred gallons of water.

Rainy River was used as the susceptible parent in the inheritance studies and the recurrent parent and female in the backcrosses. Pollen was always obtained from resistant plants in successive backcrosses.

All varieties involved in this work were resistant to the beta and gamma races of *Colletotrichum lindemuthianum* with the exception of Z-1 (Topcrop). Resistance to the alpha race of *Colletotrichum lindemuthianum* was obtained from Emerson 51, a garden (snap) bush bean, and Emerson 847, a large white navy bean. Both varieties were developed by the late Dr. R. A. Emerson (Cornell University), but neither are commercially important.

The virus 15 resistant varieties used in these studies are also resistant to virus 1. The genes governing resistance to both virus strains must either occupy the same loci or be closely linked. Therefore, in breeding for resistance to both, only tests for virus 15 resistance were necessary. This resistance was obtained from three varieties: (a) Trag 279-1, U. S. D. A. foreign plant introduction from Mexico, a field bean with a black seed coat; (b) Cornell 46-62, a white navy bean, developed by Dr. H. M. Munger (Cornell University) from crosses between Michelite and Great Northern U. I. No. 1; (c) Z-1, now called Topcrop, a garden (snap) bean developed by Dr. W. J. Zaumeyer (U. S. D. A.).

The hybridization was started in October, 1949. A crossing technique similar to that described by Down and Thayer (11) was used. The procedure was essentially as follows:

1. The flower buds were emasculated the day before the flowers normally open and shed their pollen.

2. Pollination was accomplished by removing a pollen covered stigma from a flower that had opened during the previous night or early morning and rubbing it over the surface of the stigma of a newly emasculated flower.

3. The pollinated flower was tagged in order to identify the cross.

4. Self-pollinated flowers on the same plant were removed each day until the pods from the crosses were at least one inch long. It appeared that this procedure helped retain a larger number of successful crosses.

When mature, the seed were shelled, placed in envelopes, and allowed to dry for at least seven days before being planted for the next generation.

Stock cultures of the alpha race of *Colletotrichum lindemuthianum* were obtained from Dr. A. L. Andersen (Michigan State College) and maintained on bean pod agar slants in test tubes. About 14 days before plant inoculation, sterilized barley grain cultures were seeded with a spore suspension of the fungus to obtain large quantities of inoculum. The substrate was prepared by soaking a 1 to 1 mixture by weight of dry grain and water in Erlenmeyer flasks in an Arnold steamer until all the water was absorbed by the grain. The media was autoclaved thirty minutes at 250° F. and 15 pounds of pressure.

After seeding the medium, the cultures were incubated at about 72° F. for 7 to 15 days. A spore suspension was prepared from the grain cultures and sprayed on the plants, which were then placed in a moist chamber for 48 hours to establish infection.

A culture of virus 15 was obtained from Dr. A. L. Andersen (Michigan State College). The virus was maintained in the greenhouse on the Michelite variety.

The following rub-inoculation method was used to test plants segregating for resistance:

1. Carborundum powder (320 to 600 mesh) was sprinkled on the primary leaves to be inoculated.

2. Leaves of diseased plants were macerated with a mortar and pestle or in a Waring Blendor and the virus infected juice removed by filtration through a fine mesh cheesecloth.

3. The virus infected juice was diluted with nine parts water to one part juice and rubbed lightly into the primary leaves with the cheesecloth.

4. The inoculated leaves were washed immediately with water.

When a large number of plants were to be inoculated, carborundum powder was added to the infective plant extract and sprayed on the primary leaves with a suction-feed glass atomizer at a pressure of thirty pounds or more (25). It was not necessary to wash the leaves afterwards when this method was used.

EXPERIMENTAL RESULTS

The greenhouse growing conditions were very satisfactory for the development of strong plants. However, a higher percentage of pods were set during the spring and summer months (over 90 per cent) than during the fall and winter months (40 to 50 per cent).

To reduce the time required to produce a crop, newly harvested seed were picked before fully dry and allowed to dry in envelopes. Seed allowed to dry for less than seven days germinated much slower than seed dried for seven days or more.

A. Inheritance Studies

1. Anthracnose resistance (Alpha)

Heavy inoculum dosages of viable spores were obtained by growing the fungus on the barley grain substrate. After inoculation and incubation, susceptible plants showed anthracnose lesions in less than a week. Plate II shows one resistant and two susceptible plants about ten days after inoculation.

(a) Rainy River X Emerson 51. Reciprocal crosses were made between Rainy River and Emerson 51. The F_1 hybrids were resistant, indicating that resistance to alpha is dominant and

Mendelian in nature. However, a few of the F_1 plants were susceptible because Emerson 51 was not homozygous for resistance.

The crosses between Emerson 51 and Rainy River were used to make the first backcross since they were planted a few days sooner than the reciprocals. After three generations of backcrossing to Rainy River, some of the resistant plants were allowed to segregate to further study the genetic behavior of resistance. In each generation of a backcross, the selected plants are F_1 hybrids for the character in question. The next generation segregates into an F_2 distribution and is referred to throughout these studies as BC_n F_2 (n equals the number of generations backcrossed).

Table 1 shows the BC_3 F_2 distribution of resistant and susceptible plants. Out of 155 plants, 111 were resistant and 44 were susceptible. The distribution fits a 3 to 1 ratio, indicating that a single dominant gene governs resistance to alpha.

If resistance is due to one dominant gene, each backcross generation should segregate into a ratio of 1 resistant plant to 1 susceptible. The distribution of four backcross generations is shown in Table 2. The data consisted of 51 resistant and 71 susceptible plants. The chi-square value is rather high for a 1 to 1 ratio and would be considered as a poor fit.

TABLE 1

INHERITANCE OF RESISTANCE TO ALPHA (ANTHRACNOSE) BC_3 F_2 GENERATION FROM CROSSES BETWEEN RAINEY RIVER AND EMERSON 51

Progeny Number	Plant Reaction		Total
	Resistant	Susceptible	
359101	14	8	22
02	18	6	24
03	9	5	14
04	15	4	19
05	15	5	20
06	11	4	15
07	15	7	22
08	14	5	19
Grand Total	111	44	155
Ratio tested	3	1	

Chi-square	.948
Probability range	30 to 50 per cent

TABLE 2

INHERITANCE OF RESISTANCE TO ALPHA (ANTHRACNOSE) IN FOUR BACKCROSS GENERATIONS FROM CROSSES BETWEEN RAINY RIVER AND EMERSON 51

B. C. Generation	Plant Reaction		Total
	Resistant	Susceptible	
2	3	15	18
3	13	10	23
4	32	38	70
5	3	8	11
Grand Total	51	71	122
Ratio tested	1	1	

Chi-square	3.280
Probability range	5 to 10 per cent

(b) Rainy River X Emerson 847. The general procedure in this study was the same as that in crosses between Rainy River and Emerson 51. The F_1 generations were resistant. This indicated that resistance to alpha was dominant and Mendelian in nature. The F_1 plants, in which Rainy River was the female parent, were used in the first backcrosses because the seed produced by Rainy River (selfed or cross pollinated) matured about ten days earlier than seed produced by Emerson 847. The only advantage was to save time in the backcross studies.

After the third backcross, some of the resistant plants were allowed to segregate in order to further study the inheritance of resistance. Table 3 shows the number of resistant and susceptible plants in the F_2 generation following the third backcross. From a total of 165 plants, 114 were resistant and 51 were susceptible. This segregation poorly fits a 3 to 1 ratio as indicated by the chi-square value.

From the five backcross generations, as shown in Table 4, 62 plants were resistant and 89 susceptible. This data approaches a 1 to 1 ratio.

TABLE 3

INHERITANCE OF RESISTANCE TO ALPHA (ANTHRACNOSE) BC_3 F_2 GENERATION FROM CROSSES BETWEEN RAINY RIVER AND EMERSON 847

Progeny Number	Plant Reaction		Total
	Resistant	Susceptible	
358901	14	6	20
02	4	5	9
03	12	5	17
04	15	2	17
05	9	6	15
06	10	7	17
07	15	5	20
08	8	3	11
09	2	5	7
10	16	4	20
11	9	3	12
Grand Total	114	51	165
Ratio tested	3	1	
Chi-square	3.070		
Probability range	5 to 10 per cent		

TABLE 4

INHERITANCE OF RESISTANCE TO ALPHA (ANTHRACNOSE) IN FIVE BACKCROSS GENERATIONS FROM CROSSES BETWEEN RAINY RIVER AND EMERSON 847

B. C. Generation	Plant Reaction		Total
	Resistant	Susceptible	
1	9	11	20
2	4	12	16
3	14	10	24
4	28	45	73
5	7	11	18
Grand Total	62	89	151
Ratio tested	1	1	
Chi-square	4.830		
Probability range	2 to 5 per cent		

2. Virus 15 resistance

Both the mechanical rub and pressure spray methods of inoculation produced 100 per cent infection when susceptible plants were tested. Usually these plants showed mosaic symptoms about two weeks after inoculation (Plates III and VI). Occasionally, an inoculated plant would show necrosis (Plates III, IV, and V).

(a) Rainy River X Trag 279-1. Crosses between Rainy River and Trag 279-1 and reciprocals were made. The F_1 hybrids were resistant, indicating a Mendelian type of inheritance with resistance being dominant.

The F_2 and backcross generations exhibited three types of reaction to virus 15: (a) healthy plants; (b) top necrotic plants; and (c) mosaic plants (Plate III). The necrotic plants usually died about two weeks after inoculation but in one case necrosis was delayed until crosses had been made to susceptible plants. Plate IV shows the necrotic plant after it had produced blooms and set at least one pod. The progeny from these crosses segregated into healthy and mosaic types indicating that this necrotic reaction was shown by a heterozygous resistant plant rather than a susceptible or mosaic one.

Table 5 shows the F_2 distribution following inoculation. From a total of 328 plants, 246 were resistant and 82 were

TABLE 5

INHERITANCE OF RESISTANCE TO VIRUS 15 IN THE F_2 GENERATION FROM CROSSES BETWEEN RAINY RIVER AND TRAG 279-1 AND RECIPROCALS

Progeny Number	Plant Reaction			Total
	Top necrotic	Healthy	Mosaic	
355301	4	9	9	22
02	0	23	2	25
03	0	20	9	29
04	0	26	5	31
05	2	19	6	27
06	2	19	7	28
07	3	14	10	27
08	0	18	7	25
355401 (Recip-rocals)	0	2	2	4
02	3	4	1	8
03	0	10	1	11
04	0	7	4	11
05	0	13	3	16
06	1	17	4	22
07	0	17	5	22
08	0	13	7	20
	(15) plus	(231)		
Grand Total	246		82	328
Ratio tested	3		1	
Chi-square	0.000			
Probability range	100 per cent			

susceptible. An exact ratio of 3 resistant plants to 1 susceptible indicates that a single dominant gene governs resistance to virus 15 in Trag 279-1. For additional proof, records were kept of the backcross segregations (Table 6). In the five backcross generations, 68 plants were resistant and 77 susceptible. This segregation fits a 1 to 1 ratio.

(b) Z-1 (Topcrop) X Trag 279-1. Since Trag 279-1 is a foreign introduction that carries a dominant type of resistance, crosses were made with Z-1 to determine if they both possessed the same genes for resistance. Z-1 obtains its resistance from Corbett Refugee. If the resistant factors in each are located on the same loci, all of the F_2 progeny of such a cross will be resistant. However, if resistance in each is due to separate independent factor pairs, the F_2 progeny will segregate into a ratio of 15 resistant plants to 1 mosaic. The crosses were made and the F_1 generation was found to be resistant. The F_2 generation contained 58 resistant plants, 3 plants with top necrosis, but none with mosaic as shown in Table 7. Although no chi-square was run, due to the small number of F_2 plants, it appears highly probable that resistance in both varieties is controlled by the same genes.

(c) Rainy River X Cornell 46-62. The symbol B. C. in this section refers to the number of backcrosses made with one

TABLE 6

INHERITANCE OF RESISTANCE TO VIRUS 15 IN FIVE BACKCROSS GENERATIONS FROM CROSSES BETWEEN RAINY RIVER AND TRAG 279-1

B. C. Generation	Plant Reaction			Total
	Top necrotic	Healthy	Mosaic	
1	2	28	23	53
2	6	5	5	16
3	2	8	11	21
4	9	5	22	36
5	0	3	16	19
	(19) plus	(49)		
Grand Total	68		77	145
Ratio tested	1		1	
Chi-square	.559			
Probability range	30 to 50 per cent			

TABLE 7

INHERITANCE OF RESISTANCE TO VIRUS 15 IN THE F_2 GENERATION FROM CROSSES BETWEEN Z-1 (TOPCROP) AND TRAG 279-1

Progeny Number	Plant Reaction				Total
	Top necrotic		Healthy	Mosaic	
354301	0		17	0	17
02	2		19	0	21
03	1		22	0	23
	(3)	plus	(58)		
Grand total		61		0	61

generation of segregation between each cross. Some of the F_1 hybrids were tested and found to be susceptible. This indicates a recessive type of resistance. The remaining F_1 plants were not inoculated and the resulting F_2 generation segregated into 148 healthy plants to 292 diseased (Table 8). This segregation is close to a 1 to 2 ratio, but a chi-square value was not determined because such a ratio in this case was proved to be incorrect by the studies that follow. Even though 100 per cent infection was obtained when susceptible varieties were inoculated, it was suspected that some of the F_2 plants in the above cross either masked or failed to respond to the virus. To confirm this assumption, progeny from seven F_2 resistant appearing plants of the first backcross were inoculated by the pressure spray method and the following results noted: (a) three lines were resistant; (b) three lines were found to be segregating for resistance; and (c) one line was completely susceptible.

Because of these results, a similar study was conducted by testing the remaining BC_1 F_2 population. The plants were inoculated by the pressure spray method and carefully grouped according to the disease symptoms. Unfortunately, the seed produced by the resistant plants of the BC_1 F_1 generation had been combined before the inheritance studies were made. Thus, it was necessary to assume that the previous backcrosses attempted

TABLE 8

INHERITANCE OF RESISTANCE TO VIRUS 15 IN THE F_2 GENERATION FROM CROSSES BETWEEN RAINY RIVER AND CORNELL 46-62

Progeny Number	Plant Reaction		Total
	Healthy	Diseased	
852402	11	18	29
03	8	15	23
04	11	14	25
05	3	11	14
06	14	11	25
07	4	7	11
08	7	17	24
09	10	22	32
11	5	13	18
12	13	19	32
13	5	27	32
14	11	20	31
352601	8	12	20
352801	12	2	14
02	7	16	23
03	5	21	26
04	5	8	13
05	2	11	13
07	3	10	13
?	4	18	22
Grand total	148	292	440
Ratio	1	2	

were successful and not selfs. Table 9 shows the distribution of the BC_1 F_2 generation according to healthy and diseased plants. From a total of 161 plants, 38 were healthy and 123 diseased. This segregation fits a 1 to 3 ratio as shown by the chi-square value. Such a ratio indicates that resistance is due to a single recessive factor pair of genes. The diseased plants could be classified into two groups: (a) necrotic plants, which died (plate V); and (b) mosaic plants, which lived (Plate VI). The distribution of the BC_1 F_2 generation according to mosaic, healthy, and necrotic plants is shown in Table 10. Of the 161 plants, 96 were mosaic, 38 healthy, and 27 necrotic. This distribution fits a 9 to 4 to 3 ratio, indicating that a second and modifying factor was present and when in recessive condition induced necrosis in susceptible plants infected with virus 15.

For additional proof in support of the 1 to 3, and 9 to 4 to 3 ratios, the individual lines of the BC_2 F_2 generation were inoculated by the mechanical rub method and the temperature maintained at 75° F. to hasten the disease symptoms. Nine of the fourteen lines tested contained only susceptible plants, indicating that some of the crosses attempted were actually selfs. Table 11 shows the remaining five lines classified according to healthy and diseased plants. Out of a total of 76 plants, 18 were healthy and diseased plants. The chi-square value indicates a

TABLE 9

INHERITANCE OF RESISTANCE TO VIRUS 15 IN THE $BC_1 F_2$ GENERATION FROM CROSSES BETWEEN RAINY RIVER AND CORNELL 46-62

Total		Plant Reaction	
		Healthy	Diseased
161		38	123
Ratio tested		1	3
Chi-square	.168		
Probability range	.50 to .70 per cent		

TABLE 10

INHERITANCE OF RESISTANCE TO VIRUS 15 IN THE $BC_1 F_2$ GENERATION FROM CROSSES BETWEEN RAINY RIVER AND CORNELL 46-62

Total	Plant Reaction		
	Mosaic	Healthy	Necrotic
161	96	38	27
Ratio tested	9	4	3
Chi-square	.789		
Probability range	30 to 50 per cent		

TABLE 11

INHERITANCE OF RESISTANCE TO VIRUS 15 IN THE $BC_2 F_2$ GENERATION FROM CROSSES BETWEEN RAINY RIVER AND CORNELL 46-62

Progeny Number	Plant Reaction		Total
	Healthy	Diseased	
360601	2	21	23
03	5	10	15
08	3	8	11
10	6	14	20
14	2	5	7
Grand Total	18	58	76
Ratio tested	1	3	
Chi-square	.070		
Probability range	70 to 80 per cent		

close fit to a 1 to 3 ratio. The same data based on mosaic, healthy, and necrotic plants is given in Table 12. From the 76 plants, 48 were mosaic, 18 healthy, and 10 necrotic. This segregation fits a 9 to 4 to 3 ratio.

When the data in both studies were combined, a chi-square value was obtained that fits a 1 to 3 ratio as summarized in Table 13. The combined data also fit a 9 to 4 to 3 ratio (Table 14).

To satisfy the 9 to 4 to 3 ratio in both studies, it is necessary to assume that the resistant grandparents of both the BC_1 F_2 and BC_2 F_2 generations carried the necrotic factor in the homozygous recessive condition. At present there is not sufficient evidence to confirm this assumption.

(d) Trag 279-1 X Cornell 46-62. If resistance is governed in Trag 279-1 by a dominant pair of genes and in Cornell 46-62 by a recessive pair, a ratio of 13 non-mosaic plants to 3 mosaic would be expected in the F_2 generation from such a cross. Out of a total of 166 plants, 130 were healthy, 5 were necrotic, and 31 were mosaic (Table 15). When the 5 plants with necrosis were grouped with the 130 healthy ones, as done in the crosses between Rainy River and Trag 279-1, 135 were non-mosaic and 31 mosaic. This segregation is a close fit to a 13 to 3 ratio (Table 15). On the other hand, when the 5 necrotic plants were included with the 31 mosaic ones, as in crosses between Rainy

TABLE 12

INHERITANCE OF RESISTANCE TO VIRUS 15 IN THE BC_2 F_2 GENERATION FROM CROSSES BETWEEN RAINY RIVER AND CORNELL 46-62

Progeny Number	Plant Reaction			Total
	Mosaic	Healthy	Necrotic	
360601	18	2	3	23
03	8	5	2	15
08	5	3	3	11
10	13	6	1	20
14	4	2	1	7
Grand Total	48	18	10	76
Ratio tested	9	4	3	

Chi-square	1.965
Probability range	30 to 50 per cent

TABLE 13

INHERITANCE OF RESISTANCE TO VIRUS 15 IN THE $BC_1 F_2$ AND $BC_2 F_1$ GENERATIONS FROM CROSSES BETWEEN RAINY RIVER AND CORNELL 46-62

Generation	Plant Reaction		Total
	Healthy	Diseased	
$BC_1 F_2$	38	123	161
$BC_2 F_2$	18	58	76
Grand Total	56	181	237
Ratio tested	1	3	
Chi-square	.238		
Probability range	50 to 70 per cent		

TABLE 14

INHERITANCE OR RESISTANCE TO VIRUS 15 IN THE $BC_1 F_2$ AND $BC_2 F_2$ GENERATIONS FROM CROSSES BETWEEN RAINY RIVER AND CORNELL 46-62

Generation	Plant Reaction			Total
	Mosaic	Healthy	Necrotic	
$BC_1 F_2$	96	38	27	161
$BC_2 F_2$	48	18	10	76
Grand Total	144	56	37	237
Ratio tested	9	4	3	
Chi-square	2.280			
Probability range	30 to 50 per cent			

TABLE 15

INHERITANCE OF RESISTANCE TO VIRUS 15 IN THE F_2 GENERATION FROM CROSSES BETWEEN TRAG 279-1 AND CORNELL 46-62

Progeny Number	Plant Reaction			Total
	Healthy	Mosaic	Necrotic	
353001	14	3	3	20
02	9	2	1	12
03	11	4	0	15
04	15	4	1	20
05	12	4	0	16
353101	22	6	0	28
02	25	4	0	29
03	22	4	0	26
Grand Total	130	31	5	166

Grouping	135 Non-mosaic 31 Mosaic	130 Healthy 36 Diseased	130 Healthy 31 Mosaic 5 Necrotic
Ratios tested	13 to 3	13 to 3	52 to 9 to 3
Chi-square	.0006	.940	3.681
Probability range	95 to 100 per cent	30 to 50 per cent	10 to 20 per cent

River and Cornell 46-62, 130 plants were healthy and 36 were diseased. This grouping assumes that a third and modifying factor, when present in the recessive condition, causes necrosis in the susceptible plants. The calculated ratio, considering all three factors, would be 52 healthy plants to 9 mosaic to 3 necrotic or 52 healthy plants to 12 diseased, which reduces to a 13 to 3 ratio as before. The data, so arranged, fit this ratio (Table 15). Likewise, the data of 130 healthy plants to 31 mosaic to 5 necrotic fit the calculated ratio of 52 to 9 to 3 (Table 15). This is additional proof that a third and modifying factor may be present in crosses involving Cornell 46-62.

B. Backcross and Selection Studies

For the most part, the materials and methods used in the inheritance studies and in the backcross program were the same. Four successive backcross generations were grown every 11 months. The time depended upon the number of days it took the female parent, Rainy River, to reach maturity and the number of days for the male parent to produce pollen. For example, Rainy River and most of the progeny from the various backcrosses bloomed about five weeks after planting. Another week was required to make a sufficient number of backcrosses to Rainy River in which the disease resistant progeny from the preceding backcross generation were used as pollen parents. Then a period of five weeks was necessary for the seed to mature, plus another week after maturity to dry, before the next generation could be planted. This makes a sum total of 12 weeks or approximatdy 84 days. Table 16 shows the time required to grow one generation.

By the time the sixth backcross was completed, the general procedure had been worked out fairly well as to the minimum amount of time and material required to obtain enough crosses for the next generation. Table 17 shows a part of the data that concern the sixth backcross. Rainy River was planted at three different times in order to provide enough blooms during the crossing period. In each case, the actual number of resistant plants was less than the expected number. A total of 13 resistant plants provided pollen for crossing onto 28 plants of Rainy River. In other words, an approximate ratio of 1 male plant to 2 females worked out quite well. From a total of 65 attempted backcrosses, 30 were successful. An average of 4.43 seeds per pod was obtained from all the successful crosses.

1. Anthracnose resistance

(a) Rainy River X Emerson 51. As previously mentioned, one source of anthracnose resistance came from Emerson 51. Since the F_1 hybrids from crosses between Emerson 51 and Rainy

TABLE 16

TIME REQUIRED TO GROW ONE GENERATION OF RAINY RIVER AND THE VARIOUS BACKCROSS MATERIAL

Planting to First Bloom	5 weeks
First Bloom to Last Cross-Pollination	1 week
Last Cross-Pollination to Harvest	5 weeks
Harvest to Planting	1 week
Total	12 weeks
	approximately 84 days

TABLE 17

DATA THAT CONCERN THE SIXTH BACKCROSS TO RAINY RIVER

Original Parent	Rainy River	Emerson 51	Emerson 847	Trag 279-1
Resistance	-	Anthrac-nose	Anthrac-nose	Virus 15
Dates Planted	1/10/51 1/14/51 1/19/51	1/14/51	1/14/51	1/14/51
Material Planted	Parent	BC_5	BC_5	BC_5
Total Number of Plants	28	11	19	19
Expected Number of Resistant Plants	-	5.5	9.5	9.5
Actual Number of Resistant Plants	-	3	7	3
Number of Backcrosses Attempted	-	19	28	18
Number of Backcrosses Successful	-	8	14	8
Number of Seed from Crosses	-	36	63	34
Average Number of Seed per Pod	-	4.5	4.5	4.25

River were found to be resistant, they could be crossed back to Rainy River, the recurrent and susceptible parent. The second cross is known as the first backcross; the third and next cross as the second backcross; etc. Anthracnose resistance was found to be controlled by a dominant pair of genes. Thus, approximately one-half of the progeny from any backcross would be resistant. These plants were used to make the next backcross.

In addition to selecting for anthracnose resistance, it was possible to eliminate plants with colored stems. The stem color came from Emerson 51 and appeared to be correlated with seed color, an undesirable character in navy beans. This color was completely eliminated during the second backcross.

As a general rule, at least four backcrosses, preferably more, should be made to Rainy River before segregation and final selection. However, in this study, some lines were allowed to segregate for three generations following the third backcross. One resistant F_1 plant was saved and in turn 13 resistant F_2 plants were retained from which homozygous resistant lines were selected in the F_3 generation. The F_3 lines that contained resistant plants, but no susceptible ones, were considered to be homozygous for anthracnose resistance, and at this time, they are still growing. The F_4 generations may be tested later in the field for earliness, yield, type, and other characters. Table 18

TABLE 18

THE F_1, F_2 AND F_3 GENERATIONS THAT FOLLOW THE THIRD BACKCROSS TO RAINY RIVER. EMERSON 51 IS THE NON-RECURRENT AND ANTHRACNOSE RESISTANT PARENT

Resistant F_1	Resistant F_2		F_3 Distribution	
Progeny No.	Progeny No.	Growth Habit	Resist.	Susc.
3591	359101	determinate	3	2
	02	do	3	4
	03	do	3	2
	04	do	5	0
	05	do	4	0
	06	do	4	0
	07	do	4	0
	08	indeterminate	3	3
	09	do	8	2
	10	do	6	2
	11	do	7	0
	12	do	9	0
	13	do	8	0

shows the first three segregating generations that follow the third backcross. Apparently the F_1 plant carried the recessive factor for determinate growth habit as found in Emerson 51. After three backcrosses to Rainy River, an indeterminate type, the probability of one plant out of 32 would be expected to carry this factor if it is not linked with anthracnose resistance. Since three of the seven lines that possessed the determinate growth habit segregated for anthracnose resistance in the F_3 generation, it was assumed that no linkage was present. The seed from all of the F_2 plants closely resembled Rainy River.

The backcross studies were continued and at present the sixth backcross has been completed. In a continuous backcross program of this nature, it was practically impossible to select for Rainy River characters without some segregation under field conditions. However, in an effort to retain earliness and at the same time speed up the program, pollen was always obtained from the first blooms of the resistant backcross progeny. Table 19 shows the planting date and days to first bloom of each backcross generation. From a general inspection of the date in Table 19, it is evident that the resistant progeny from each backcross bloomed about the same time as Rainy River, sometimes slightly earlier, other times slightly later. Variations between seasons, for example day length and light intensity, appeared to

TABLE 19

PLANTING DATE AND DAYS TO FIRST BLOOM OF EACH BACKCROSS GENERATION

Material	Date Planted	Days to First Bloom
Rainy River	9/23/49	34
Emerson 51	do	34
Rainy River	12/20/49	37
F_1	do	35
Rainy River	3/16/50	33
BC_1	do	29
Rainy River	5/30/50	34
BC_2	do	36
Rainy River	8/6/50	35
BC_3	do	36
Rainy River	10/29/50	34
BC_4	do	31
Rainy River	1/14/51	31
BC_5	do	33

to have no effect upon the length of time required for Rainy River to bloom. The extremes, 31 and 37 days, fell within the same season but on different years.

(b) Rainy River X Emerson 847. The other source of anthracnose resistance was obtained from Emerson 847. The general procedure was similar to that used with Emerson 51. It was not necessary to select against stem color as it is absent in Emerson 847. The segregation that follows the third backcross to Rainy River is shown in Table 20. Only the homozygous resistant F_3 lines were saved for segregation of other characters. The general appearance of these plants was similar to Rainy River and to the indeterminate types (Table 16) in which resistance was obtained from Emerson 51.

The backcross studies were continued and the sixth backcross has been completed. Table 21 shows the planting date and days to first bloom of each backcross generation. In this case, the backcross generations, except for the first and fourth, bloomed slightly later than Rainy River; the non-recurrent parent, Emerson 847, was even later.

2. Virus 15 resistance

(a) Rainy River X Trag 279-1. When the dominant type of resistance, as found in Trag 279-1, was used in the backcrosses,

TABLE 20

THE F_1, F_2 AND F_3 GENERATIONS THAT FOLLOW THE THIRD BACKCROSS TO RAINY RIVER. EMERSON 847 IS THE NON-RECURRENT AND ANTHRACNOSE RESISTANT PARENT

Resistant F_1	Resistant F_2	F_3 Distribution	
Progeny No.	Progeny No.	Resistant	Susceptible
3609	360901	8	1
	02	8	2
	03	8	3
	04	6	2
	05	9	1
	06	4	6
	07	7	0
	08	7	0
	09	6	3
	10	9	2
	11	10	0
	12	2	1
	13	9	2

TABLE 21

PLANTING DATE AND DAYS TO FIRST BLOOM OF EACH BACKCROSS GENERATION

Material	Date Planted	Days to First Bloom
Rainy River	9/23/49	34
Emerson 847	do	43
Rainy River	12/20/49	37
F_1	do	40
Rainy River	3/16/50	33
BC_1	do	31
Rainy River	5/30/50	34
BC_2	do	35
Reiny River	8/6/50	35
BC_3	do	36
Rainy River	10/29/50	34
BC_4	do	34
Rainy River	1/14/51	31
BC_5	do	33

a similar procedure was employed as that in the anthracnose studies. Stem color was present in Trag 279-1 but it was eliminated during the second backcross to Rainy River. Table 22 shows the segregation that follows the third backcross; it is similar to the segregation in the anthracnose studies. One of the F_3 resistant plants from 360808 had top necrosis. The other plants were either healthy or mosaic. The seed from the F_2 population closely resembled Rainy River as to size, shape, and color. However, this resemblance was no closer than the F_2 seed from the anthracnose resistant material. The foliage of the F_2 and F_3 generations were darker green in color than Rainy River; somewhat intermediate between Rainy River and Trag 279-1.

This study was carried to the sixth backcross generation. Table 23 shows the planting dates and days to first bloom of each backcross generation. Trag 279-1 required about two weeks longer than Rainy River to bloom, whereas the F_1 hybrids were intermediate. The first backcrosses bloomed two days later than Rainy River, which indicated that rapid progress was made in selecting early blooming plants; but in the backcross generations that followed, little or no progress appeared to be made towards earlier blooming. However, the seed produced by the

TABLE 22

THE F_1, F_2 AND F_3 GENERATIONS THAT FOLLOW THE THIRD BACKCROSS TO RAINY RIVER. TRAG 279-1 IS THE NON-RECURRENT AND VIRUS 15 RESISTANT PARENT

Resistant F_1	Resistant F_2	F_3 Distribution	
Progeny No.	Progeny No.	Resistant	Susceptible
3608	360801	9	1
	02	10	3
	03	4	3
	04	9	1
	05	6	2
	06	10	0
	07	6	4
	08	5	1
	09	6	3
	10	8	2
	11	6	1
	12	8	4
	13	10	0

TABLE 23

PLANTING DATES AND DAYS TO FIRST BLOOM
OF EACH BACKCROSS GENERATION

Material	Date Planted	Days to First Bloom
Rainy River	9/23/49	34
Trag 279-1	9/20/49	48
Rainy River	12/20/49	37
F_1	do	41
Rainy River	3/16/50	33
BC_1	do	35
Rainy River	5/30/50	34
BC_2	do	36
Rainy River	8/6/50	35
BC_3	do	37
Rainy River	10/29/50	34
BC_4	do	32
Rainy River	1/14/50	31
BC_5	do	33

BC_5 F_1 resistant plants appeared to be almost the same in size, shape, and color as those of Rainy River (Plate VII).

(b) Rainy River X Cornell 46-62. When virus 15 resistance was obtained from Cornell 46-62, the F_1 hybrids and backcross progeny were allowed to segregate one generation between each cross because the genetic factors for resistance are recessive. Only two backcrosses had been made by the end of the studies. Table 24 shows the planting dates and days to first bloom for each backcross generation. Cornell 46-62 was slightly earlier to bloom than Rainy River.

TABLE 24

PLANTING DATES AND DAYS TO FIRST BLOOM
IN EACH BACKCROSS GENERATION

Material	Date Planted	Days to First Bloom
Rainy River	9/23/49	34
Cornell 46-62	-	31
Rainy River	3/30/50	33
F_2	do	30
Rainy River	8/27/50	35
BC_1	do	35
Rainy River	1/16/51	31
BC_2	1/28/51	33

DISCUSSION

Inheritance of resistance to the alpha race of *Colletotrichum lindemuthianum* (bean anthracnose) was found to be governed by a single dominant Mendelian factor. The study was based on crosses that involved a susceptible variety. Rainy River, and two resistant ones, Emerson 51 and Emerson 847. In the generations that segregated for resistance, the observed number of susceptible plants was always a little higher than the expected number, especially in the backcross ratios. This should be expected, however, because the most essential part of the study was to select resistant plants for the next backcross. A few resistant plants could have been classified as susceptible since small anthracnose lesions occasionally appear on resistant genotypes. In earlier studies on alpha, McRostie (18) also obtained a single factor difference in which resistance was dominant to susceptibility in crosses between Well's Red Kidney and Robust.

Although only a small number of plants were tested for virus 15 resistance, certain conclusions can be drawn from the data as to the genotypes of the varieties used in the inheritance studies. Resistance in Trag 279-1 and X-1 (Topcrop) was found to be controlled by a dominant pair of factors (II). Occasionally, plants that possessed this resistance in the heterozygous condition died as a result of top necrosis when inoculated with virus 15. In one instance necrosis was even delayed until after several pollinations had been made to the susceptible parent. The next generation segregated into resistant and susceptible (mosaic) plants, which proved that the necrotic parent possessed the resistant factor. Grogan and Walker (13) and Ali (1), in work with virus 1, explained that varieties carrying the dominant type of resistance should be considered only as field resistant because if the virus inoculum escapes into the vascular system top necrosis and black root occur. The resistance in Cornell 46-62 was found to be governed by a recessive pair of factors (aa). In addition, this variety appeared to possess a second and modifying recessive factor (nn) that induced necrosis when present in susceptible plants infected with virus 15. No attempt was made to determine how this type of necrosis differed histologically from that occasionally found in other plants carrying the dominant type of resistance. The F_2 or equivalent segregating generations in crosses between Rainy River and Cornell 46-62 may be grouped in three ways: (a) 3 diseased plants to 1 healthy; (b) 9 mosaic plants to 4 healthy to 3 necrotic; and (c) 9 mosaic plants to 7 non-mosaic.

The letters II and aa that stand for resistance to virus 15 are the same symbols used by Ali (1) for resistance to virus 1. This would imply that resistance to both strains of common mosaic virus, virus 1 and virus 15, are controlled by genes that occupy the same loci. If this is true, then 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 susceptible to virus 15, as present in Michelite and Robust. According to Ford (12), the genotype a-1 a-15 (Michelite X Cornell 46-62) would be resistant to virus 15 at low temperatures and susceptible at high temperatures. The response of this genotype to virus 15, in the presence of the recessive necrotic factors (nn), has not been determined.

During the short period of time the backcross studies were conducted, it was not possible to obtain either anthracnose or virus 15 resistant strains of navy beans that were identical to Rainy River for most characters. A breeding program of this nature requires several generations of segregation and field selection following the backcrosses. The characters selected for in the backcrosses were anthracnose resistance, virus 15 resistance, non-colored stems, and earliness. Earliness was based on the number of days from planting to first bloom; the most progress towards earliness was evident in the

F_1 generations of the parental crosses and the first backcrosses. After the third backcross some lines carrying the dominant factor for resistance to anthracnose and virus 15, respectively, were allowed to segregate for three generations. The object was to obtain anthracnose resistant and virus 15 resistant navy beans that would closely resemble Rainy River. This was justified as Rickey (26) has given the percentage of plants homozygous for (n) factors entering the cross only from the recurring homozygous parent in each of (r) successive generations, calculated from the formula: $\left(\left(2^r - 1\right)/2^r\right)^n$. Linkage is considered to be absent. For example, after three generations of backcrossing without selection, 88 per cent of the plants would be homozygous for one factor pair, 51 per cent for five factor pairs, and so on. If linkage is considered to be present and no crossing-over takes place, then after three generations of backcrosses to the recurrent parent, followed by segregation and selection, at least one of the 11 pairs of chromosomes would have come from the non-recurrent or resistant parent. In other words approximately 91 per cent of the genotype would be the same as the recurrent parent. Thus, we may assume that a high percentage of the genotype was the same as Rainy River.

Whenever anthracnose resistance was obtained from Emerson 51, the factor for determinate growth habit was present in some segregates from the third backcross. Since earliness and determinate growth habit appear to be correlated, it would be easy and perhaps desirable to add this character to Rainy River along with anthracnose resistance. From the general appearance of the BC_3 F_3 segregates, the plants, in which Trag 279-1 was the non-recurrent parent, appeared to be further away from the desired type than where Emerson 51 and Emerson 847 were used. This should be expected as Trag 279-1 is quite different in appearance from Rainy River. However, by the end of the fifth backcrosses, there were no apparent differences between seed of Rainy River and BC_5 F_2 in which Trag 279-1 was the non-recurrent parent.

The studies have been carried to the sixth backcross in which anthracnose resistance was obtained from Emerson 51 and Emerson 847 and virus 15 resistance came from Trag 279-1. The backcross studies are being continued. In addition, the anthracnose and virus 15 resistant material that has been backcrossed six times will be combined and from these, resistant strains of navy beans can be selected that should be the same as Rainy River for other characters.

Only two backcrosses have been made in which resistance to virus 15 is recessive in nature and came from Cornell 46-62. This variety more nearly resembles Rainy River than the others used in this work. Therefore, a fewer number of backcrosses should be necessary to obtain the desired type. Furthermore, the recessive type of virus 15 resistance has the advantage of not showing top necrosis as in the dominant inherited type and may prove to be more desirable under field conditions.

SUMMARY

Studies were made on the inheritance of resistance to the alpha race of *Colletotrichum lindemuthianum* (bean anthracnose) and the variant strain of common bean mosaic, virus 15, in conjunction with the preliminary development of disease resistant strains of Rainy River navy beans by backcrossing.

In two intervarietal crosses that involved three varieties, inheritance of anthracnose resistance was found to be dominant to susceptibility and governed by one pair of genes.

Inheritance of virus 15 resistance was interpreted in terms of two factor pairs that exhibited dominant and recessive epistasis, respectively. A few plants from crosses between a susceptible parent and one that carried the dominant type of resistance had top necrosis. It was shown that these necrotic plants possessed the dominant factor for resistance. A similar type of necrosis was present in segregates from crosses between a susceptible parent and one that carried the recessive type of resistance. This necrosis appeared to be controlled by a second pair of recessive factors that were expressed only in susceptible plants infected with virus 15.

Selections were made for anthracnose resistance, virus 15 resistance, non-colored stems, and earliness in the breeding

program. After the third backcross to Rainy River, some anthracnose and some virus 15 resistant plants were allowed to segregate to obtain homozygous resistant strains for a comparison of other characters with Rainy River. The sixth backcross to Rainy River has been completed with regard to anthracnose resistance and virus 15 resistance.

LITERATURE CITED

1. Ali, M. A. Genetics of resistance to the common bean mosaic virus (bean virus 1) in the bean (Phaseolus vulgaris L.) Phytopath. 40:69-79. 1950.

2. Andersen, A. L. Observations on bean diseases in Michigan during 1949 and 1950, U. S. Dept. Agr., Plant Dis. Rptr. 35(2):89-90. 1951.

3. Andrus, C. F., and Wade, B. L. The factorial interpretation of anthracnose resistance in beans. U. S. Dept. Agr. Tech. Bul. 810, 29 pp., 1942.

4. Barrus, M. F. Variation of varieties of beans in their susceptibility to anthracnose. Phytopath. 1:190-195, 1911.

5. _______, Varietal susceptibility of beans to strains of Colletotrichum lindemuthianum (Sacc. and Magn.) Briosi and Cav. Phytopath. 8:589-614, 1918.

6. Briggs, F. N. Breeding wheats resistant to bunt by the backcross method. Jour. Am. Soc. Agron. 22:239-244. 1930.

7. _______, The backcross method in plant breeding. Jour. Am. Soc. Agron. 27:971-973. 1935.

8. _______., The use of the backcross in crop improvement. Amer. Nat. 72:285-292. 1938.

9. Burkholder, W. H. The production of an anthracnose-resistant White Marrow bean. Phytopath. 8:353-359. 1918.

10. _______, The gamma strain of Colletotrichum lindemuthianum (Sacc. and Magn.) Briosi and Cav. Phytopath. 13:316-323. 1923.

11. Down, E. E. and Thayer, J. W. The Michelite bean. Mich. Agr. Expt. Sta. Spec. Bul. 295, 23 pp. 1938.

12. Ford, H. P. Studies on the resistance of two strains of navy (pea) beans to virus 15. "Unpublished M. S. thesis" Mich. State Coll. 18 numb. leaves. 1950.

13. Grogan, R. G. and Walker, J. C. The relation of common mosaic to black root of bean. Jour. Agr. Res. 77: 315-331. 1948.

14. Harlan, H. V. and Pope, M. N. The use and value of back-crosses in small grain breeding. Jour. Hered. 13: 319-322. 1922.

15. Harter, L. L. and Zaumeyer, W. J. A monographic study of bean diseases and methods for their control. U. S. Dept. Agr. Tech. Bul. 868, 160 pp., 1944.

16. Johnson, I. J. and Hayes, H. K. The inheritance of pericarp tenderness in sweet corn. Jour. Am. Soc. Agron. 30:220-231. 1938.

17. Leach, J. G. The parasitism of *Colletotrichum lindemuthianum*. Minn. Agr. Expt. Sta. Tech. Bul. 14, 41 pp., 1923.

18. McRostie, G. P. Inheritance of anthracnose resistance as indicated by a cross between a resistant and a susceptible bean. Phytopath. 9:141-148. 1919.

19. ________, Inheritance of disease resistance in the common bean. Jour. Amer. Soc. Agron. 13:15-32. 1921.

20. Muncie, J. H. Experiments on the control of bean anthracnose and bean blight. Mich. Agr. Expt. Sta. Tech. Bul. 38, 50 pp., 1917.

21. Nelson, R. Investigations in the mosaic disease of bean (*Phaseolus vulgaris* L.) Mich. Agr. Expt. Sta. Tech. Bul. 118, 71 pp., 1932.

22. Parker, M. C. Inheritance of resistance to the common mosaic virus in the bean. Jour. Agr. Res. 52:895-915, 1936.

23. Pierce, W. H. The inheritance of resistance to common bean mosaic in field and garden beans. Phytopath. 25:875-883. 1935.

24. Richards, B. L., and Burkholder, W. H. A new mosaic disease of beans. (abst.) Phytopath. 33:1215-1216. 1943.

25. Richards, B. L., and Munger, H. M. A rapid method for mechanically transmitting plant viruses (abst.) Phytopath. 34:1010. 1944.

26. Rickey, F. D. The convergent improvement of selfed lines of corn. Amer. Nat. 61:430-449. 1927.

27. Schrieber, F. Resistenzzuchtung bei Phaseolus vulgaris. Phytopath. Ztschr. 4:415-454. 1932.

28. ________, Resistenz-zuchtung bei buschbohnen. Kuhn Arch. 38:287-292. 1933.

29. Spragg, F. A., and Down, E. E. The Robust bean. Mich. Agr. Expt. Sta. Spec. Bul. 108, (9) pp., 1921.

30. Suneson, C. A., Riddle, O. C., and Briggs, F. N. Yields of varieties of wheat derived by backcrossing. Jour. Amer. Soc. Agron. 33:835-840. 1941.

31. Wade, B. L., and Andrus, C. F. A genetic study of common bean mosaic under conditions of natural field transmission. Jour. Agr. Res. 63:389-393. 1941.

PLATE I

Greenhouse grown seed of Rainy River navy beans.

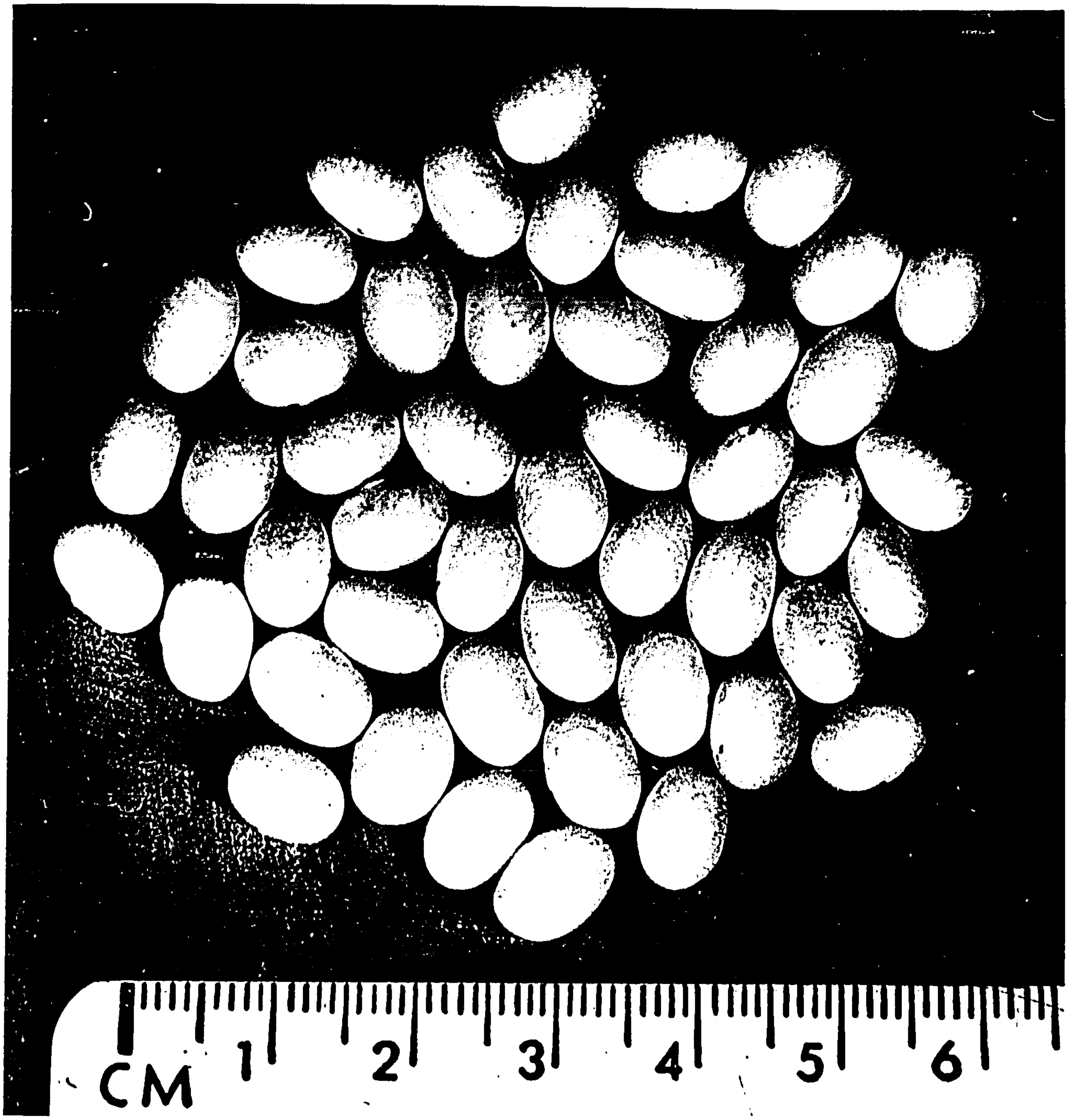
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PLATE II

Anthracnose reaction on beans. F_1 progeny of the third backcross to Rainy River; resistance from Emerson 847. The center plant is resistant.

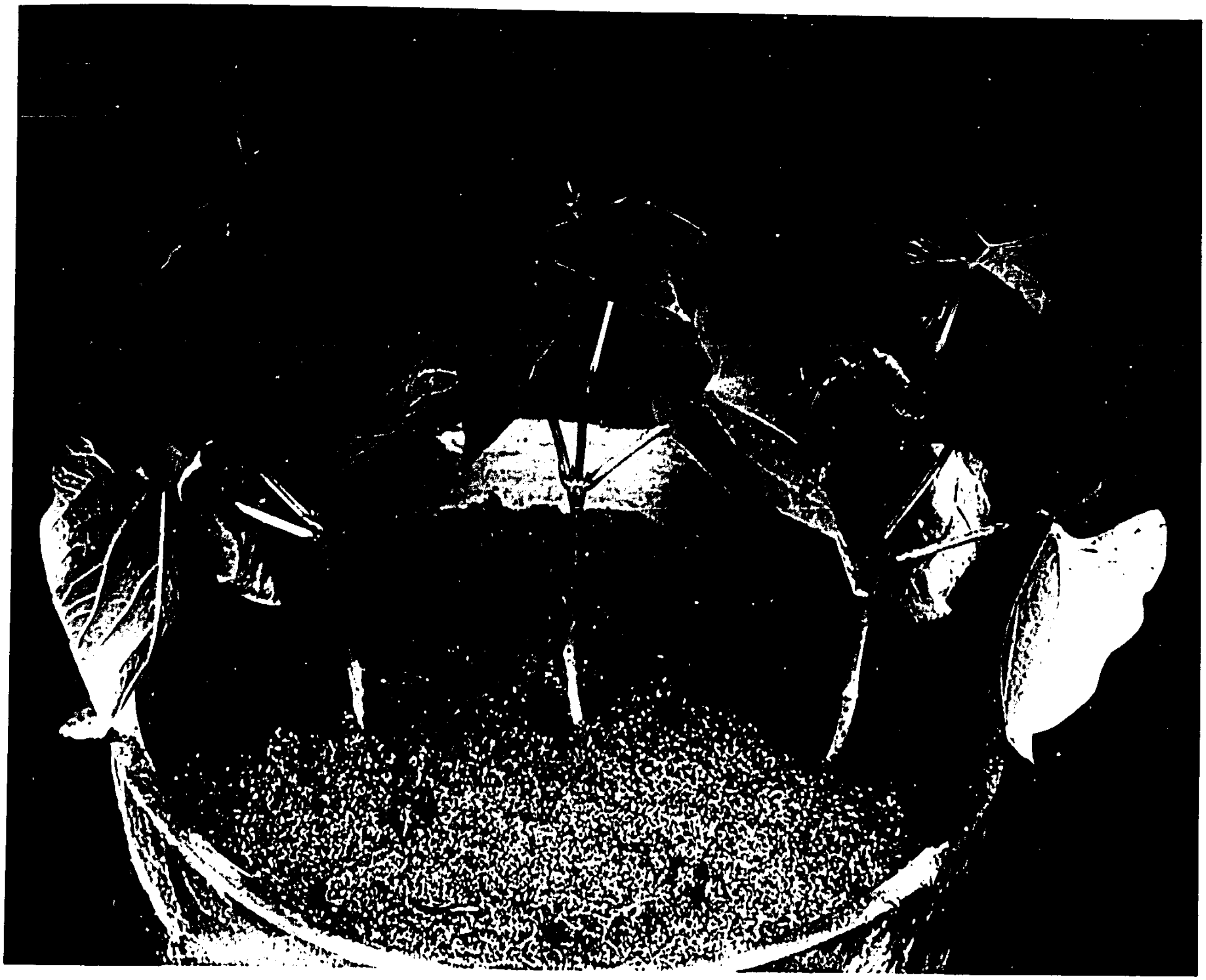

PLATE III

Virus 15 reaction on beans. F_1 progeny of the third backcross to Rainy River; resistance from Trag 279-1. Top right: resistant; bottom right: top-necrosis; and bottom left: mosaic. The primary leaves show inoculation injury.

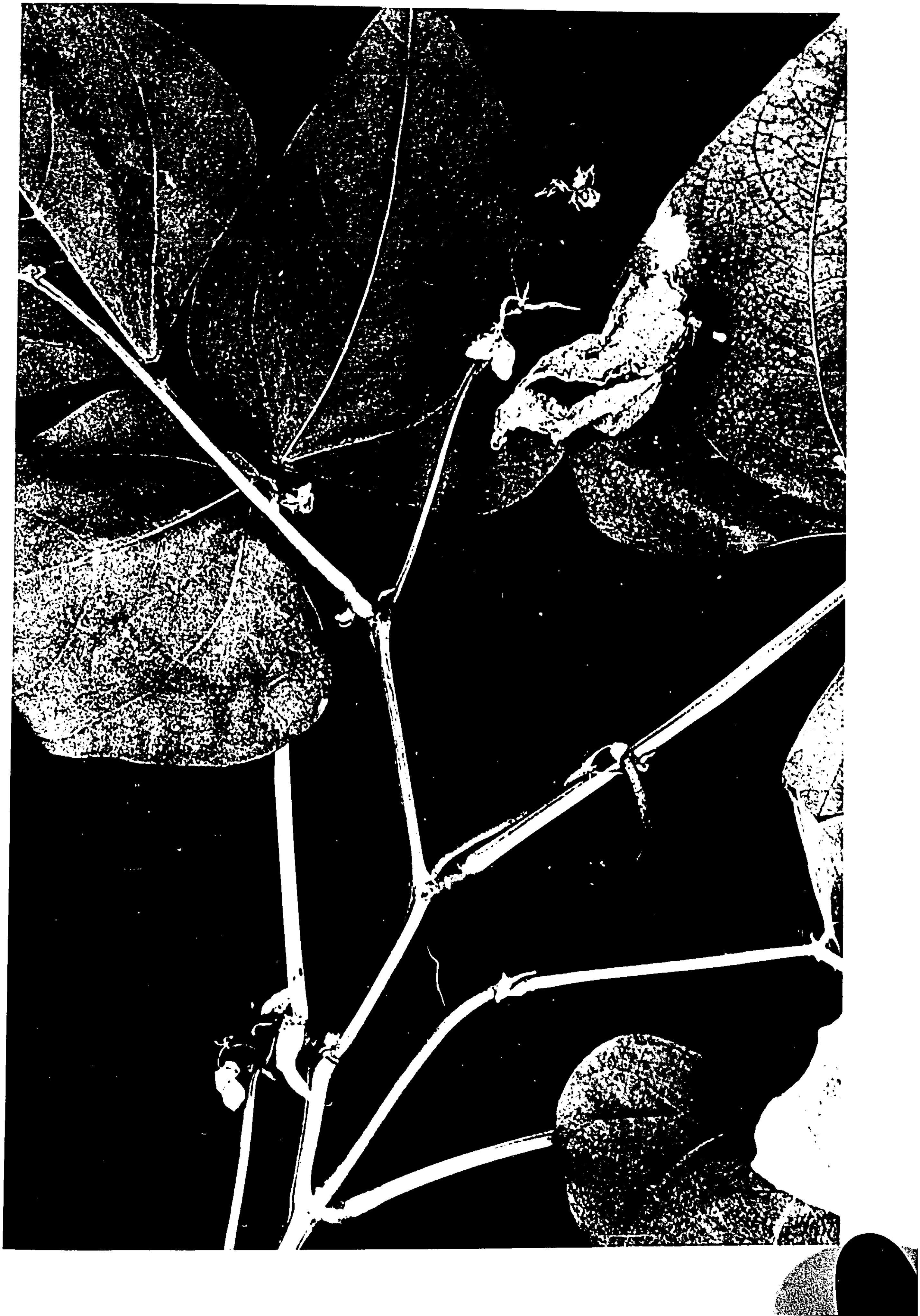

PLATE V

Necrotic reaction after inoculation with virus 15. F_2 progeny of the first backcross to Rainy River; resistance from Cornell 46-62.

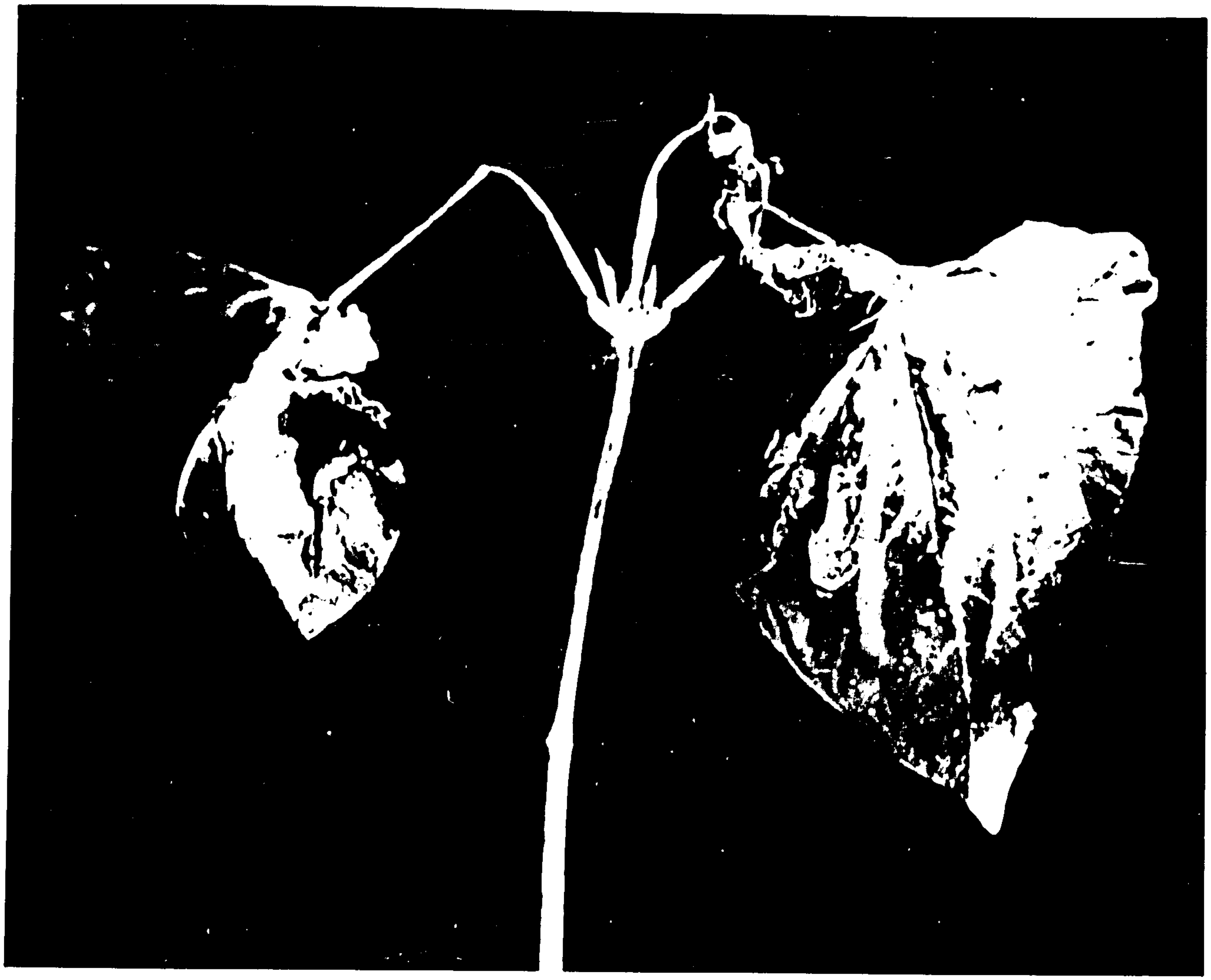

PLATE VI

Virus 15 reaction (mosaic) on a trifoliate leaf. From the F_1 progeny of the second backcross to Rainy River; resistance from Cornell 46-62.

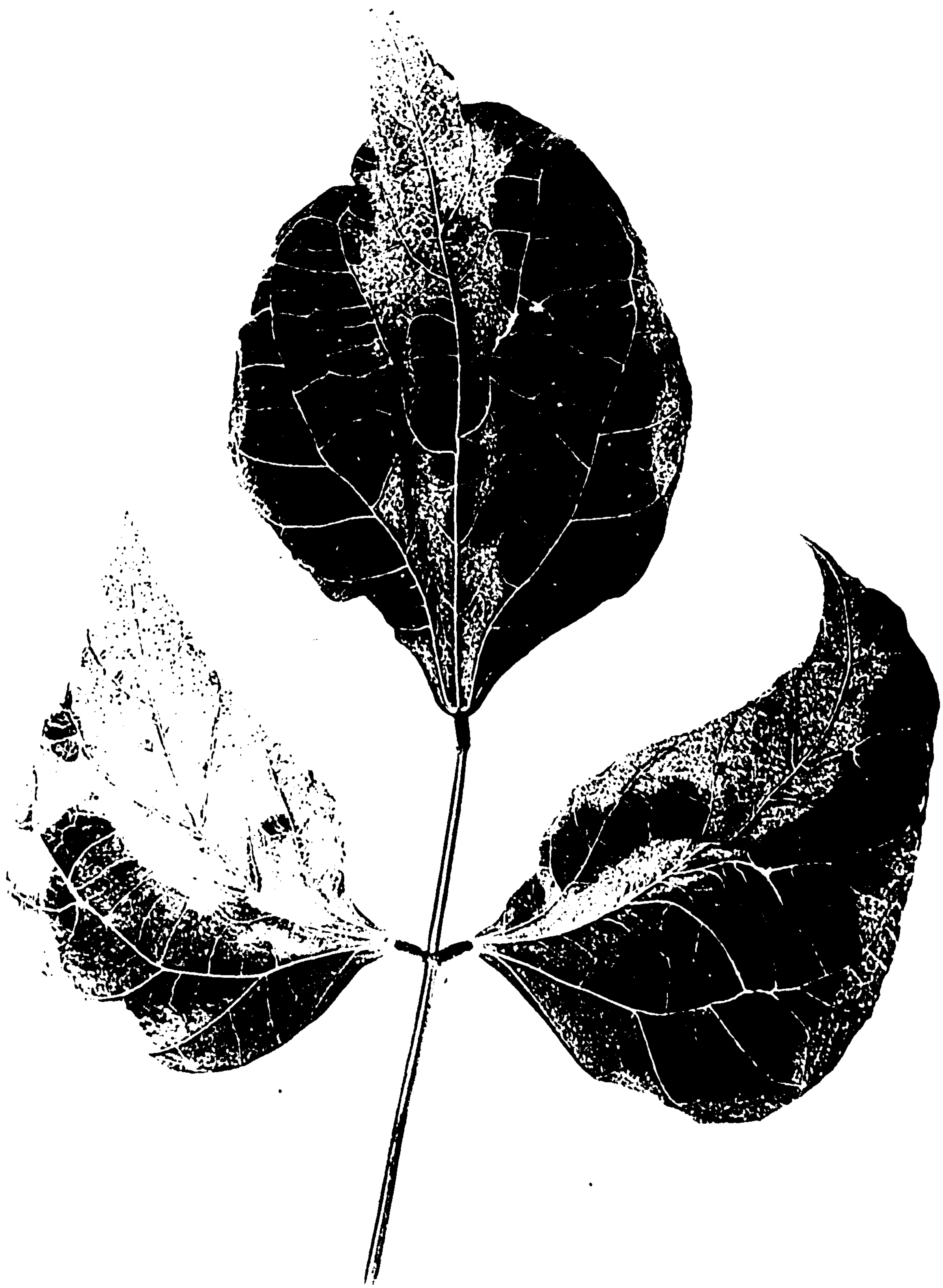

PLATE VII

Parental and BC_5 F_2 seed used in the virus 15 studies. Top left: Rainy River (recurrent parent); top right: Trag 279-1 (non-recurrent parent); and bottom: BC_5 F_2 (from a resistant BC_5 F_1 plant).