



**AgEcon** SEARCH  
RESEARCH IN AGRICULTURAL & APPLIED ECONOMICS

*The World's Largest Open Access Agricultural & Applied Economics Digital Library*

**This document is discoverable and free to researchers across the globe due to the work of AgEcon Search.**

**Help ensure our sustainability.**

Give to AgEcon Search

AgEcon Search  
<http://ageconsearch.umn.edu>  
[aesearch@umn.edu](mailto:aesearch@umn.edu)

*Papers downloaded from **AgEcon Search** may be used for non-commercial purposes and personal study only. No other use, including posting to another Internet site, is permitted without permission from the copyright owner (not AgEcon Search), or as allowed under the provisions of Fair Use, U.S. Copyright Act, Title 17 U.S.C.*

TECH. BULL. (1942)

USDA TECHNICAL BULLETINS

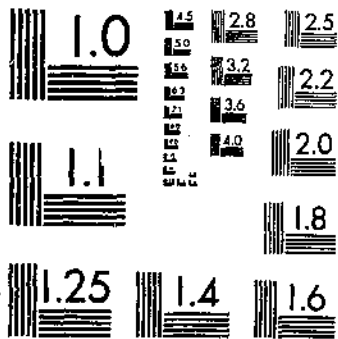
UPDATA

THE FACTORIAL INTERPRETATION OF ANTHRACNOSE RESISTANCE IN BEANS

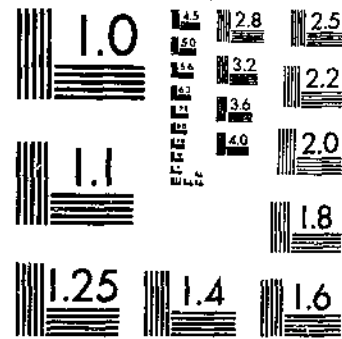
ANDRUS, C. F. WADE, B. L.

1 OF 1

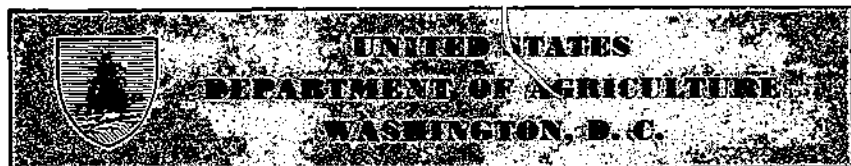
# START



MICROCOPY RESOLUTION TEST CHART  
NATIONAL BUREAU OF STANDARDS-1963-A



MICROCOPY RESOLUTION TEST CHART  
NATIONAL BUREAU OF STANDARDS-1963-A



# The Factorial Interpretation of Anthracnose Resistance in Beans<sup>1</sup>

By C. F. ANDRUS, pathologist, and B. L. WADE, senior geneticist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry

## CONTENTS

	Page		Page
Introduction.....	1	Inheritance of resistance to gamma—Con.	
Methods.....	2	Tolerant X susceptible.....	18
Inheritance of resistance to beta.....	6	Susceptible X susceptible.....	20
Resistant X resistant.....	6	Interpretation of gamma.....	20
Resistant X susceptible.....	6	Inheritance of resistance to delta.....	21
Resistant X tolerant.....	8	Resistant X susceptible.....	21
Tolerant X tolerant.....	11	Susceptible X susceptible.....	24
Susceptible X tolerant.....	11	Interpretation of delta.....	24
Interpretation of beta.....	13	Linkage.....	25
Inheritance of resistance to gamma.....	16	Discussion.....	26
Resistant X susceptible.....	16	Summary.....	26
Resistant X tolerant.....	16	Literature cited.....	20

## INTRODUCTION

It is advantageous for the plant breeder to be able to conceive of a definite system of fixed genes operating in relation to the characters in which he is momentarily interested. But if the gene system becomes too complex there is a tendency to avoid a factorial interpretation and to rely only on the easily demonstrable fact that the characters are inheritable and that with suitable perseverance he can hope to obtain desirable new combinations. In resistance to parasitic diseases in plants there are specific instances in which attempts at a complete factorial interpretation are discouraged because of complexities attending an unstable symptomatology and an involved host-parasite interaction, especially where there are an indefinite number of forms of the pathogen; yet it is conceivable that inheritance of disease reaction may have a comparatively simple factorial basis in spite of the outward complexities.

The sharp differentiation of the several pathogenic strains of *Colletotrichum lindemuthianum* (Sacc. and Magn.) Briosi and Cav. on suitable bean (*Phaseolus vulgaris* L.) varieties, together with the complicated though sharply differentiated symptomatology, seemed to suggest that bean anthracnose would offer a favorable set-up for a comprehensive study of the inheritance of disease resistance. The

<sup>1</sup> Submitted for publication May 28, 1941. This work was performed chiefly under an allotment from the Special Research Fund authorized by Title I of the Bankhead-Jones Act of June 20, 1935.

case with which the host can be cultivated in greenhouse and field, the low percentage of cross-pollination, the fairly large sib populations that can be obtained, and the adaptability of the pathogen to pure-culture manipulation were other advantages which the project seemed to offer. Several contributions already published on the genetics of bean anthracnose (1, 3, 4, 6, 7, 8, 9)<sup>2</sup> will be referred to in the discussion of data.

The work was begun in 1932 with 8 intervarietal crosses and parental selfed lines, and over a period of 6 years was supplemented by 22 additional intervarietal crosses. A total of 398  $F_1$  plants have been carried through the  $F_2$  generation, many of them through the  $F_3$  and a few through the  $F_4$ ; 145  $F_1$  plants were inoculated. An approximate total of 32,600 plants have been inoculated and classified in  $F_2$ , 1,900 families (108,000 plants) analyzed in  $F_3$ , and a considerable number in  $F_4$ . Although the development of anthracnose-resistant varieties was not an original objective of the investigation, many strains have been isolated that are resistant to several of the known physiological forms of *Colletotrichum lindemuthianum*.

## METHODS

Methods of handling the anthracnose organism in culture and of applying inoculum had been developed previous to 1932 in connection with a study of physiological forms of the pathogen. Cultures used for inoculation were invariably grown on cooked bean pods, usually in tubes but occasionally in small flasks and Petri dishes. On this medium they produced a profusion of pink- to orange-colored spore masses, which could easily be washed off into water with a camel's-hair brush. A rough uniformity in spore concentration was obtained by allowing one bean pod culture to each 200 cc. of water. It was observed, however, that a wide range of dilution exerted no appreciable effect on the amount or character of infection. The condition of the culture used, on the other hand, exerted an important effect on the amount of infection. Cultures in which the spore masses had begun to turn white, or had become colorless and watery, were unfit for use.

The most suitable age of culture was affected vastly by differences in temperature. Also exposure to direct sunlight caused them to deteriorate rapidly—an observation earlier made by Budde (2) and others. In the winter months, cultures at laboratory temperature were usually in prime condition at 6 to 14 days of age. It was possible to prolong the useful life of cultures by putting them at 10° to 14° C. refrigeration after the seventh day. During the summer months the cultures were incubated at about 14° during their entire period of growth.

Six physiologic forms of *Colletotrichum lindemuthianum* were available. Four of these were known to occur in the United States, and the other 2 had been isolated from material from Brazil and from Jamaica. The first 4 were selected for use in this study because of their possibly greater economic importance. They comprised the alpha, beta, and gamma forms, obtained from Prof. W. H. Burkholder, of Cornell University, and a new form, delta, isolated from North Carolina material. From the data available it is not possible

<sup>2</sup> Italic numbers in parentheses refer to Literature Cited, p. 23.

to identify delta with any of the 34 physiologic forms of *C. lindemuthianum* described by Schreiber (8). Later it was found necessary to eliminate the alpha form from the inheritance study until further preliminary work could be done, particularly with reference to developing parental lines having a high degree of resistance to it.

The method of applying inoculum underwent a considerable evolution during a 6-year period. The 2-ounce DeVilbiss atomizers used during the early part of the investigation were supplemented by 1-quart continuous atomizers as more space became available and the scope of the project enlarged. The 1-quart sprayers were supplemented by 14-quart knapsack sprayers in the later field inoculations. The 2- by 3-foot glass cages, used as infection chambers in the early experiments, were very soon supplemented by especially built glass-covered benches accommodating approximately 500 4-inch pots. Field inoculations were in all cases made under overhead irrigation.

The time during which the plants were held in the infection chamber varied from 24 to 48 hours, and no effect of time on infection was observed within these limits. Usually plants were put in the chamber in late afternoon and removed on the second following morning, a period of about 42 hours.

On the other hand, conditions inside the chamber exerted an important effect on the amount of infection. Methods were standardized to such an extent as practically to insure moisture deposition on the plants inside the chamber, a condition that seemed to be necessary for maximum infection. The more important factors in this procedure probably were an initial excess of moisture and a falling temperature. The first condition was met by a liberal application of water in the empty chamber, and the second by covering the glass tops with a double thickness of cheesecloth, which was frequently sprinkled and which provided a broad evaporation surface.

The reaction of a large number of bean varieties to the 4 forms of anthracnose was known from preliminary tests; also methods of handling large numbers of bean plants in the greenhouse were to some extent standardized before the genetic study began. In all the larger samples, representatives of each parent were inoculated side by side with their hybrid population. Plants to be inoculated were customarily handled in 4-inch pots and moved in trays of a convenient size, holding 15 or 18 pots. The  $F_1$  plants were planted 1 seed per pot, the  $F_2$  2 to 4 seeds per pot, and the  $F_3$  usually 4 seeds per pot. Less than 50 percent of the  $F_1$  plants were inoculated, the others being planted directly in the field to obtain higher yields. The inoculated  $F_1$  plants were transplanted to soil in a screenhouse or to field plots, and with individual care, many of these produced large  $F_2$  populations. One  $F_1$  plant, grown in a 6-inch pot on a screenhouse ground bed, produced the phenomenal yield of 1,396 seed, or 382 gm.

A number of inoculated  $F_2$  plants, after classification, were transplanted to bench soil in the greenhouse, and many of these produced large  $F_3$  families when given special care. Most of the  $F_3$  families, however, were from plants propagated in the field. In certain crosses the larger  $F_3$  families were divided into two parts and inoculated separately with forms beta and gamma. In some instances it was possible to divide them into three parts and inoculate with delta as well.

The selection of varieties for crossing was made so as to include representatives of several different reaction classes in respect to the 4 forms of anthracnose. The original hybrid material involved intercrosses of 8 varieties, and, in the many new crosses made, only 4 additional varieties and 3 new selections were used; the object was to determine the anthracnose reaction genotype by intercrossing a few varieties in several combinations. The 15 varieties used represent 6 reaction classes (table 1).

TABLE 1.—Reaction of 15 parent bean varieties and selections to 4 physiological forms of *Colletotrichum lindemuthianum*

Variety or selection	Reaction to form—			
	Alpha	Beta	Gamma	Delta
Dark Red Mahogany U. S. No. 1 Refugee Selection No. 1 <sup>1</sup> Geneva Red Kidney	Susceptible	Susceptible	Susceptible	Susceptible
Boston Marrow Perry Marrow selection Robust Perry Marrow	do	Resistant	do	Do.
Kentucky Wonder Wax Corbett Refugee	do	do	Resistant	Do.
Idaho No. 1 Mosaic Resistant Great Northern, <sup>2</sup> Selection No. 2 <sup>3</sup>	do	Tolerant	Tolerant	Do.
Canadian Wonder bush selection <sup>4</sup> Small White (California) selection <sup>5</sup> Selection No. 3 <sup>6</sup>	do	Resistant	Susceptible	Resistant
	do	do	Resistant	Do.

<sup>1</sup> From Giant Stringless × Wells Red Kidney.

<sup>2</sup> Designated subsequently in this bulletin as Great Northern.

<sup>3</sup> From Small White (California) × Dark Red Mahogany.

<sup>4</sup> Designated subsequently in this bulletin as Canadian Wonder.

<sup>5</sup> Designated subsequently in this bulletin as Small White.

<sup>6</sup> From Robust × Small White (California).

The most favorable age for the plant to be inoculated had been determined previously in an extensive series of variety tests. Except for irregularities due to differences in rate of germination and the natural heterogeneity of hybrid populations, all greenhouse plants were inoculated in the primary leaf stage. However, in the field it was found desirable to delay inoculation until the plant had developed a considerable bush. In populations from crosses involving hard seed coats, all seed were scarified before planting, to insure a high percentage of and more uniform germination.

A few of the parent varieties were known to be heterogeneous in respect to reaction to anthracnose, but only lines of known homogeneity were used in the actual crosses. For example, one strain of Perry Marrow is resistant to gamma and another is susceptible. Both strains were used in the crosses but were kept separate and the parent lines checked repeatedly along with the hybrid populations. Seven of the varieties were selfed for two or more generations preceding the hybridization, and of the remaining varieties, five were selfed preceding supplementary crosses but not preceding the original ones. In several instances a parent variety used in later crosses was not known to be a lineal descendant of the same parent used in an earlier cross; the infection pattern, however, was always the same, and data from such sources were combined only when there was no reason to suspect heterogeneity.



FIGURE 1.—Classes of anthracnose reaction on beans 13 days after inoculation: *A*, Plants (left to right) classified as *R*, *L*, *S*, *R*, *S*, and *S*; *B*, plants classified as *S*, *I*, *S*, *I*.

With the exception of one group of  $F_3$  families, all plants were classified as to infection type by the senior author personally, but over the period of several years there were, unavoidably, some changes in the system of classification. The system finally used, and upon which most of the data are based, consisted of three classes defined as follows:

- R*. Resistant - ranging from no visible injury to a faint browning or scarring of leaf veins, petioles, and stems.
- I*. Intermediate - noticeable leaf flecking and with linear lesions principally on the upper stem. These lesions differ in color and usually in shape from those on a fully susceptible plant and also contain few or no conidia. The tolerant parents would fall in this class.



S=Susceptible—plants in this class seldom survive to maturity in the greenhouse but usually survive in the field. A small amount of error may be introduced by lethal agents other than anthracnose.

It is probable that there are two quite different types included in the intermediate class, one (corresponding to the tolerant parents) being due to the action of a particular gene or pair of genes and the other being due to the lack of dominance in heterozygous genotypes. It was impossible to distinguish these types except in their breeding behavior.

Figure 1 includes examples of the three reaction types. Plants were always classified on the seventh day after inoculation but frequently were observed over a longer period. For the purpose of testing for Mendelian segregation, the first two classes were usually combined as resistant; in a few instances, however, the proportion of intermediate phenotypes was such that they could be fitted to a particular genotype. Yates' continuity correction was applied to the estimates of chi-square ( $\chi^2$ ) deviation of all  $F_2$  Mendelian ratios and to all two-part  $F_3$  distribution  $\chi^2$  ratios. The continuity correction was not applied to  $F_3$  ratios used in calculating heterogeneity or total  $\chi^2$  values.

## INHERITANCE OF RESISTANCE TO BETA

### RESISTANT $\times$ RESISTANT

In the cross Robust  $\times$  Small White all of 50  $F_2$  plants inoculated with beta proved to be resistant. In the cross Small White  $\times$  Boston Marrow and reciprocal all of 131 plants were resistant in the  $F_2$  generation. The cross selection No. 3  $\times$  Boston Marrow segregated in  $F_2$  generation 99 resistant to 7 susceptible, a good approximation to a 15 to 1 Mendelian segregation ( $\chi^2=0.003$ ). Presumably both parents carried at least 1 recessive factor for beta susceptibility. No  $F_3$  families from these crosses were inoculated with beta.

### RESISTANT $\times$ SUSCEPTIBLE

Resistance was dominant in the  $F_1$  generation of the cross Dark Red Mahogany  $\times$  Geneva Red Kidney. The other  $F_1$  plants were not inoculated. A lack of complete dominance in crosses of beta resistant  $\times$  beta susceptible is shown in subsequent generations where intermediate phenotypes appear in the several crosses. Whenever tested in  $F_3$  most of the individuals in the intermediate class were proved to be heterozygous. Data involving 1,744  $F_2$  plants from 5 crosses of beta resistant  $\times$  beta susceptible as well as 130  $F_3$  families from 3 crosses are shown in table 2.

The total  $\chi^2$  of 14.031 for a 3:1 ratio in the 5 crosses shown in table 2 is considerably outside the 5-percent point (11.070); hence a single-factor hypothesis will hardly suffice for all the data. It may be considered possible, therefore, that the cross Dark Red Mahogany  $\times$  Geneva Red Kidney, which gives the poorest fit to a 3:1 ratio, is actually segregating 11:5. An 11:5 Mendelian ratio results from the introduction of both a dominant and a recessive gene for the same character in a cross and involves a rather complex series of interactions. Interaction between a dominant and recessive gene for the same phenotype in different allelomorph series results in a 13:3 ratio,

TABLE 2.—Inheritance of resistance to beta in  $F_2$  and  $F_3$  generations of crosses resistant  $\times$  susceptible or the reciprocal

No. and cross	$F_2$ plants <sup>1</sup>		$F_3$ families <sup>1</sup>							
	Observed segregation	$\chi^2$	Classification in $F_2$	All R	Segregating	All S	Distribution $\chi^2$	Population $\chi^2$ of segregating families	Heterogeneity $\chi^2$	Total $\chi^2$
1. U. S. No. 1 Refugee $\times$ Geneva Red Kidney	344 R:106 S	<sup>3</sup> 0.427	Unclassified (Class R and I)	Number 6 9	Number 16 14	Number 9 2	0.613 .346	} 0.340	55.995**	4 56.335**
2. Selection No. 1 $\times$ Geneva Red Kidney	131 R:54 S	<sup>3</sup> 1.515	Unclassified	3	10	8	2.420			
3. Perry Marrow $\times$ U. S. No. 1 Refugee	396 R:158 S	<sup>3</sup> 3.475	Unclassified (Class R)	7 11	21 8	6 0	1.941	16.641**	77.723**	94.363*
4. Dark Red Mahogany $\times$ Geneva Red Kidney	217 R:97 S	<sup>2</sup> 5.503*						<sup>3</sup> 4.175*	<sup>3</sup> 40.440*	<sup>3</sup> 44.614*
5. Canadian Wonder $\times$ Dark Red Mahogany	191 R:50 S	<sup>6</sup> 6.006 <sup>2</sup> 2.104 <sup>7</sup> 7.507								

<sup>1</sup> \* = Significant at 5-percent level. \*\* = Significant at 1-percent level.

<sup>2</sup> Based on 3:1 ratio.

<sup>3</sup> Omitted from  $\chi^2$  calculation.

<sup>4</sup> By elimination of the 2 most divergent populations, population  $\chi^2$  is reduced to 0.004, total  $\chi^2$  to 25.380, and heterogeneity  $\chi^2$  to 25.379; all nonsignificant values.

<sup>5</sup> By elimination of the 2 most divergent families.

<sup>6</sup> Based on 11:5 ratio.

<sup>7</sup> Based on 13:3 ratio.

but an additional interaction between alleles of the same series can produce an 11:5 ratio. If the 11:5 hypothesis is valid, the Dark Red Mahogany parent must carry one dominant factor for susceptibility, and the same factor would upset the ratio in the cross of Canadian Wonder  $\times$  Dark Red Mahogany, which is seen to give a closer approximation to a 13:3 than to a 3:1 ratio. Unfortunately, no  $F_3$  data are available with which to test the irregularity in the two crosses involving Dark Red Mahogany. Evidence that Dark Red Mahogany does carry a dominant factor for susceptibility will be presented in a succeeding section (p. 11).

In respect to the first 3 crosses in table 2,  $F_3$  data tend to confirm the 3:1 hypothesis. The proportion of all-resistant, segregating, and all-susceptible families (from plants not tested in  $F_2$ ) conforms satisfactorily with the calculated 1:2:1 ratio in all 3 crosses represented. Analysis based on the ratio of resistant to susceptible plants in each segregating family shows that in the cross U. S. No. 1 Refugee  $\times$  Geneva Red Kidney 30 families segregated 3:1 with a total  $\chi^2$  of 56.335 and heterogeneity  $\chi^2$  of 55.995, slightly outside the 1-percent point. The total resistant and susceptible in the 30 segregating families also approximated a 3:1 ratio (population  $\chi^2=0.340$ ).

Data on 10 segregating families from the cross selection No. 1  $\times$  Geneva Red Kidney are less conclusive, but the small sample would not justify rejection of the 3:1 hypothesis. Heterogeneity  $\chi^2$  is low, but the population  $\chi^2$  is high and indicates a deficiency of susceptibles.

The 29 segregating families from the cross Perry Marrow  $\times$  U. S. No. 1 Refugee give a total  $\chi^2$  of 94.363 and a heterogeneity  $\chi^2$  of 77.723, which is far outside the 1-percent level of significance. Most of the deviation was contributed by 2 families which segregated 95 resistant to 3 susceptible and 17 resistant to 24 susceptible, and when they are removed from the calculation the heterogeneity  $\chi^2$  is reduced to approximately the 5-percent level for 26 degrees of freedom.

The excess of homozygous resistant families from 19 parents classified as *R* in  $F_2$  of the Perry Marrow  $\times$  U. S. No. 1 Refugee cross might be due to the fact that most plants classified as *I* in  $F_2$  were eliminated because of weak growth; the intermediate class was presumably heterozygous in genotype. This was verified only in the case of 3 *I* plants in the U. S. No. 1 Refugee  $\times$  Geneva Red Kidney cross, all of which proved to be heterozygous.

#### RESISTANT $\times$ TOLERANT

The two varieties Corbett Refugee and Great Northern, although both were called tolerant on the basis of slight flecking of the leaf veins and lamina, actually differed from each other slightly in the extent of injury. From a practical point of view, both varieties are highly resistant to both beta and gamma. The crosses resistant  $\times$  tolerant, therefore, are between varieties that differ but slightly in their anthracnose reaction.

Five resistant  $\times$  tolerant crosses were made and 3 types of segregations obtained in  $F_2$  (table 3). Corbett Refugee was the tolerant parent in 4 crosses, and the results point to the likelihood that 3 different genotypes are represented among the 4 resistant parents. Most of the plants classified as intermediate in  $F_2$  of the Perry Marrow  $\times$  Corbett Refugee cross appear to be of the hypothetical genotypes *Aabb* or *aaBb*. Of 16 plants so classified, 12 were proved to be heterozygous.

TABLE 3.—Inheritance of resistance to beta in  $F_2$  and  $F_3$  generations of the crosses resistant  $\times$  tolerant or the reciprocal

No. and cross	$F_2$ plants <sup>1</sup>		$F_3$ families <sup>1</sup>					
	Observed segregation	$\chi^2$	Classification in $F_3$	All R	Segregating	All S	Distribution $\chi^2$	Population $\chi^2$ of segregating families
1. Perry Marrow $\times$ Corbett Refugee and reciprocal	978 R:63 S	<sup>2</sup> 0.040	Class R and I	Number 21	Number 29	Number 0	<sup>3</sup> 0.269	<sup>4</sup> 3.153
2. Boston Marrow $\times$ Corbett Refugee	275 R:16 S	<sup>2</sup> 1.187						
3. Canadian Wonder $\times$ Corbett Refugee	220 R:24 S	<sup>2</sup> 4.234*	Class R and I (classified in field).	228	133	0	<sup>7</sup> 2.737	<sup>8</sup> 30.365**
4. Geneva Red Kidney $\times$ Corbett Refugee and reciprocal	<sup>5</sup> 1,923 R:64 S	<sup>6</sup> 34.482**						
5. Perry Marrow $\times$ Great Northern and reciprocal	<sup>9</sup> 989 R:18 S 368 R:85 S	<sup>6</sup> 20.1 <sup>10</sup> 0.003						

<sup>1</sup> \* = Significant at 5-percent level. \*\* = Significant at 1-percent level.

<sup>2</sup> Based on 15:1 ratio.

<sup>3</sup> Based on 7:3 ratio.

<sup>4</sup> Based on 27:5 ratio.

<sup>5</sup> Greenhouse test.

<sup>6</sup> Based on 63:1 ratio.

<sup>7</sup> Based on 37:26 ratio.

<sup>8</sup> Based on 378:38 ratio in a total population of 6,585.

<sup>9</sup> Field test.

<sup>10</sup> Based on 13:3 ratio.

The first 3 crosses entered in table 3 segregated 15 resistant to 1 susceptible in  $F_2$ . The combined data for the 3 crosses also closely approximate a 15:1 ratio. The 15:1 hypothesis is supported further by  $F_3$  data on 50 families from the Perry Marrow  $\times$  Corbett Refugee cross (table 3), where the calculated proportions of all-resistant and segregating families and the ratio of total resistant to total susceptible plants in the segregating families are nearly realized.

The cross Geneva Red Kidney  $\times$  Corbett Refugee seems to exhibit a 63:1 type of inheritance. Actually the  $F_2$  population segregated in the proportion of 62:2, which corresponds to a 14:2 type of inheritance to be described later in the discussion of gamma inheritance (p. 16). The 62:2 hypothesis, however, is not supported by the  $F_3$  data, which on the contrary indicate a 63:1 ratio. Apparently one or more of the genes entering into the cross are especially sensitive to environmental conditions; therefore, the response to different environments of the heterozygote derived from this gene pair could account for the variable proportions of resistant and susceptible phenotypes repeatedly observed in different samples of the  $F_2$  population.

Another factor conducive to error in this cross is the occurrence of a semilethal (principally a chlorophyll deficiency), which affects approximately 7 percent of the  $F_2$  plants. Individuals weakened or killed by the lethal factor are difficult to classify in respect to anthracnose reaction. In view of this situation a rather large deviation might be expected in the population  $\chi^2$  for segregating families.

Theoretically the  $F_3$  data could be subjected to the following measures of goodness of fit:

- (1) The proportions of all-resistant, segregating, and all-susceptible families.
- (2) The ratio of the total number of resistant and susceptible plants within the segregating families.
- (3) The proportions of different classes of segregating families.

Actually only the first two measures are available, since, so far as the present authors are aware, no method has been devised for equably separating different Mendelian segregating classes from a mixed population. The method of subjecting each segregating family to a  $\chi^2$  test for two ratios and assigning the family to the class that it most nearly approximates may (except by chance) lead to a false interpretation.<sup>3</sup>

A total of over 16,000  $F_3$  plants from the cross Geneva Red Kidney  $\times$  Corbett Refugee have been inoculated with beta. Most of these, 14,516, represent 307 families from  $F_2$  plants classified in the field and verified in the greenhouse. Smaller groups of  $F_3$  families from plants classified in the greenhouse were verified both in the greenhouse and in the field. The families varied in size from 6 to 269 individuals and averaged 47.

Thirteen of the  $F_3$  families were from plants classified as susceptible in the field and each proved to be all susceptible in the greenhouse. The remaining 361 families were from plants resistant in  $F_2$ ; it is therefore possible to consider only the ratio of all-resistant to segregating families. On that basis the data conform with the 63:1 hypothesis. According to a 63:1 hypothesis,  $F_3$  families should occur in the ratio

<sup>3</sup> It would be inappropriate here to discuss the mathematical basis for rejection of the method. The objection is based, however, on errors introduced by the zone of overlapping of two distribution systems, as represented by a bimodal frequency curve involving percentage classes (or ratios).

of 37 all-resistant to 26 segregating to 1 all-susceptible. Actually the 37:26 ratio is realized in table 3.

The ratio of resistant to susceptible plants in all segregating families combined does not conform satisfactorily to the 63:1 ratio. According to a 63:1 hypothesis the segregating families would be 6/26, 48:16 (3:1); 12/26, 60:4 (15:1); and 8/26, 63:1; and the combined ratio of resistant to susceptible plants would be 378:38. The observed data (table 3) show a significant excess of susceptibles, or 731 where the calculated number would be 601 out of a total population of 6,585. Perhaps it should be pointed out that the excess of susceptibles, although highly significant from a statistical standpoint, involves only about 2 percent of the total population.

#### TOLERANT × TOLERANT

Among the 15 parent varieties and selections, there were 3 that were classed as tolerant to the beta anthracnose fungus (table 1). Seven  $F_1$  plants from the cross Corbett Refugee × Great Northern were inoculated with beta. The  $F_1$  plants, as well as the parents, were tolerant to beta.

Segregation in  $F_2$  was as shown in table 4. Although an excellent 15:1 ratio is obtained by combining all resistant and intermediate plants into one class, the 13:2:1 ratio is more satisfactory in that it associates the plants classified as intermediate with a definite genotype. According to the authors' interpretation, beta resistance in the cross Great Northern × Corbett Refugee follows a modified 13:3 ratio, in which the two  $AA'bb$  genotypes are partially susceptible whereas the one  $A'A'bb$  genotype is fully susceptible. No  $F_2$  data are available for this cross.

TABLE 4.—Inheritance of resistance to beta in the  $F_2$  generation of the cross Great Northern × Corbett Refugee

Infection type	Total	15:1 ratio				13:2:1 ratio			
		Observed	Calculated	$\chi^2$	P	Observed	Calculated	$\chi^2$	P
R	500	573	570			500	494		
I	73					73	70		
S	35					35	38		
Total	608	608	608	0.178	0.70	608	608	0.428	0.80

12 degrees of freedom.

#### SUSCEPTIBLE × TOLERANT

Susceptibility was dominant in the cross Dark Red Mahogany × Great Northern and the reciprocal; 7  $F_1$  plants in the field were all susceptible to beta. A progeny test of 222 random  $F_2$  plants confirmed the observation that susceptibility is dominant in this cross (fig. 2) and incidentally tends to strengthen the belief, expressed in the discussion of resistant × susceptible crosses (p. 6), that Dark Red Mahogany carries 1 dominant susceptible pair of factors.

The actual segregation of beta reaction does not conform to any simple Mendelian ratio. Of the 222 families, 5 were all resistant, 169

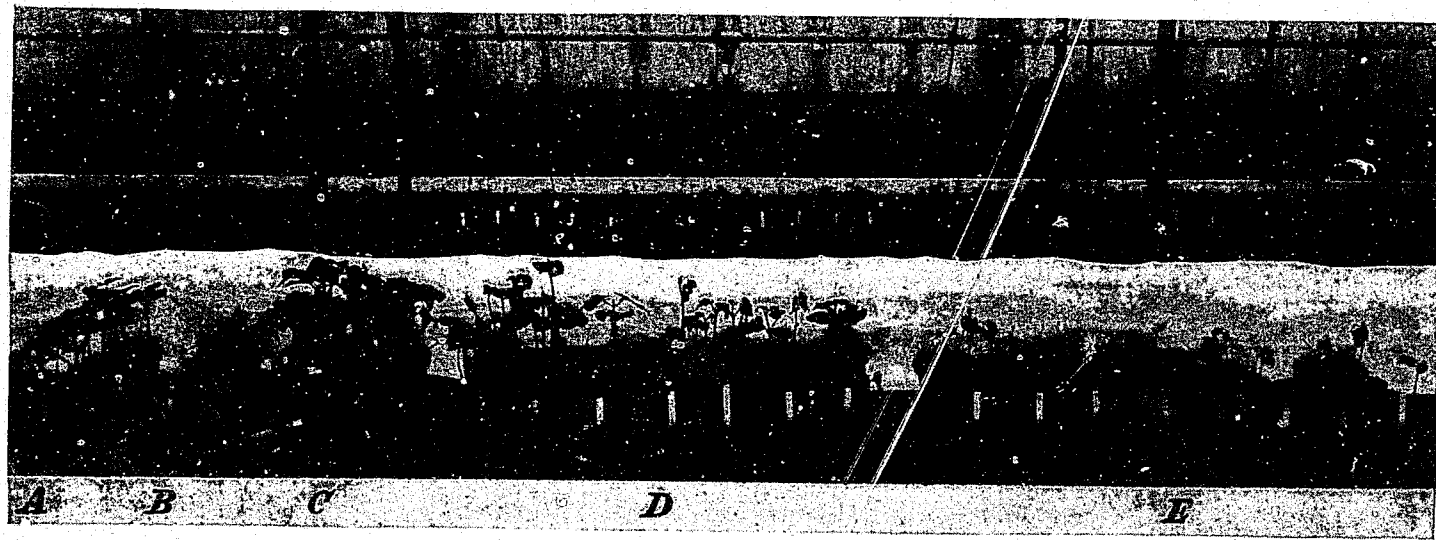


FIGURE 2.— $F_2$  segregation in the susceptible  $\times$  tolerant cross: *A*, The tolerant parent; *B*, the susceptible parent; *C*, two all-resistant families; *D*, seven segregating families; *E*, eight all-susceptible families.

segregated, and 48 were all susceptible. In the segregating families the proportion of intermediates was high, and there was almost complete intergradation of infection types ranging from dead to completely resistant. The individual ratios observed among the segregating families suggest a 15:1 type of inheritance, but the number of segregating families is excessive. It is possible that 3 pairs of factors are segregating in the cross, and that certain of them are cumulative in effect.

#### INTERPRETATION OF BETA

In the inoculations with the beta anthracnose fungus on nine intervarietal crosses there were obtained in the  $F_2$  generation five possibly different Mendelian ratios, some of which seem to be wholly incompatible (fig. 3). The three ratios, 3:1, 15:1, and 63:1, all supported by  $F_2$  data, are adequately explained on the assumption that there are three independent pairs of factors controlling beta reaction, with resistance dominant. But subsidiary evidence, based principally on

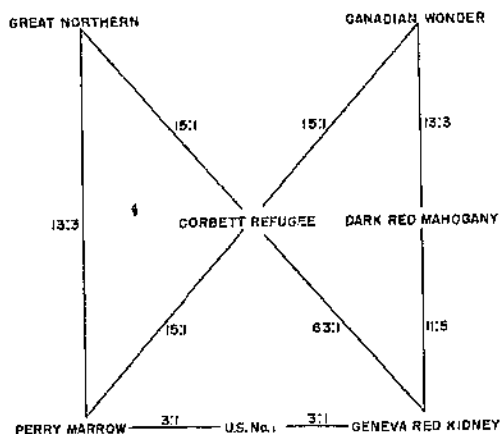


FIGURE 3.—The  $F_2$  ratios obtained when seven varieties were intercrossed in nine directions and the crosses were inoculated with the beta anthracnose fungus. The ratios for the following crosses are supported by  $F_2$  data: Corbett Refugee  $\times$  Perry Marrow, Corbett Refugee  $\times$  Geneva Red Kidney, Perry Marrow  $\times$  U. S. No. 1 Refugee, and Geneva Red Kidney  $\times$  U. S. No. 1 Refugee

$F_2$  data, indicates strongly that the interpretation of beta inheritance will need to include factors dominant for susceptibility as well as for resistance (the 13:3, 11:5 ratios, and the Dark Red Mahogany  $\times$  Great Northern cross). It would need also to account for the presence of intermediate grades of injury and include certain genotypes that are peculiarly susceptible to environmental conditions. Since there is never any evidence of more than a trihybrid segregation, the factors should probably not extend beyond three allelic series. To be fully useful such an explanation should provide a basis for predicting the results of crosses not yet made.

After rejecting many tentative hypotheses, one involving three series of alleles combined with gene interactions at two points was selected as one of the few which would explain all the data at hand and



still provide for fixity of gene action. The allelic series would be defined as follows:

A series <sup>4</sup>	B series <sup>4</sup>	C series <sup>4</sup>
A = R (dominant)	B = R (dominant)	C (alone or with A', C', or B) = S
A' (alone or with C) = S	B' (alone) = S	C' (with A or B') = R
A' (with B' or C') = R	B' (with A', C', or C) = R	C' (alone or with C) = S
a = S (recessive)	b = S (recessive)	C' (with A' or B') = R
		c = S
		c' = S

A series of genotypes	B series of genotypes	C series of genotypes
AA' = R	BB' = R	CC' = S
Aa = R	Bb = R	Cc = S
A'a = S	B'b = S	Cc' = R
		C'c = S
		C'c' = S
		cc' = R

With the 10 factors in 3 series, 36 homozygous genotypes are possible—11 susceptible and 25 resistant. If the 62:2 type of inheritance, first observed in the F<sub>2</sub> generation of the Corbett Refugee × Geneva Red Kidney cross, should be proved invalid, it would be necessary only to eliminate the hypothetical gene *c'* and consequently the interaction between *c* and *c'*, which was introduced to account for the 62:2 ratio. It should be borne in mind that the gene hypothesis is offered only to show the sort of set-up that would be required if all the data are to be interpreted along Mendelian lines. The possibility of non-Mendelian inheritance, in certain crosses at least, is not excluded. It is possible also, and perhaps even probable, that the Corbett Refugee and certain other parental varieties have introduced lethal or semilethal genes that upset normal ratios to such an extent as to make a factorial interpretation too difficult.

The F<sub>2</sub> ratios that would be expected, according to the hypothesis, when 22 of the 36 possible genotypes are intercrossed, are shown in table 5, and the 9 beta-inoculated crosses from which the hypothesis is constructed are outlined in figure 3. If the 7 parent varieties are fitted to their appropriate genotypes in table 5, there is presented a working hypothesis for predicting the results of many future crosses. Table 5, however, should be regarded only as an illustration of how predictions might be made and not as a serious attempt at making them, because the parental genotypes shown are tentative and would not be completely known until all possible intervarietal crosses had been made.

<sup>4</sup> Symbols R=resistant and S=susceptible, as explained on p. 5.

TABLE 5.—Theoretical  $F_2$  ratios from all possible intercrossings of 22 of 36 possible genotypes, including tentative genotypes of 7 parents tested for resistance to beta

Genotype No. <sup>1</sup>	Genotype constitution <sup>1</sup>	Segregation ratio or injection type for indicated genotype <sup>1</sup>																														Parent of crosses tested for resistance to beta
		11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32									
11	<i>A.Abbcc</i> .....	R	R	51:13	63:1	<sup>2</sup> 15:1	<sup>3</sup> 63:1	<sup>2</sup> 15:1	63:1	15:1	{ 63:1 62:2 }	3:1	12:4	3:1	{ 15:1 14:2 }	15:40	15:1	15:1	{ 63:1 62:2 }	57:7	<sup>2</sup> 57:7	12:4	56:8	Corbett Refugee.								
12	<i>A.Abbc'e</i> .....		R	50:5	63:1	{ 63:1 62:2 }	{ 63:1 62:2 }	63:1	{ 63:1 62:2 }	15:1	{ 15:1 14:2 }	15:1	{ 15:1 14:2 }	3:1	47:17	15:1	{ 63:1 62:2 }	15:1	59:5	57:7	56:8	12:4										
13	<i>A'A'BBCC</i>			S	3:1	3:1	3:1	13:3	13:3	{ 15:1 14:2 }	S	13:3	3:13	11:5	S	1:3	3:1	3:1	3:1	13:3	51:13	59:5	Great North-orn.									
14	<i>A'A'BBc'C'</i>				R	R	R	13:3	R	R	R	1:3	R	15:1	15:1	1:3	R	R	R	13:3	R	63:1		63:1								
15	<i>A'A'BBcc</i>					R	R	<sup>2</sup> 13:3	R	R	R	3:13	15:1	3:1	{ 15:1 14:2 }	1:3	R	R	R	51:13	15:1	15:1	{ 63:1 62:2 }									
16	<i>A'A'BBc'e</i>						R	15:1	R	R	R	<sup>2</sup> 11:5	15:1	{ 15:1 14:2 }	3:1	<sup>2</sup> 3:1	R	R	R	50:5	15:1	{ 63:1 62:2 }	15:1									
17	<i>A'A'B'B'CC</i>								R	R	R	3:1	13:3	3:1	{ 15:1 14:2 }	<sup>2</sup> 3:1	15:1	51:13	50:5	R	R	15:1	15:1									
18	<i>A'A'B'B'C'C'</i>									R	R	R	13:3	R	15:1	15:1	13:3	R	63:1	R	R	15:1	15:1									
19	<i>A'A'B'B'cc</i>										R	R	3:1	R	3:1	{ 15:1 14:2 }	51:13	57:7	15:1	{ 63:1 62:2 }	15:1	15:1	3:1									
20	<i>A'A'B'B'c'e</i>										R	{ 15:1 14:2 }	15:1	{ 15:1 14:2 }	3:1	15:1	57:7	{ 63:1 62:2 }	15:1	15:1	15:1	{ 15:1 14:2 }	3:1									
21	<i>A'A'bbCC</i>											S	1:3	S	1:1	S	1:3	10:54	11:5	3:1	<sup>2</sup> 51:13	47:17	51:13									
22	<i>A'A'bbC'C'</i>											R	3:1	3:1	15:40	15:1	57:7	15:1	15:1	15:1	54:10	54:10	Dark Red Mahogany.									
23	<i>A'A'bbcc</i> .....													S	S	S	57:7	3:1	{ 15:1 14:2 }	15:1	51:13	9:7		50:14								
24	<i>A'A'bbc'e</i>														S	1:1	57:7	{ 15:1 14:2 }	3:1	{ 63:1 62:2 }	51:13	50:14	9:7									
25	<i>aaBBCC</i>															S	1:3	1:3	3:1	3:1	13:3	3:1	{ 15:1 14:2 }									
26	<i>aaBBC'C'</i>																R	R	R	13:3	R	15:1	15:1									
27	<i>aaBBcc</i>																	R	3:1	15:1	3:1	15:1	14:2									
28	<i>aaBBc'e</i>																		R	{ 15:1 14:2 }	15:1	{ 15:1 14:2 }	3:1									
29	<i>aaB'B'CC</i>																			R	R	3:1	3:1									
30	<i>aaB'B'C'C'</i>																				R	3:1	3:1									
31	<i>aaB'B'cc</i>																					S	1:1									
32	<i>aaB'B'c'e</i>																						S									

<sup>1</sup> Genotype numbers of susceptible genotypes are shown in bold face and genotype constitutions in bold-face italic.

<sup>2</sup> Ratios actually obtained with beta anthracnose.

<sup>3</sup> Supported by  $F_1$  data.

## INHERITANCE OF RESISTANCE TO GAMMA

RESISTANT  $\times$  SUSCEPTIBLE

The three resistant by susceptible crosses probably involve simple monohybrid and dihybrid types of inheritance, although better fits are obtained when more complex gene systems are hypothesized (table 6). The ratios, 13:3, 11:5, 57:7, all suggest the existence of either fixed dominant susceptible genes or an unstable dominance of resistant genes. The  $F_2$  data are from inoculations made in the greenhouse at a time when no facilities were available for carrying plants to maturity, consequently  $F_3$  data were not obtained.

RESISTANT  $\times$  TOLERANT

Only three  $F_1$  plants from resistant  $\times$  tolerant parents (selection No. 3  $\times$  Great Northern) were tested and all were resistant. Five crosses were tested in the  $F_2$  generation and five different ratios were obtained (table 7). A significant difference appeared in reciprocals of the Corbett Refugee  $\times$  Perry Marrow cross, 14:2 in one direction and 13:2:1 in the other. Reciprocals were combined in other crosses. The populations were adequate in size and the segregation of fully susceptible plants was unusually distinct; the evidence therefore indicates that the five parental varieties represent five different genotypes.

TABLE 6.—Inheritance of resistance to gamma in the  $F_2$  generation of the crosses resistant  $\times$  susceptible or the reciprocal

Cross	Total	Observed segregation	Ratio tested	$\chi^2$	P
	<i>Number</i>				
Selection No. 3 $\times$ Boston Marrow	409	373 R:36 S	57:7	1.702	0.20
Boston Marrow $\times$ Small White	233	180 R:44 S	15:1	4.121*	.04
			3:1	4.323*	.04
Small White $\times$ Dark Red Mahogany	94	63 R:31 S	13:3	.001	.96
			3:1	2.780	.10
			11:5	.062	.80

\* = Significant at 5-percent level.

Conceivably the tolerant parents carry unstable genes that are particularly susceptible to environmental effects or are peculiar in their interactions with other allelomorphs. The important effect of environment is suggested in the unusually large number of intermediate grades of disease reaction. An interesting observation is the fact that selection No. 3 (table 7, cross No. 5) seems to carry no recessive gene or genes for susceptibility to the gamma anthracnose fungus.

An apparent difference in reciprocals of the Corbett Refugee  $\times$  Perry Marrow cross (No. 2, table 7) is possibly due to the small population in the one direction. Combined reciprocals give a fairly satisfactory 14:2 ratio, a type of inheritance discussed more fully on page 19.  $F_3$  data from the Corbett Refugee  $\times$  Perry Marrow cross tend to support the 14:2 hypothesis, which is based on interaction of two susceptible genes.

A total of 82 families were studied in the  $F_3$  generation. According to the 14:2 hypothesis, a random sample of  $F_3$  families would be all-

TABLE 7.—Inheritance of resistance to gamma in  $F_2$  and  $F_3$  generations of the crosses resistant  $\times$  tolerant or the reciprocal

No. and cross	$F_2$ plants		$F_3$ families <sup>1</sup>					Population $\chi^2$ of segregating families
	Observed segregation	$\chi^2$ for ratio indicated	Classification in $F_2$	All R	Segregating	All S	Distribution $\chi^2$	
				Number	Number	Number		
1. Small White $\times$ Corbett Refugee	511 R: 5 S	0.827 (63:1)						
2. Corbett Refugee $\times$ Perry Marrow	716 R: 101 S	.004 (14:2)						
Perry Marrow $\times$ Corbett Refugee	228 R: 48 I: 14 S	1.820 (13:2:1)						
Combined	902 R: 115 S	4.322 (14:2)	{ Class R Class I Unclassified	9 10 5	1 30 23	0 0 4	1.741 1.156	5.444*
3. Great Northern $\times$ Small White and reciprocal	1,239 R: 81 S	.013 (15:1)	{ Class R Class I	10 0	16 8	0 0	3.406	
4. Great Northern $\times$ Perry Marrow and reciprocal	333 R: 295 S	2.524 (9:7)	{ Class R Class I	7 3	4 36	0 0	3.240	.168
5. Selection No. 3 $\times$ Great Northern	411 R: 0 S							

<sup>1</sup> \* = Significant at 5-percent level. \*\* = Significant at 1-percent level.  
<sup>2</sup> Based on 4:10 ratio.  
<sup>3</sup> Heterogeneity  $\chi^2$  for reciprocals = 11.129, which is just beyond 1-percent level.  
<sup>4</sup> Based on 4:10:2 ratio.

<sup>5</sup> Based on 7:8 ratio.  
<sup>6</sup> Based on 27:5 ratio.  
<sup>7</sup> Based on 1:8 ratio.  
<sup>8</sup> Based on 21:11 ratio.

TABLE 8.—Inheritance of resistance to gamma in  $F_2$  and  $F_3$  generations of the crosses susceptible  $\times$  tolerant or the reciprocal

No. and cross	$F_2$ plants <sup>1</sup>		$F_3$ families					Population $\chi^2$ of segregating families
	Observed segregation	$\chi^2$	Classification in $F_2$	All R	Segregating	All S	Distribution $\chi^2$	
				Number	Number	Number		
1. Corbett Refugee $\times$ Geneva Red Kidney and reciprocal	1,717 R: 250 S	{ <sup>2</sup> 0.061 <sup>4</sup> 138.931** 1.071	{ Class S Class R (classified in field)	0 144	8 169	45 8	0.032	0.043
2. Corbett Refugee $\times$ Dark Red Mahogany	243 R: 29 S	{ <sup>3</sup> 27.750** <sup>5</sup> .686 <sup>6</sup> .130						
3. Corbett Refugee $\times$ Perry Marrow selection	28 R: 54 I: 30 S	{ <sup>7</sup> 3.967* <sup>10</sup> .197						
4. Boston Marrow $\times$ Corbett Refugee	172 R: 36 S	{ <sup>11</sup> 1.515 <sup>12</sup> .005						
5. Canadian Wonder $\times$ Corbett Refugee	367 R: 139 S							
6. Perry Marrow selection $\times$ Great Northern	16 R: 51 S							

<sup>1</sup> \* = Significant at 5-percent level. \*\* = Significant at 1-percent level.  
<sup>2</sup> Greenhouse test.  
<sup>3</sup> Based on 14:2 ratio.

<sup>4</sup> Based on 15:1 ratio.  
<sup>5</sup> Field test.  
<sup>6</sup> Omitted from  $\chi^2$  calculation.

<sup>7</sup> Based on 7:8 ratio.  
<sup>8</sup> Based on 27:5 ratio.  
<sup>9</sup> Based on 1:2:1 ratio.

<sup>10</sup> Based on 13:3 ratio.  
<sup>11</sup> Based on 3:1 ratio.  
<sup>12</sup> Based on 1:3 ratio.

resistant to segregating to all-susceptible in the proportion of 4:10:2. The 32 families from plants not classified in the  $F_2$  generation (table 7) constitute an unbiased sample, and they give an excellent approximation of the 4:10:2 ratio. The samples from plants classified in  $F_2$  also support the 14:2 hypothesis and incidentally show a tendency for certain heterozygous genotypes to give an intermediate disease reaction, whereas the presumably homozygous resistant genotypes are less often represented in the intermediate grades.

The second measure of goodness of fit applied to the  $F_3$  data is based on the assumption that in the 14:2 inheritance the segregating families would be of three classes: 2/10, 1:1; 4/10, 3:1; and 4/10, 14:2. From this it can be calculated that the total of resistant and susceptible plants in the segregating families would be in the ratio of 3:1. The observed data (table 7) approach this calculation with a fair degree of accuracy, being outside the 5-percent point of probability but within the 1-percent point for 1 degree of freedom.

The meager  $F_3$  data from the Small White  $\times$  Great Northern cross scarcely support the 15:1  $F_2$  hypothesis. The 34 families (cross No. 3, table 7) were all from parents classified in the  $F_2$  generation, and since the classes are not represented in their true proportions, the ratio of all-resistant to segregating families would not be expected to conform to any calculated ratio; actually the deviation probability is still within the 5-percent point for a 7:8 ratio. The data indicate also that plants giving the intermediate reaction ( $I$ ) are predominately heterozygous and that dominance is incomplete. Considering the fact that the proportion of  $I$  plants varies enormously even in different samples from the same cross, however, it could be concluded that dominance of certain genes at least is extremely variable.

The second measure of goodness of fit applied to the Small White  $\times$  Great Northern  $F_3$  data shows an excess of susceptibles in the calculated 27:5 ratio (table 7). This is insufficient to invalidate the 15:1  $F_2$  hypothesis, in view of the small number of families and the small family size. Families varied in size from 11 to 74 and averaged 30.

When the same measures of goodness of fit are applied to  $F_2$  data from the Great Northern  $\times$  Perry Marrow cross, excellent support for the 9:7  $F_2$  hypothesis is obtained (table 7). The  $F_2$  phenotypes,  $R$  and  $I$ , are represented in approximately their observed proportions, and the ratio of all-resistant to segregating conforms to the calculated 1:8. The ratio of total resistant to total susceptible in the 40 segregating families conforms to the calculated 21:11 ratio based on an equal number of 3:1 and 9:7 families. The actual ratios observed in the separate  $F_3$  families were quite variable, but heterogeneity  $\chi^2$  cannot be used here. It is probable that considerable fluctuation of dominance was taking place in this cross, due perhaps to the presence of a single unstable gene from the tolerant parent.

#### TOLERANT $\times$ SUSCEPTIBLE

Of 21  $F_1$  plants tested in the greenhouse, 2 showed a degree of leaf flecking comparable with that on the Corbett Refugee (tolerant) parent and 19 showed no injury. One cross, Corbett Refugee  $\times$  Geneva Red Kidney, was tested in both field and greenhouse in the  $F_2$  generation, and a significant difference in the proportion of susceptible plants

was noted (table 8). Intermediate phenotypes that segregate out in the greenhouse usually fail to show up in the field. No significant difference was obtained in reciprocals, which were therefore combined.

Although great variability characterized the tolerant  $\times$  susceptible crosses (table 8), it should be observed that the tolerant parent was the same (Corbett Refugee) in five crosses, and probably is the source of any unstable genes. The sixth cross, with Great Northern as the tolerant parent, is unique in that susceptibility to gamma is dominant over tolerance or resistance, an observation that has since been verified in the  $F_1$  generation. An earlier instance of dominance of susceptibility was described in the study of beta inheritance.

A clue to the cause of variability in disease reaction is to be found in the Corbett Refugee  $\times$  Geneva Red Kidney data in which the cross and reciprocal were both represented in comparatively large numbers. No significant differences were observed between the cross and reciprocal, but a highly significant difference occurred between greenhouse and field data in both the cross and the reciprocal. It can be said with a reasonable degree of certainty, therefore, that environment is an especially important factor in reaction to anthracnose where certain genotypes are involved.

It is unlikely that the 14:2 ratio is one that might be expected to occur by chance. The  $F_2$  data presented are compounded of numerous samples acquired on different dates and from different individual parents. The 14:2 ratio recurred with remarkable constancy in the different samples of greenhouse data. It is probable, therefore, that a certain amount of fixity of gene action is involved in the 14:2 ratio and a hypothesis involving interaction of two susceptible genes (p. 14), would suffice to explain this peculiar expression of inheritance.

Of 75  $F_2$  plants of Corbett Refugee  $\times$  Geneva Red Kidney parentage classified as susceptible in the field, 53 were grown to maturity. The 53 families ranged in size from 9 to 232 and averaged 43 plants each. Of 1,082  $F_2$  plants classified as resistant in the field, 321 were grown to maturity. The 321 families ranged in size from 10 to 232 but averaged 56. A total of 20,274 plants are included in the  $F_3$  analysis.

Of the 53 families from plants susceptible in the field, 8 were definitely heterozygous. These are considered to be due to error in field classification. Sixteen other families contained a small proportion of resistant plants which is attributed to cross-pollination in the field (the  $R$  plants being of the  $F_1$  generation), known to occur to the extent of 5 percent or more under favorable circumstances. Families from parents susceptible in the field therefore segregated 45 homozygous susceptible to 8 heterozygous.

$F_3$  data obtained in greenhouses at the United States Regional Vegetable Breeding Laboratory, Charleston, S. C., with 321 families from resistant parents failed to confirm the 14:2 hypothesis for  $F_2$  greenhouse reaction obtained at the United States Horticultural Station, Beltsville, Md. On the contrary it is rather plain (table 8) that  $F_3$  families segregated according to a 15:1 type of inheritance, which would correspond with the  $F_2$  field data obtained at Beltsville. One irregularity in the 15:1 interpretation is the presence among 321 families of 8 all-susceptible families, whereas none were expected. The occurrence of 8 all-susceptible among 321 families indicates an error of 2 or 3 percent in field classification in the  $F_2$  generation.

Also, the distribution of segregating families is not the bimodal distribution that would be expected if only two classes were present (3:1 and 15:1); instead there is an excessively large number of families intermediate between 3:1 and 15:1 that fail to approximate either of those ratios (fig. 4). The multimodal distribution suggests that there may be as many as six segregating classes. However, considerable variability among progenies must be expected even from a regular 15:1 inheritance.

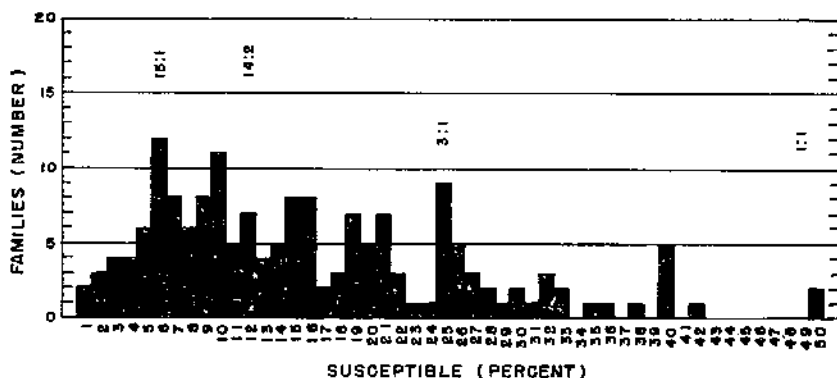


FIGURE 4.—Frequency distribution of 169  $F_3$  segregating families from the cross Corbett Refugee  $\times$  Geneva Red Kidney arranged according to percentage classes. Significant numerical ratios are superposed at their approximate percentage classes.

It is likely that certain genes, probably derived from the Corbett Refugee parent, are so susceptible to environmental effects that variability in anthracnose reaction occurs not only between greenhouse and field but also between greenhouses situated in different climatic areas. With such material one can scarcely hope to approach a correct analysis of the parental genotypes in respect to anthracnose reaction. It is probable, therefore, that the factorial interpretation cannot be applied to the Corbett  $\times$  Geneva Red Kidney cross inoculated with the gamma anthracnose fungus without introducing a number of dubious hypotheses.

#### SUSCEPTIBLE $\times$ SUSCEPTIBLE

Samples of  $F_2$  populations totaling 263 plants from 4 crosses of susceptible  $\times$  susceptible were all fully susceptible to gamma in the greenhouse. No field tests were made. The crosses were U. S. No. 1 Refugee  $\times$  Geneva Red Kidney, selection No. 1  $\times$  Geneva Red Kidney, Perry Marrow selection  $\times$  U. S. No. 1 Refugee, and Boston Marrow  $\times$  selection No. 2.

#### INTERPRETATION OF GAMMA

The assortment of ratios obtained in intervarietal crosses inoculated with beta is paralleled by the gamma data. The similar character of the ratios would seem to indicate that the same genetic principles are operating in the inheritance of resistance to both forms of the disease. For example, 3 pairs of independent factors are all that seem to be operating in any one cross; there is evidence of dominant factors both

for resistance and for susceptibility; the 62:2 ratio obtained with beta in the  $F_2$  generation of the Corbett Refugee  $\times$  Geneva Red Kidney cross (greenhouse data) is supported by the 14:2 ratio obtained in  $F_2$  with gamma with a similar deviation in  $F_2$  data; finally, if there are only 3 series of alleles, in order to account for the different ratios in different parental combinations there must be more than 2 alleles in each series. It is not surprising therefore to find that the system of 10 alleles in 3 series, which sufficed to explain the beta inheritance, would suffice also to explain the inheritance of reaction to gamma.

If the assumptions made regarding the anthracnose gene system have any basis in fact, there would seem to be a clear indication that, in any one bean variety, the genes that control reaction to beta and those that control reaction to gamma are identical, but that their influence on the host-parasite interaction is different in respect to the two forms of the pathogen. Proof that the same gene or genes are actually operating in the control of reaction to more than one form of the pathogen would be hard to obtain.

## INHERITANCE OF RESISTANCE TO DELTA

### RESISTANT $\times$ SUSCEPTIBLE

Eight crosses of resistant  $\times$  susceptible parents were tested with delta. Twenty-six  $F_1$  plants from three crosses were all resistant. Five of the eight crosses segregated 3:1 (table 9) in  $F_2$  and three crosses segregated 9:7 (table 10). Four of the 3:1 crosses and one of the 9:7 crosses were carried through  $F_3$ . The five 3:1 crosses still give a 3:1 ratio when combined, and no heterogeneity is indicated. The genes segregating are not necessarily the same in all five crosses, and it is conceivable that certain of them are more susceptible to environmental effects than others.

The  $F_3$  data for the 3:1 crosses conform satisfactorily to the monofactorial hypothesis at most points. Families from unclassified parents are the only reliably random samples, and in each case these approximate the 1:2:1 ratio of all-resistant to segregating to all-susceptible families (distribution  $\chi^2$ ). The measures of goodness of fit applied to the combined segregating families show them to vary far beyond the normal expectation. It is probable, however, that where variability in expression of a character is high, as in the case of disease reaction, one must especially rely on the distribution of the  $F_3$  families and place very little emphasis on the variations within those families.

The 9:7 ratios are represented in the  $F_3$  generation only by the Small White  $\times$  Great Northern cross. Over 1,000 families from this cross (including reciprocal) were tested in  $F_3$ . The comparatively large amount of  $F_3$  data was obtained in order to clarify the apparent effect of direction of cross on proportions of phenotypes evident in  $F_2$ . However, the  $F_3$  data revealed a certain amount of misclassification, and when an appropriate correction is applied to the original ( $F_2$ ) data the resulting ratios are brought much closer to a calculated 9:7 ratio (table 10), and the apparent difference between reciprocals becomes less. That a difference between reciprocals still exists is further indicated by the tendency for misclassification to occur to a greater extent in the susceptible  $\times$  resistant than in the resistant  $\times$  susceptible cross.



TABLE 9.—Monofactorial inheritance of resistance to delta in  $F_2$  and  $F_3$  generations of crosses resistant  $\times$  susceptible or the reciprocal

No. and cross	$F_2$ plants		$F_3$ families <sup>1</sup>							
	Observed segregation	$\chi^2$	Classification in $F_3$	All R	Segregating	All S	Distribution $\chi^2$	Population $\chi^2$ of $F_3$ segregating families	Heterogeneity $\chi^2$	Total $\chi^2$
1. Small White $\times$ Corbett Refugee.....	344 R: 116 S.....	<sup>1</sup> 0.003	Unclassified (Unclassified Class I.....	Number 18 6	Number 31 24	Number 11 9	<sup>3</sup> 0.900 <sup>2</sup> 2.538	<sup>1</sup> 0.809 <sup>2</sup> 32.039**	27.312 181.562**	28.120 213.601**
2. Small White $\times$ Robust and reciprocal.....	1,979 R: 645 S.....	<sup>1</sup> .224	Class I Class R and I Combined Unclassified.....	12 70 16	50 127 50	<sup>4</sup> 6 25	<sup>3</sup> 2.070	<sup>1</sup> .049 <sup>2</sup> .079 <sup>3</sup> 3.153 <sup>1</sup> .031	55.996 121.894**	56.046 121.925**
3. Small White $\times$ Boston Marrow and reciprocal.....	809 R: 264 S.....	<sup>1</sup> .070	Unclassified.....	21	39	18	<sup>3</sup> 2.228	<sup>2</sup> 24.277	57.164*	81.440**
4. Selection No. 3 $\times$ Boston Marrow and reciprocal.....	77 R: 33 S.....	<sup>1</sup> 1.212	Unclassified.....	61	144	63	<sup>3</sup> 1.889			
5. Selection No. 2 $\times$ Kentucky Wonder Wax.....	229 R: 65 S.....	<sup>1</sup> 1.161	Unclassified (Unclassified Class R and I.....	143	327		<sup>3</sup> 1.702			
Combined (5 crosses).....	3,438 R: 1,123 S.....	<sup>1</sup> .328								

<sup>1</sup> \* = Significant at 5-percent level, \*\* = Significant at 1-percent level.  
<sup>2</sup> Based on 3:1 ratio.

<sup>3</sup> Based on 1:2:1 ratio.  
<sup>4</sup> Omitted from  $\chi^2$  calculation.

<sup>5</sup> Based on 1:2 ratio.

TABLE 10.—Bifactorial inheritance of resistance to delta in  $F_2$  and  $F_3$  generations of crosses resistant  $\times$  susceptible or the reciprocal

No. and cross	$F_2$ plants <sup>1</sup>		$F_3$ (173 unclassified families)				$F_3$ (433 segregating families)	
	Segregation	$\chi^2$	All R	Segregating	All S	Distribution $\chi^2$	Resistant plants	Susceptible plants
6. Small White $\times$ Great Northern:								
Observed.....	3,841 R: 2,781 S.....	<sup>1</sup> 8.204**	Number 7	Number 86	Number 80	<sup>1</sup> 1.207	19,107	12,700
Adjusted for 4-percent escape.....	3,687.4 R: 2,934.6 S.....	<sup>1</sup> 8.41	10.8	86.5	75.7		20,873.4	10,033.6
Reciprocal:								
Observed.....	875 R: 455 S.....	<sup>1</sup> 48.794**						
Adjusted for 7-percent escape.....	813.8 R: 516.3 S.....	<sup>1</sup> 12.958*						
Direction of cross uncertain:								
Observed.....	286 R: 229 S.....	<sup>1</sup> .080						
Combined data:								
Observed.....	5,002 R: 3,465 S.....	<sup>1</sup> 27.371**						
Adjusted for 5.5-percent escape.....	4,726.9 R: 3,740.1 S.....	<sup>1</sup> 5.98						
7. Selection No. 3 $\times$ Great Northern and reciprocal:								
Observed.....	373 R: 340 S.....	<sup>1</sup> 4.330*						
8. Canadian Wonder $\times$ Corbett Refugee:								
Observed.....	133 R: 93 S.....	<sup>1</sup> 5.19						

<sup>1</sup> \* = Significant at 5-percent level, \*\* = Significant at 1-percent level.

Based on 9:7 ratio.

<sup>1</sup> Based on 1:8:7 ratio.

The only unbiased sample of  $F_2$  families is that from unclassified parents, and the calculated 1:8:7 ratio of all-resistant to segregating to all-susceptible families is closely approached (table 10). When the segregating families are separately analyzed, however, it is found that susceptible individuals are occurring in a proportion greatly in excess of that expected according to a 9:7 type of inheritance. Since the two expected classes of segregating families, 3:1 and 9:7, cannot be separated equably (see p. 18), a calculated ratio of 21:11 (12:4+9:7) is used for the whole population (table 10). The observed ratio deviates extremely from the 21:11, and the deviation was in the direction of excess susceptibles in all samples.

Finally, the frequency distribution of 433 segregating families, based on percent of susceptibles in each family (fig. 5), shows distinctly the expected bimodal curve with modes in the vicinity of 3:1 (25 percent) and 9:7 (44 percent). It is significant that the 9:7 portion of the distribution is definitely skewed in the direction of 7:9 and that a faint indication of a third modal class is present in the vicinity of 1:3, which may indicate a tendency toward reversal of dominance. Obviously something is upsetting the inheritance in this cross, and since the deviation is consistently in one direction the possibility of reversal of dominance seems likely. Such a hypothesis would imply that certain heterozygous genotypes, which often were observed to give an intermediate reaction in  $F_2$ , are under different environmental conditions falling into the fully susceptible class. The action of lethals could account also for the deviations in this cross, but no direct evidence of the presence of lethals was found.

The Small White  $\times$  Great Northern cross illustrates once again the difficulties in trying to impose a strict gene interpretation of disease reaction where there is an obvious shift in phenotype from resistant to susceptible or from susceptible to resistant as a result of differences in level of infection in different samples. It is doubtful if any system of modifiers, linkages, or gene interactions would explain adequately the kind of variability that is experienced in disease reactions. There seems to be a tendency for the inheritance of anthracnose reaction to conform to Mendelian principles, but the ordinary measures of probability will not encompass the degree of variability that apparently must be expected when dealing with disease reaction classes. It is assumed that the Small White  $\times$  Great Northern cross exhibits a 9:7 type of inheritance, because the many samples of data tend to vary around

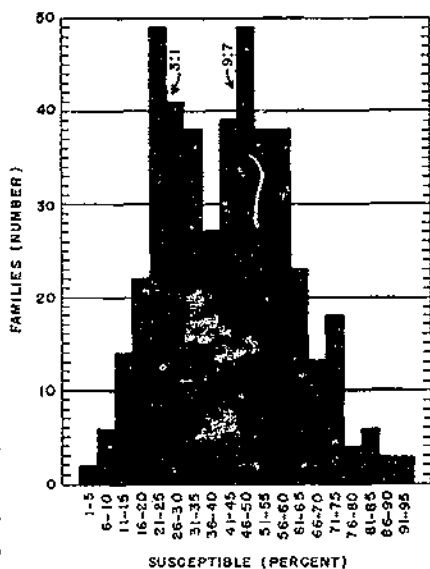


FIGURE 5.— Distribution into percentage classes of 433  $F_2$  segregating families from the cross Small White  $\times$  Great Northern and reciprocal. The modes approximate 3:1 and 9:7 classes.

that ratio and because no other simple factorial interpretation will explain the results to a greater satisfaction.

### SUSCEPTIBLE $\times$ SUSCEPTIBLE

Eight crosses of susceptible  $\times$  susceptible varieties were tested with the delta anthracnose fungus in the  $F_2$  generation. At the time these tests were made the natural supposition was that all progeny from such crosses would be susceptible to delta, and for that reason only small populations were sacrificed for the purpose (table 11).

A few apparently resistant plants might occur as a result of escape; plants with intermediate reaction, however, obviously were not escapes and it is probable that higher grades of reaction are actually segregating from certain susceptible  $\times$  susceptible crosses. Such a result is not unexpected, since the 9:7 ratios obtained in resistant  $\times$  susceptible crosses (table 10) imply that one pair of dominant factors for resistance to delta may be carried in susceptible plants. If several varieties susceptible to delta can carry among them different factors for resistance to delta, the appropriate intercrosses should produce a proportion of resistant segregants.

The actual ratios observed in table 11 are unimportant, because the populations are small. It may be borne in mind, however, that ratios of 1:1 and 1:3 are predicted from susceptible  $\times$  susceptible crosses in the hypothesis first suggested in the discussion of beta inheritance (p. 14).

TABLE 11.—Inheritance of resistance to delta in the  $F_2$  generation of crosses susceptible  $\times$  susceptible

No. and cross	Total plants	Observed segregation		
		Resistant	Intermediate	Susceptible
	Number	Number	Number	Number
1. Selection No. 1 $\times$ Geneva Red Kidney.....	10	0	0	10
2. Corbett Refugee $\times$ Perry Marrow.....	20	0	0	20
3. Boston Marrow $\times$ Great Northern.....	56	0	0	56
4. Great Northern $\times$ Perry Marrow selection.....	129	1	3	125
5. U. S. No. 1 Refugee $\times$ Geneva Red Kidney.....	30	2	8	20
6. Perry Marrow $\times$ U. S. No. 1 Refugee.....	77	5	15	56
7. Corbett Refugee $\times$ Geneva Red Kidney.....	70	17	15	38
8. Perry Marrow $\times$ Great Northern.....	10	10	0	0

### INTERPRETATION OF DELTA

According to the simplest explanation of a 9:7 inheritance, the resistant parent would be of the genotype  $AABB$  and the susceptible parent  $aabb$ . A 3:1 ratio would result if the susceptible parent were of the genotype  $AAbb$  or  $aaBB$ . However, due to the fact that two resistant parents (Canadian Wonder and Small White) give a 9:7 and 3:1 ratio, respectively, with the same susceptible parent (Corbett Refugee), it is necessary to suppose that there are at least two genotypes represented among the resistant parents; hence there should be involved at least three pairs of genes for delta resistance. It is interesting to note that the gene set-up proposed in explanation of beta inheritance is not excluded in the case of delta. An extension of table 5 would provide for a 9:7 ratio in the cross  $A'A'B'B'cc'$

$\times aabbc$  and  $A'A'B'B'c'c'$   $\times aabbc'$  and a 3:1 ratio in other appropriate combinations. Also the hypothesis anticipates the irregular recessive  $\times$  recessive data described in the preceding section.

## LINKAGE

There are only nine pairs of chromosomes in beans, and since genes governing anthracnose reaction are carried on at least three chromo-

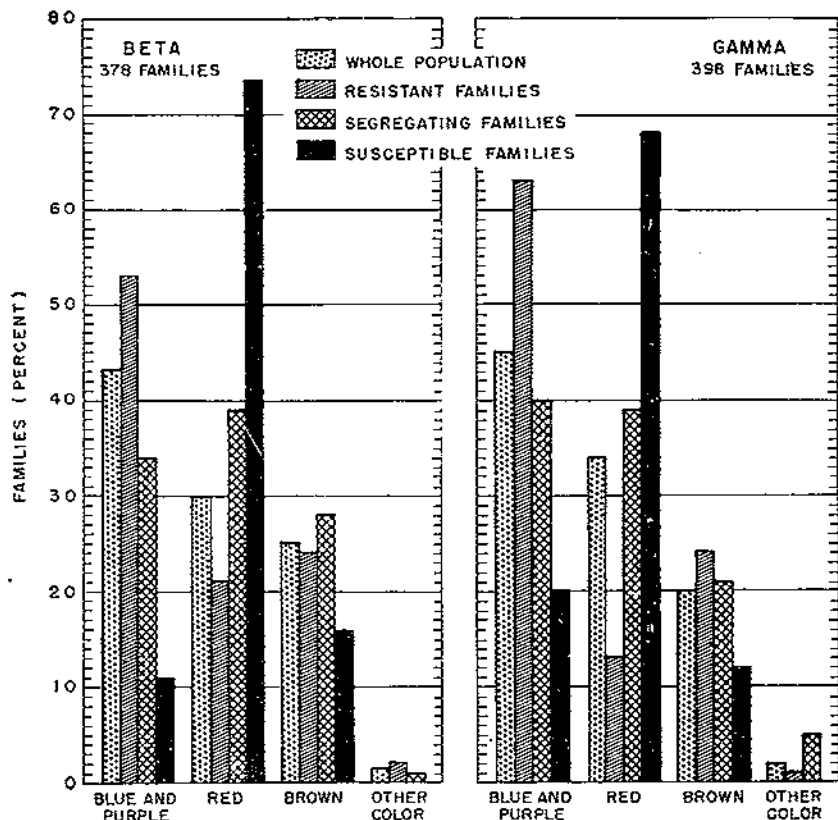


FIGURE 6.—Correlation between  $F_2$  seed-coat color and susceptibility to beta and gamma anthracnose fungi in the  $F_3$  generation of the cross Corbett Refugee  $\times$  Geneva Red Kidney and the reciprocal.

somes, the probability is high that linkage is involved in some of the intervarietal crosses made during the course of this study. Most of the irregularities observed in disease reaction, however, were of a sort that could hardly be due to linkage, and it is concluded that, in spite of probabilities in its favor, linkage is not involved to any important extent in the inheritance of anthracnose reaction.

In certain crosses data were taken on seed-coat color, among the few characters in addition to anthracnose reaction. Linkage was observed between red seed-coat color and susceptibility to the beta and gamma anthracnose fungi in the cross Corbett Refugee  $\times$  Geneva Red Kidney and the reciprocal. The involved genetics of both

characters (seed-coat color and anthracnose reaction) makes calculation of the actual percent linkage especially difficult by the usual methods, but the fact of its occurrence is demonstrated arithmetically in figure 6.

### DISCUSSION

It would seem to be self-evident in the field of plant breeding that any vegetable as highly developed and interbred as, for example, tomatoes, melons, peas, and beans would possess extreme intervarietal heterogeneity in respect to genotypes, and that any study of inheritance based on the results of a single intervarietal cross, or even few crosses, would set forth a small fraction of the information pertaining to the species. The present study, based on only 30 intervarietal crosses and representing only 15 out of a possible 200 or more varieties of beans, amply demonstrates the heterogeneity of genotypes in respect to one character, anthracnose reaction.

Many difficulties were encountered in trying to apply a factorial interpretation to the bean anthracnose data. Certain crosses would not conform to any such interpretation. The question arose: should the factorial interpretation be rejected because some crosses do not conform to any simple Mendelian type of inheritance? The situation is perhaps similar with many plant diseases. Although it is probable that disease reactions are subject to gene control, the tendency of phenotypes to shift from one reaction class to another in response to differences in level of infection at times would render a factorial interpretation practically invalid. There has been proposed here a factorial interpretation that will account for most of the irregularities observed in the bean anthracnose data, but the future usefulness of the hypothesis remains to be determined. It is assumed that a certain cross exhibits a 15:1 type of inheritance, for example, because many samples of data tend to vary around that hypothesis and because no other interpretation will explain the results with a greater degree of satisfaction. At the same time it must be observed that the ordinary measures of probability do not countenance the degree of variability that apparently is to be expected when dealing with disease reaction classes.

Genetic studies based on one or a few intervarietal crosses have often led to an impression that the characters in question are controlled by one or two simple Mendelian factors when a broader survey of parental material might reveal many exceptions. The earliest study reported on the inheritance of resistance to anthracnose in beans was based on five intervarietal crosses involving six varieties (6, 7). Resistance to alpha anthracnose was found to be controlled by a single dominant Mendelian factor. Dihybrid ratios were obtained only when alpha and beta were both present in the inoculum. Fortunately the research was continued, and, in two interesting and important papers (8, 9), Schreiber was able to give evidence of the operation of not less than eight pairs of factors in the determination of anthracnose reaction.

Schreiber's conclusions were based primarily on 2 intervarietal crosses involving 3 parental varieties, with a total  $F_2$  population of 1,032 and  $F_3$  plants to the number of 5,520. His technique was to inoculate samples with 1 physiological form of *Colletotrichum lindemuthianum* and with mixtures of 2, 3, and 4 physiological forms. A

monohybrid ratio was obtained in the sample inoculated with a single culture and dihybrid, trihybrid, etc., ratios when 2 or more strains were used in mixed inoculum.

The present authors were led to reject the mixed-inoculum technique because in some preliminary experiments two physiological forms (alpha and beta) in mixed suspension seemed to experience an interaction which influenced the host response. A phenomenon probably of a similar nature has been described by Leitzke (5). The experiments have not continued far enough to determine the nature of the interaction but only far enough to demonstrate that an important element of uncertainty exists in the use of mixed cultures of the anthracnose fungus. The writers were not inclined to reject Schreiber's conclusions, but it seemed desirable in the projected research to analyze the inheritance of resistance to each physiological form separately.

In respect to the likelihood that there are a relatively large number of Mendelian factors concerned in the inheritance of anthracnose reaction the present data tend to confirm Schreiber's findings, but uncertainty exists, at least in some instances, as to whether the writers are dealing with simple Mendelian factors only or with a complex of cytoplasmic and external environmental factors as well.

Contrary to the previous observations on the inheritance of anthracnose resistance (1, 6, 7, 8, 9), all of which agree that resistance to any single form of *Colletotrichum lindemuthianum* is controlled by a single dominant gene, the present results bring to light a variety of dihybrid and trihybrid types of inheritance as well. Several of these were studied on an extended scale and leave no reason to suppose that they represent only deviations from simpler Mendelian ratios but that they faithfully reflect a complex mode of inheritance.

Three forms of bean anthracnose were investigated separately, and the conclusions, based only on those crosses that were represented by both  $F_2$  and  $F_3$  data, are as follows: Control of reaction to each of the 3 forms of anthracnose rests in not less than 3 pairs of alleles in not less than 3 allelic series. Supplementary evidence based on  $F_2$  data alone or on  $F_3$  data alone indicate that in addition to the 3 dominant resistant genes there is 1 dominant susceptible gene operating in relation to forms beta and gamma. Also a peculiar 14:2  $F_2$  ratio, apparently well-substantiated by  $F_3$  data, requires the action of an additional gene pair to explain fully the inheritance of reaction to gamma. A tentative hypothesis involving 10 genes in 3 allelic series will apparently satisfy all the data.

The very existence of a large number of physiologic forms of a parasite would seem to call for a corresponding multiplicity of genotypes among the differential varieties of the host. This assumption is borne out in the data for 3 physiologic forms of the anthracnose fungus on 15 varieties and selections of garden bean. The data permit assigning a theoretical genotype to only a few of the parental varieties.

Table 12 illustrates how the genotype of 5 varieties will need to be expressed in order to explain the ratios obtained both with beta and with gamma anthracnose pathogen. Corbett Refugee reacts alike to forms beta and gamma, and its presumed genotype is the same for both. Great Northern is tolerant to both beta and gamma, and its calculated genotype shifts in one series from  $c$  to  $C'$ , both of which symbolize susceptible genes that differ only in their interactions with

two other members of the same allelomorphous series (see p. 14). The remaining three varieties are resistant to form beta and susceptible to gamma and in each case there is a shift in symbolic expression from a resistant to a susceptible genotype.

TABLE 12.—Hypothesized genotypes of parental bean varieties in respect to the beta and gamma forms of anthracnose

Variety or selection	Pathogen form	Genotype
Corbett Refugee	Beta	AAbbcc
	Gamma	AAbbcc
Great Northern	Beta	A'A'BBcc
	Gamma	A'A'BBc'C'
Perry Marrow selection	Beta	A'A'B'B'CC
	Gamma	A'A'bbCC
Geneva Red Kidney	Beta	A'A'BBc'c'
	Gamma	aaB'B'c'c'
Canadian Wonder	Beta	aaB'B'c'C'
	Gamma	A'A'bbcc

Do these different denominations mean that a different set of genes is operating in the reactions to the two forms of the pathogen, or are the same genes reacting differently to different environments furnished by the two strains of the pathogen? It can be conceived that a comparatively simple system of fixed genes could control reaction to many or all forms of the parasite, and that their symbolic denomination alone would need to be altered in order to express the possible different types of host-parasite interaction.

### SUMMARY

The inheritance of resistance to three physiologic forms of *Colletotrichum lindemuthianum* (beta, gamma, and delta) has been studied in intervarietal crosses of *Phaseolus vulgaris*. Fifteen parent varieties and selections were used in 30 combinations. Inoculations were made in field or greenhouse on 145 first-, about 32,600 second-, 108,000 third-, and a considerable number of fourth-generation plants.

Parent varieties were resistant, tolerant, or susceptible. In crosses of resistant  $\times$  tolerant and resistant  $\times$  susceptible, resistance was always dominant. In two crosses of tolerant  $\times$  susceptible, susceptibility was dominant in the F<sub>1</sub> generation and subsequent generations.

A few resistant  $\times$  resistant crosses segregated a proportion of susceptibles; likewise certain susceptible  $\times$  susceptible crosses segregated a proportion of resistant plants. It is suggested that such crosses offer the quickest way to ascertain the existence of heterogeneity of genotypes in host species.

Monohybrid and dihybrid ratios were obtained with all 3 forms of the pathogen, and trihybrid ratios also were obtained with 2 forms. A system of 10 genes in 3 allelomorphous series, involving both duplicate and complementary genes for resistance, 1 dominant gene for susceptibility, and gene interactions at 3 points, is proposed as the simplest Mendelian hypothesis that will coordinate all the data for beta and gamma anthracnose. A simpler explanation (3 independent pairs of genes) would suffice for delta, but the more complex gene system is not thereby excluded.

The hypothesis calls for 11 susceptible and 25 resistant parental genotypes of which 2 susceptible and 5 resistant were apparently realized in the beta data alone.

In certain instances differences were noted in the proportion of susceptible segregants as between greenhouse and field, between second and third generations, and between reciprocals. It is considered that one gene could be responsible for all the irregularities.

It could be presumed that the same genes are operating in respect to all three forms of the pathogen, but that they exercise a modified or reversed function, depending upon the form to which the host is exposed. Although the genotype of any individual is strictly speaking unchangeable, it would be necessary to express the disease reaction genotype by different symbols expressive of the host-parasite interaction. On this basis the number of genes involved in anthracnose reaction is not necessarily proportional to the number of physiologic forms of the parasite.

Linkage was observed in one cross between red seed-coat color and susceptibility to beta and gamma anthracnose.

### LITERATURE CITED

- (1) BREDEMANN, G., and DOORNKAAT-KOOLMAN, HEINZ TEN.  
1927. ZUR IMMUNITÄTSZÜCHTUNG BEI PHASEOLUS VULGARIS GEGENÜBER COLLETOTRICHUM LINDEMUTHIANUM UND SEINEN BIOTYPEN. Ztschr. f. Pflanzenzücht. 12: [209]-217.
- (2) BUDDE, ALOIS.  
1928. UEBER RASSENBILDUNG PARASITISCHER PILZE UNTER BESONDERER BERÜCKSICHTIGUNG VON COLLETOTRICHUM LINDEMUTHIANUM (SACC. ET MAGN.) BRI. ET CAV. IN DEUTSCHLAND. Forsch. auf dem Geb. Pflanzenkrank. u. Immunität im Pflanzenz. 5: [115]-147, illus.
- (3) DOORNKAAT-KOOLMAN, H. TEN.  
1927. DIE BRENNFLECKENKRANKHEIT DER GARTENBOHNE IM LICHT DER VERERBUNG. VERSUCHE ZUR IMMUNITÄTSZÜCHTUNG BEI PHASEOLUS VULGARIS GEGENÜBER COLLETOTRICHUM LINDEMUTHIANUM [SACC. & MAGN.] UND SEINEN BIOTYPEN. Forsch. auf dem Geb. Pflanzenkr. u. Immunität im Pflanzenz. 4: 112-225, illus.
- (4) KOOLMAN, H. N.  
1931. MONOGRAPH ON THE GENETICS OF PHASEOLUS (ESPECIALLY PH. VULGARIS AND PH. MULTIFLORUS. Bibliog. Genetica 8: [295]-413, illus.
- (5) LEITZKE, BENNO.  
1937. INFektionsversuche mit Haferflugbrand-Sporen-Gemischen. Phytopath. Zeitschr. 10: [504]-553, illus.
- (6) McROSTIE, G. P.  
1919. INHERITANCE OF ANTHRACNOSE RESISTANCE AS INDICATED BY A CROSS BETWEEN A RESISTANT AND A SUSCEPTIBLE BEAN. Phytopathology 9: [141]-148.
- (7) ———  
1921. INHERITANCE OF DISEASE RESISTANCE IN THE COMMON BEAN. Amer. Soc. Agron. Jour. 13: 15-32.
- (8) SCHREIBER, FRITZ.  
1932. RESISTENZ-ZÜCHTUNG BEI PHASEOLUS VULGARIS. Phytopath. Zeitschr. 4: [415]-454.
- (9) ———  
1933. RESISTENZ-ZÜCHTUNG BEI BUSCHBOHNEN. Kühn-Arch. 38: [287]-292.



**END**