Inheritance of Resistance to Cercospora Leaf Spot in Sugarbeet[1]

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Received for publication March 26, 1970

Despite the importance of resistance to leaf spot of sugarbeet, caused by *Cercospora beticola* Sacc., and the attention it has received in breeding programs, there have been few reports of actual experiments designed to provide information concerning the inheritance of resistance. Although experimental evidence is lacking, resistance is belived to be a quantitative character, apparently governed by several pairs of genes and subject to a considerable amount of environmental influence (1,3,5,7)[3].

Knowledge of the heritability of a character is important to the breeder, since it indicates the extent and rate of improvement attainable through selection. The extent of genetic segregation in advanced generations of a cross is a reflection of the heritability of the character in question. Lush (4) defined heritability in two ways. In the broad sense, heritability refers to the ratio of genetic variance to total variance. In the narrow sense, heritability is defined as the ratio of additive genetic variance to total variance. Using *Beta maritima* as a source of leaf spot resistance, Bilgen *et al.* evaluated the backcross method of plant breeding as a tool for transferring the higher resistance of *B. maritima* to sugarbeet. They concluded that estimates of genetic variation and heritability ratios for leaf spot resistance were relatively low in open-pollinated backcross populations, probably because of over estimation of environmental variances.

The present investigation is intended to provide information on the heritability of resistance to *Cercospora* and to provide an estimate of the minimum number of genes governing resistance.

Materials and Methods

The following sugarbeet populations were used in this study:

1. 51-319 Leaf spot susceptible (LSS)
2. 52-334 Leaf spot susceptible (LSS)
3. US 201 Leaf spot resistant (LSR)
4. 51-319 × 52-334, F_1
5. US 201 × 51-319, F_1
6. US 201 × 52-334, F_1

[1] Report of research conducted by the Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, in cooperation with the Colorado Agricultural Experiment Station and the Beet Sugar Development Foundation; publication approved by the Director, Colorado Agricultural Experiment Station, as Scientific Series Article No. 1507.

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[3] Numbers in parentheses refer to literature cited.

7. 51-319 × 52-334, F_2
8. US 201 × 51-319, F_2
9. US 201 × 52-334, F_2

Populations 1 and 2, inbred lines developed by the late G. W. Deming at Fort Collins, are quite homozygous. Homozygosity of population 3 is high for leaf spot resistance and relatively low for various other characters.

The nine populations were grown in the field in 1959 and 1960, in a randomized complete block design with 40 replications each year. Plots consisting of single rows 15 feet long in 1959 and 14 feet long in 1960, were alternated with rows of a leaf spot susceptible sugarbeet line. Rows were 20 inches apart. Plants were thinned to a spacing of 10 to 12 inches within the row. All plants in the entire experimental area were inoculated with a spore suspension prepared from diseased sugarbeet leaves collected the preceding year. Supplemental sprinkling of the field, in addition to normal furrow irrigation, was used to aid in developing a leaf spot epidemic. Visual leaf spot ratings were made on 8 individual, consecutive plants in each plot at the peak of leaf spot development each year. The scale used for leaf spot ratings was "0" for no leaf spot and "10" for complete defoliation.

Broad sense heritability estimates for resistance to leaf spot were calculated by using (Variance F_2 − Variance Pooled Parents) ÷ Variance F_2 (2,4,8). The environmental variance in the heritability formula which is the Variance of the Pooled Parents was estimated in two ways. First, the variances of the two inbred parents directly involved in the F_2 cross were pooled. Second, the variances of all three parents in the study were pooled to give the environmental variance estimate. In all cases where variances were pooled, an F test was used to determine homogeneity of variances (6).

Variances used in calculating heritability estimates and in gene number estimates were obtained by calculating the variance within single plots and dividing the sum of the single-plot variances by 40 (number of replications) for a given population. This method excludes the variation due to replication and that due to the interaction of population × replications. These total within-plot variances estimate the genetic plus environmental variation for segregating populations and the environmental variation for nonsegregating populations.

Results and Discussion

The leaf spot ratings for parental, F_1, and F_2 generations are presented as frequency distributions in histogram form in Figures 1 and 2. In 1959 the 320 plants of the resistant US 201 parent ranged from 1 to 4 on the 0 to 10 leaf spot scale with a mean of 1.6.

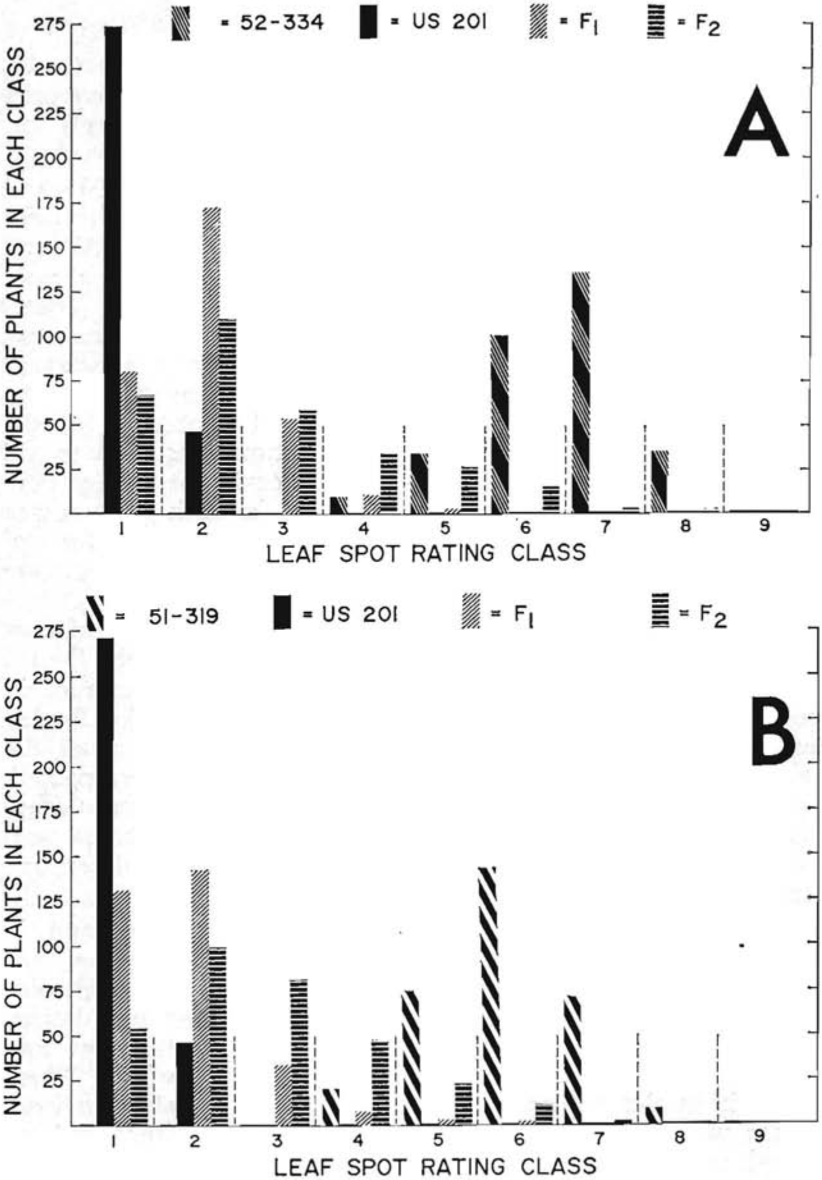

Figure 1.—Distribution of leaf spot resistant US 201 and 2 susceptible inbred parents and their F_1 and F_2 progenies in 1959: A) susceptible parent 52-334; B) susceptible parent 51-319.

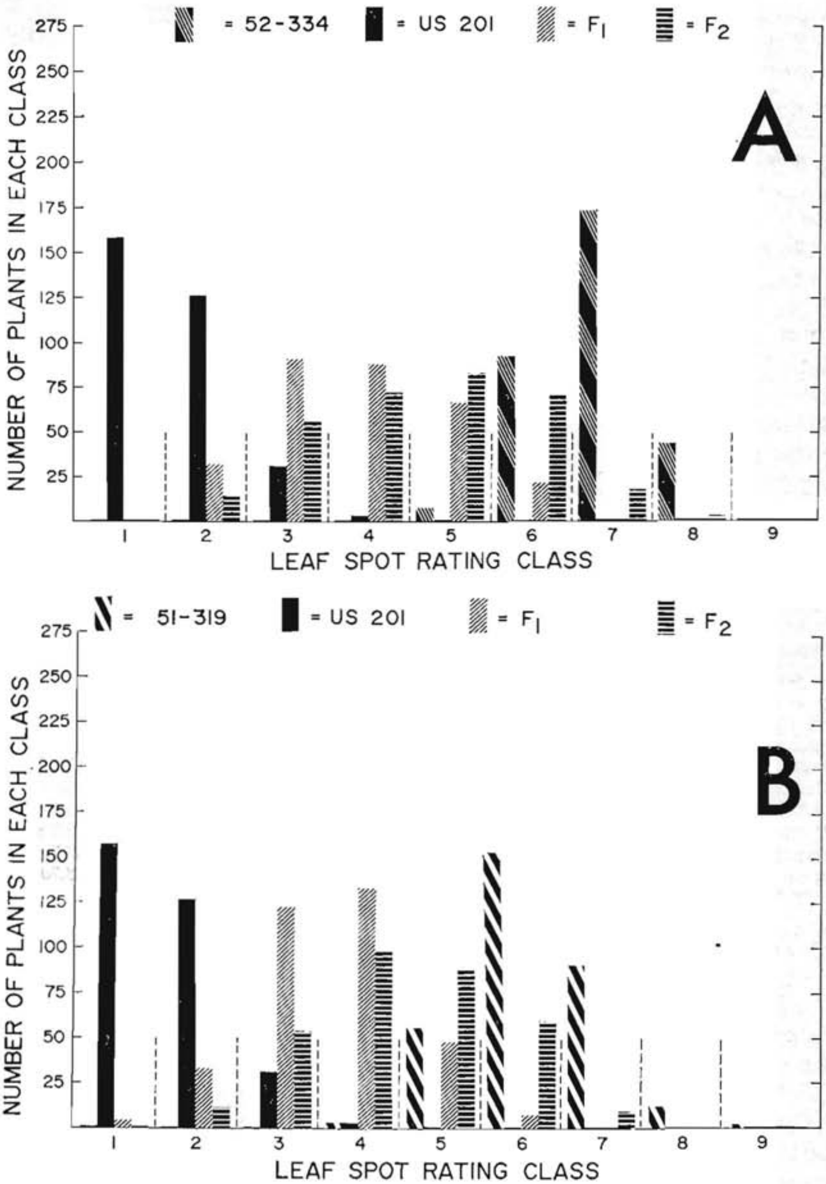

Figure 2.—Distribution of leaf spot resistant US 201 and 2 susceptible inbred parents and their F_1 and F_2 progenies in 1960: A) susceptible parent 52-334; B) susceptible parent 51-319.

The susceptible 51-319 parent plants varied from 4 to 9 and had a mean of 6.2. The susceptible 52-334 parent plants ranged from 5 to 8 with a mean of 6.8. In 1960, US 201 ranged from 1 to 2 with a mean of 1.1. The 51-319 plants varied from 4 to 8 with a mean of 5.9. The 52-334 plants varied from 4 to 8 with a mean of 6.5. Since the parents were inbreds, and thus presumably highly homozygous in leaf spot resistance or susceptibility, the plant-to-plant variation within each inbred is considered to be environmental. Consequently, a considerable degree of variation, ranging from as much as 4 to 9 may be caused by environmental influences alone. The average leaf spot ratings obtained for the parental inbreds, and for the F_1 and F_2 populations grown in 1959 and 1960, are summarized in Table 1. The level of infection in all populations was higher in 1959 than in 1960. The mean differences between the parents in 1959 was 4.6 for 51-319 vs. US 201 and 5.2 for 52-334 vs. US 201 (Table 1). The mean differences in the parents in 1960 was 4.8 for 51-319 vs. US 201 and 5.4 for 52-334 vs. US 201.

Table 1.—Average and range of leaf spot ratings for parental inbreds, F_1, and F_2 populations (320 plants per population) based on a 0 to 10 scale with 0 indicating no leaf spot and 10 indicating complete defoliation.

	1959		1960	
Population	Range	Mean	Range	Mean
51-319 (LSS)	4 to 9	6.2 b[1]	4 to 8	5.9 b
52-334 (LSS)	5 to 8	6.8 a	4 to 8	6.5 a
US 201 (LSR)	1 to 4	1.6 h	1 to 2	1.1 g
51-319 × 52-334, F_1	3 to 8	5.5 d	3 to 8	5.1 d
US 201 × 51-319, F_1	1 to 6	3.6 g	1 to 6	1.8 f
US 201 × 52-334, F_1	2 to 6	3.9 f	1 to 5	2.0 f
51-319 × 52-334, F_2	3 to 8	5.8 c	1 to 8	5.4 c
US 201 × 51-319, F_2	2 to 7	4.5 e	1 to 7	2.8 e
US 201 × 52-334, F_2	2 to 8	4.6 e	1 to 8	2.7 e
Mean		4.72[2]		3.70

[1] Any means within a year not followed by the same letter are significantly different at the .05 level.

[2] Significantly different from 3.70 at the .01 level.

In 1959 the means of the resistant by susceptible F_1 hybrids were between the values obtained for the parents, although they were somewhat below the arithmetic averages of the parents (Table 1). In 1960 the means of the resistant by susceptible F_1 hybrids were also between the parents; but the mean of US 201 × 51-319 (1.8) and the mean of US 201 × 52-334 (2.0) were considerably lower than the arithmetic average of the parents (Table 1).

The F_2 plants from US 201 × 52-334 showed a continuous range from 2 to 8 in 1959 and from 1 to 8 in 1960. The F_2 plants from US 201 × 51-319 ranged from 2 to 7 in 1959 and from 1 to 7 in 1960. These distributions are typical of quantitative inheritance. Probably the most valuable genetic information that can be gained from the data is an estimate of the number of genes involved and an estimate of the heritability of resistance.

Number of Genes Involved

Since it was obvious from distribution of the F_2 plants that resistance behaves as a quantitative character, and that no conventional Mendelian ratio was expected, it was not possible to make an exact determination of the number of genes by which the parents differed. The Castle-Wright formula,

$D^2 \div 8$ (Variance F_2—Variance F_1), is a

commonly used statistical method for estimating the minimum number of genes governing a quantitative character (9). In the formula, D refers to the mean difference between the parents. Application of the formula to the 1959 and 1960 data gave an average estimate of 4.77 for US 201 × 51-319 and 4.50 for US 201 × 52-334 (Table 2). This estimate is interpreted as indicating that at least 4 or 5 pairs of genes, and perhaps more, were involved in determining the mean difference between resistant and susceptible parents. The difference in the gene number estimates between 1959 and 1960 (Table 2) may be attributed to the difference in the severity of the leaf spot epidemic between 1959 and 1960. The lower gene number estimates for 1960 coincide with the lower average leaf spot ratings of 1960 (Table 1). These results may indicate that, in the epidemic of lower intensity (1960), some genes were not functioning or were functioning at a much lower level than others.

Table 2.—The estimated number of gene pairs controlling resistance to *Cercospora* leaf spot as determined from resistant × susceptible crosses.

Cross	Year		Combined data
	1959	1960	1959 & 1960
US 201 × 51-319	6.31	3.90	4.77
US 201 × 52-334	6.44	3.55	4.50

The Castle-Wright formula assumes equal effects of the genes involved, additive gene action, absence of dominance, and that one parent contributes only genes with plus effects and the other only genes with minus effects. Violation of any of the assumptions minimizes the estimate and leads to an underestimation of gene number. In addition, sampling error in measuring D and the variance of the F_1 and F_2 may lead to an overestimation or underestimation of gene number. Without doubt, some of the assumptions underlying use of the formula were violated. However, an estimate of 4 pairs of genes must be taken as the minimum number controlling leaf spot resistance in the sugarbeet material used in this study.

The mean difference in the leaf spot ratings of susceptible and resistant parents for the 2-year period was 5.0. If the difference were controlled by 4 pairs of genes, the average contribution per pair of genes would be 1.25 units on the visual grading scale. If the difference were governed by 5 pairs of genes, the average effect per pair would be 1.0 unit.

Heritability of Resistance

Variances of the parents and F_2 populations provide a means of estimating heritability of resistance, or the relative proportion of variation in the segregating populations which is genetic. This information can be used in determining how effective selection for high leaf spot resistance among individual F_2 plants will be.

The mere fact that the F_2 populations were a great deal more variable than the homozygous parents (Table 3) is evidence that a high proportion of the variation among F_2 plants was genetic. The statistical measure of the degree to which the F_2 variance exceeds the average variance of the parents is used as a measure of heritability, on the assumption that the difference is an indication of the genetic variance in F_2. A summary of these broad sense heritability values for resistance to leaf spot is presented in Table 4. The heritability values for the two years ranged from 60 to 71%. These values are relatively high and provide additional evidence that a high proportion of the variation among F_2

Table 3.—Within-population variances of leaf spot resistance ratings for nine populations grown in 1959 and 1960.

	Population	1959	1960	Mean[1]
	51-319	.455965	.679015	.567490
Parents	52-334	.380355	.683925	.532140
	US 201	.429470	.121880	———
	51-319 × 52-334	.582585	.569645	.576115
F_1's	US 201 × 51-319	.696868	.633935	.665401
	US 201 × 52-334	.886898	.407600	———
	51-319 × 52-334	.749993	1.006693	.878343
F_2's	US 201 × 51-319	1.108480	1.362055	1.235267
	US 201 × 52-334	1.406250	1.408933	1.407591
Coefficient of variation (%)		11.4	15.5	

[1] Homogeneity of variances between years was tested and only those variances which were homogeneous were averaged.

Table 4.—Broad sense heritability estimates (%) for leaf spot resistance using two and three parents to estimate the environmental variance.[1]

	1959		1960	
Cross	2 inbred parents	3 inbred parents	2 inbred parents	3 inbred parents
US 201 × 51-319	60.06	61.93	70.59	63.66
US 201 × 52-334	71.20	69.99	71.40	64.87

[1] Heritability estimates were computed based on the mean variance of two inbred parents of the indicated cross and on all three inbreds used in the study.

plants was genetic in nature. It must be emphasized, however, that this broad sense estimate of heritability is not an exact measure of the effectiveness of selection in the F_2, but that it is suggestive of the positive relationship between phenotype and genotype of the F_2 plants. Standard errors were not computed for heritability estimates derived by this method because some of the statistical theory necessary for computing these confidence limits has not been developed.

Since narrow sense heritability largely includes only the average effects of genes transmitted additively from parent to progeny, the magnitude of additive variance and heritability has its use in accurately predicting progress through selection in segregating populations. In the present study it was not possible to obtain a narrow sense heritability estimate. The broad sense estimates obtained, by definition, may include all types of gene action. The skewed distributions of the F_1 toward the resistant side of the scale (Figures 1 and 2) and the resistant $\times$ susceptible F_1 means (Table 1) suggest that some non-additive gene action (dominance, overdominance, or epistasis) was present.

Further, judging by the slow selection progress generally experienced by breeders, there would appear to be an apparent contradiction between the high heritability estimates of this study and realized selection progress. One explanation for high heritability estimates and slow selection progress could be the presence of a considerable portion of non-additive gene action.

To further explain the inheritance of leaf spot resistance, we are planning experiments to estimate the additive genetic variance and the degree of dominance in the F_2 hybrid material of this study, and then to compare predicted genetic advance with actual advance by selection.

Summary

Estimates of the heritability of resistance to *Cercospora* leaf spot in sugarbeet and the number of genes controlling resistance were made by means of one leaf spot resistant and two susceptible lines, three F_1 populations, and three F_2 populations. Individual-plant leaf spot ratings were made on a total of 2,880 plants in a randomized block experiment with 40 replications in each of 2 years.

Results indicated that a minimum of 4 or 5 pairs of genes control resistance to leaf spot and that, under less severe epidemic conditions, some genes may fail to function or function at a much lower level than others. Broad sense heritability estimates indicated that 60 to 71% of the variation in the F_2 populations was genetic in nature. Frequency distributions of the F_1 and F_2

populations, and the means of the F_1 and parental populations, suggested that part of this genetic variation was due to non-additive gene action.

Acknowledgments

The authors are indebted to the late Dr. LeRoy Powers, Principal Geneticist, and to Mr. Joseph A. Elder, Agricultural Research Technician (retired), Crops Research Division, Agricultural Research Service, for valuable assistance in this study.

Literature Cited

(1) BILGEN, TALAT, J. O. GASKILL, R. J. HECKER, and D. R. WOOD. 1969. Transferring *Cercospora* leaf spot resistance from *Beta maritima* to sugarbeet by backcrossing. J. Am. Soc. Sugar Beet Technol. 15: 444-449.

(2) BURTON, G. W. and E. H. DEVANE. 1953. Estimating heritability in tall fescue *(Festuca arundinacea)* from replicated clonal material. Agron. J. 45: 478-482.

(3) COONS, G. H., F. V. OWEN, and DEWEY STEWART. 1955. Improvement of the sugarbeet in the United States. Adv. in Agron. 7: 104-108.

(4) LUSH, J. L. 1949. Heritability of quantitative characters in farm animals. Proc. Eighth Int. Cong. Genetics. 1948. Hereditos Suppl. 356-375.

(5) MARGARA, J. and H. TOUVIN. 1956. Selection de betteraves sucrieres resistantes au *Cercospora*. (Selection of sugarbeets resistant to *Cercospora*). Compt. Red. Acad. Agr. France 42: 71-73.

(6) STEEL, R. G. D. and J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., New York.

(7) STEWART, DEWEY. 1948. The damages induced by a severe epidemic of *Cercospora* leaf spot on susceptible and resistant varieties of sugarbeets. Proc. Amer. Soc. Sugar Beet Technol. 5: 528-530.

(8) WEBER, C. R. and B. R. MOORTHY. 1952. Heritable and nonheritable relationships and variability of oil content and agronomic characters in the F_2 generation of soybean crosses. Agron. J. 44: 202-208.

(9) WRIGHT, S. 1921. Systems of mating. Genetics 6: 116-178.