Selection for Minor Gene Resistance to *Albugo candida* in a Rapid-Cycling Population of *Brassica campestris*

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ABSTRACT

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Three cycles of selection for resistance to *Albugo candida* race 2 were conducted within a rapid-cycling population of *Brassica campestris* that was devoid of major resistance genes. Both mass selection and selection between and within half-sib families were effective in accumulating minor genes conferring reduced pathogen sporulation. Sporulation ratings declined linearly from 4.2 in cycle 0 to 1.3 in cycle 3 of half-sib family selection and 0.95 in cycle 3 of mass selection. Evaluation of testcross generations from cycle 3 resistant × cycle 0 susceptible crosses failed to discriminate segregation of individual factors contributing to the accumulated resistance. Estimates of gene number and the degree of dominance were demonstrated to be dramatically influenced by changes in scaling of the sporulation ratings used.

Additional key words: polygenic resistance, quantitative resistance, response to selection.

Albugo candida (Pers.) Kuntze is an obligate parasite that exhibits a wide host range within the Cruciferae. Although pathogen isolates may successfully infect more than one host species, biological races have been described based on host specificities (11,15). Single, dominant genes for immunity or hypersensitive resistance to race 1 have been described in *Raphanus sativus* L., the host species from which race 1 was collected (21), and for race 2 collected from *Brassica juncea* (L.) Coss. in the host species: *B. nigra* (L.) Koch, *B. campestris* L., and *B. carinata* A. Br. (1). Intermediate levels of susceptibility to race 2 also have been reported in *B. campestris* by Pound and Williams (15) who found that some *B. campestris* individuals varied for amount as well as location of sporulation. They concluded that more than a single gene in the host must be involved in resistance based on continued segregation for susceptibility after two generations of selfing host plants. Thus, despite the *B. juncea* source of *A. candida* race 2, both major and minor genes in *B. campestris* appear to influence its reaction to race 2 of *A. candida*.

Selection for increased levels of host resistance has been effective in several pathosystems that exhibit a continuous range of disease phenotypes (4,7,8,17). Investigations into host response in other pathosystems also indicate a heritable basis for the continuous variation observed in disease phenotypes (6,13).

The purpose of this investigation was to evaluate the effectiveness of selection in accumulating favorable minor genes for resistance to *A. candida* race 2 within a susceptible *B. campestris* population. Minor genes were considered to be those that influenced disease reaction but were singly ineffective in preventing sporulation of the pathogen. A secondary objective was to compare the effectiveness of two alternative selection schemes in accumulating resistance genes. Finally, progeny were evaluated from a series of biparental matings between an original susceptible individual and selected resistant individuals to characterize the genetic basis of the accumulated resistance. The rapid generation time in the population facilitated the development of this polygenic resistance system and should benefit subsequent investigations into the behavior and mechanisms of minor gene resistance.

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MATERIALS AND METHODS

Inoculation and evaluation. All disease evaluations were conducted under controlled conditions. Seeds of the host were sown in flats filled with Jiffy-mix, and seedlings were maintained in a growth chamber at 24 C with continuous illumination at a photon flux density of 250 μmol $s^{-1}m^{-2}$ from Sylvania cool-white fluorescent bulbs with a Plexiglas barrier. Five days after sowing, seedlings were inoculated with a suspension of zoospores of *Albugo* in distilled water (concentration adjusted to $1-2 \times 10^5$ zoospores per milliliter). Inoculum increase, storage, and preparation was as described by Delwiche and Williams (1,19). To maximize uniformity of inoculation, a micropipette was used to apply four 10-microliter inoculum droplets to the cotyledons of each seedling. The inoculum flask was held in ice water and agitated to maintain uniform zoospore dispersal during inoculation.

Inoculated seedlings were placed in a dark incubation chamber at 15 C and 100% RH for 8–12 hr, then returned to the growth chamber. Seedling disease reactions were scored 7 days after inoculation using a subjective scale of estimated sporulation values from 0 to 9, with 0 representing no sporulating pustules and 9 representing the maximum proportion of the cotyledonary surface covered with pustules. The rating attempted to characterize only the apparent amount of sporulating area, without regard to the cotyledon surface (abaxial or adaxial) supporting the sporulation.

Establishment of a susceptible host population. A heterogeneous population of rapid-cycling *B. campestris*, CrGC-1, was obtained from the Crucifer Genetics Cooperative (19,20) and provided the plants that originated the base population for this investigation. This population (CrGC-1) will flower 16 days and produce mature seeds in 36 days from the date of sowing. Plants may be grown at a density greater than 600/m^2 in growth chambers, producing an average of 78 seeds per plant. Plants produce several siliques each, allowing both self-pollination and crossing of the same individuals. Although this population exhibits sporophytic incompatibility, it can be avoided and self-pollinations can be obtained by pollinating stigmas at the bud stage, 1–4 days before anthesis (14). Thus, this population was well suited to the development of a model genetic system.

Presence of major gene resistance in a population impairs selection for favorable minor genes by masking their expression (5). The establishment of a uniformly susceptible population was

sought, therefore, before the initiation of selection, an approach advocated by Robinson (16). From a population of about 600 plants of CrGC-1 inoculated with *A. candida* race 2, 42 were chosen that exhibited moderately susceptible reactions. These were a subsample of the screened individuals that were scored in interaction phenotype classes 5 and 7 according to the rating system of Williams (19), where 0 is resistant and 9 is most susceptible. Progeny testing was conducted to confirm that these plants lacked major genes for resistance before a susceptible base population was established. A minimum of 25% resistant individuals would occur in S_1 progeny if their parent carried a recessive major gene for resistance in a heterozygous state. Therefore, these 42 individuals were self-pollinated and simultaneously randomly mated in groups of three to five plants by using bee-sticks to transfer pollen (18). An average of 1.5% resistant progeny were observed among selfed progeny, with a range of 1–9% among the 42 S_1 families. This low frequency of resistance indicated that the parental plants lacked major genes for resistance. Equal numbers of seeds from the randomly mated (RM_1) progeny of 36 of these plants (the others lacked sufficient quantities of RM_1 seed) were bulked and designated as the base population for subsequent selection.

Experiment I. Two separate selection procedures were exercised among individuals in the base population of susceptible plants. The first was simple mass selection among individuals. The second was selection among and within half-sib families. Mass selection is expected to capitalize on all of the additive genetic variance (σ_a^2) among individuals; however, its great disadvantage is that selection is based on phenotypes of individual plants (3). The expected gain from selection is $k\,\sigma_a^2/\sigma_p^2$, where k is the selection differential and σ_p^2 is the phenotypic variance of individual plants. Half-sib family selection is expected to capitalize on ⅜ of the additive genetic variance among families and ¼ of the additive genetic variance within families (3). The expected gain from selection is $k_1(\frac{3}{8})\sigma_a^2/\sigma_{HS}^2 + k_2(\frac{1}{4})\sigma_a^2/\sigma_w^2$, where k_1 and k_2 are the selection differentials among and within families, respectively, and σ_{HS}^2 and σ_w^2 are the phenotypic variances among and within half-sib families, respectively. Its major advantage is that selection among families is based on family means. Because the variance of the mean expression of a family of n individuals is expected to be $1/n^{th}$ as large as the variance of its members, the heritability of the selection differential among families can be greater than that obtained for mass selection. Selection among half-sib families is progressively more effective relative to selection within half-sib families as the heritability of the trait decreases (3, p. 188).

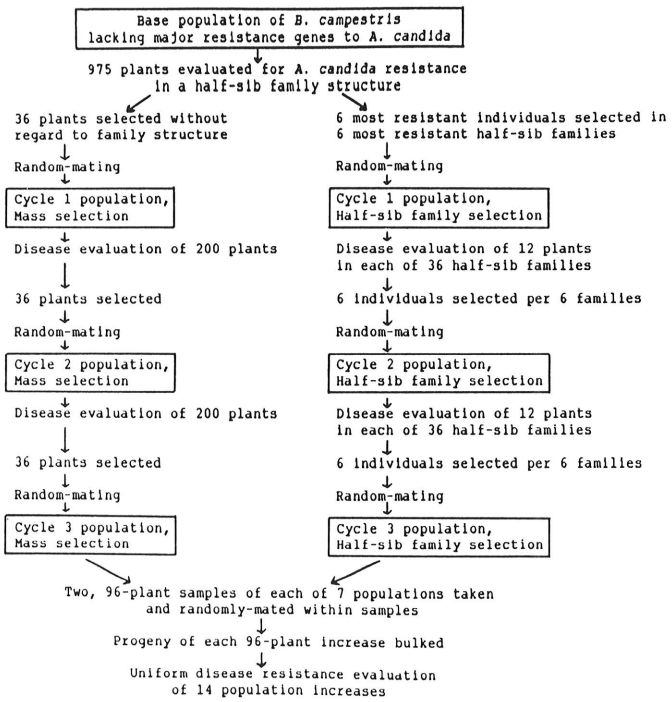

Fig. 1. Outline of mass selection and half-sib family selection procedures for resistance to *Albugo candida* race 2 in a *Brassica campestris* population.

Another potential disadvantage of mass selection for low sporulation is that the sporulation ratings used are quasicontinuous. The maximum potential selection pressure is a function of the percentage of individuals that are scored in the lowest discrete sporulation class. The experimenter has no control over this outcome and may find it difficult to exert further selection pressure once a substantial portion of the population of host plants fails to support sporulation. Conversely, selection among families is exercised on continuous values (means of discrete values) and should progress until most families produce only resistant progeny.

An outline of the selection procedures is given in Figure 1. Cycle 1 of each selection procedure was selected from among 975 plants in the base population. Half-sib family selection was for the most resistant six plants in each of the six most resistant families. Mass selection was for the most resistant 36 plants in the entire population. Because 205 of the 975 plants were scored in the lowest observed class (sporulation = 1), the 36 mass-selected individuals were randomly selected by computer from among these 205, producing a selection intensity of 21%. Thereafter, the selection procedures diverged and selection was practiced among 36 families of 12 individuals for half-sib family selection and among 200 individuals for mass selection. In each cycle of selection, the six most resistant individuals were selected from the six most resistant families in the half-sib family procedure and the 36 most resistant individuals were selected from the population at large in mass selection. Selection intensities for cycles 2 and 3 of mass selection were 30 and 29%, respectively. Selected individuals were randomly mated within each population, by using bee-sticks, after each cycle of selection to generate progeny for the next cycle of selection. Seeds from the half-sib family selected individuals were maintained separately from each plant. Equal numbers of seeds from each of the mass-selected individuals were bulked at harvest.

When the three cycles of selection had been completed, an evaluation of all the selected populations was performed to establish the effectiveness of the selection procedures under a common, uniform environment. Remnant seeds were used to produce two 96-plant increases of the base population and all cycles of both selection procedures. Plants in each increase were randomly mated and grown to maturity as described. Use of two increases per population allowed estimation of the error due to sampling of the selection cycle populations. Twenty-four individuals from each increase were evaluated for disease reaction in each of two randomized complete blocks. Blocks were inoculated by different individuals and placed in separate incubation chambers. Disease ratings were conducted separately by two individuals to provide a measure of the error associated with the subjective ratings. Mean values of disease ratings of the 24 plants in each plot were used for analysis of variance, with increases, inoculation effects, and evaluator effects considered random and all other effects considered fixed. The variance due to differences in population means was partitioned into four, nonorthogonal, linear, and quadratic contrasts to determine if population differences were due to linear or curvilinear responses to the two selection procedures. Least-squares regressions were used to estimate the linear change in resistance per cycle of selection for both selection procedures. Estimation of the heritability of sporulation ratings was determined from the slope of the linear regression of selection response upon the cumulative selection differential (2, p. 184). The selection differential for each selection cycle was simply the difference between the mean rating of the selected individuals and the mean of the population from which they were selected.

Experiment II. To examine the genetic basis of the accumulated resistance, self-pollinations and resistant × susceptible biparental crosses were conducted among individuals from the increases of cycles 0 and 3 of both selection procedures. These progeny were evaluated to establish: 1) whether individuals from the advanced

selection cycles transgressed beyond the range of resistance in the original, unselected population; 2) whether discontinuities existed in distributions of (resistant × susceptible) F_2 progeny, indicating segregation of identifiable single genes that contributed to the accumulated resistance; 3) what degree of dominance appears to characterize the accumulated resistance; and 4) what number of genes appear to be responsible for the accumulated resistance.

Plants evaluated in this experiment included the most resistant 21 of 96 plants evaluated in the increase of the unselected population (these exhibited an average sporulation rating of 0.85), 21 of 32 individuals exhibiting sporulation ratings of 0 from the increase of cycle 3 of half-sib family selection, and 26 of 44 individuals from the increase of cycle 3 of mass selection that also exhibited sporulation ratings of 0. All these individuals were self-pollinated and also crossed by a single, highly susceptible (sporulation rating = 9) individual from cycle 0. Selfed seed of the susceptible test parent were also produced.

Selfed progeny were evaluated for disease reaction in a randomized complete block design with two blocks of four S_1 progeny per family. Resistant × susceptible F_1 progeny were evaluated along with S_1 progeny of the single, susceptible parent, using a randomized complete block design with two blocks of 10 individuals per testcross family. Eighteen individuals from the F_1 families were self-pollinated to generate F_2 families. An average of 27 individuals per F_2 family were evaluated for disease reaction in two randomized complete blocks, along with individuals from remnant seed of six F_1 families, five resistant S_1 families, and S_1 progeny of the susceptible testcross parent. These S_1, F_1, and F_2 values were used to determine the apparent degree of dominance of resistance. In addition, the means and variances of these generations were used to allow estimation of the effective gene number involved in resistance, according to the methods of Lande (9). Statistics necessary for the dominance and gene number estimates were obtained by using both original and square-root-transformed sporulation values.

TABLE 1. Sums of squares and mean squares from analysis of variance of estimated sporulation ratings[a] from selection cycle populations of *Brassica campestris* after inoculation with *Albugo candida* race 2

Source	df	Estimated sporulation rating	
		Sums of squares	Mean squares[b]
Population	6	62.7	10.45*
Half-sib family linear	(1)	(35.3)	(35.3)**
Half-sib family quadratic	(1)	(1.2)	(1.2)
Mass selection linear	(1)	(49.9)	(49.9)**
Mass selection quadratic	(1)	(1.8)	(1.8)
Increase (population) (= Error A)	7	8.1	1.16
Inoculation	1	0.0	0.00
Population × inoculation	6	4.4	0.74
Increase (population) × inoculation (= Error B)	7	2.3	0.33
Evaluator	1	0.0	0.01
Error C	27	0.8	0.03
Total	55	78.3	

[a] Values pertaining to contrasts across levels of main effects are indicated in parentheses.
[b] *, ** Significant at the 5 and 1% levels, respectively.

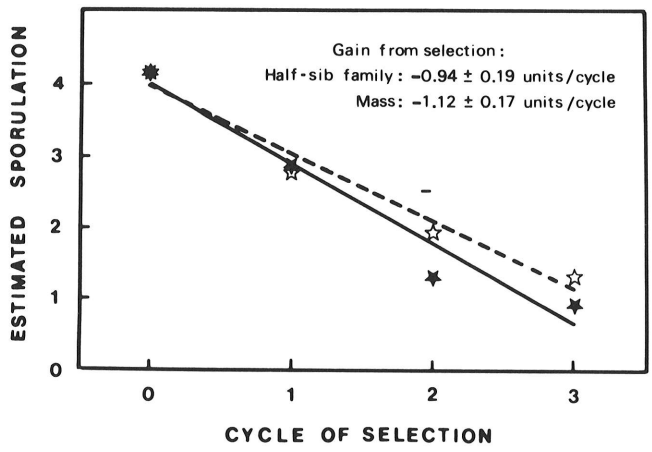

Fig. 2. Mean estimated sporulation ratings for selection cycle populations from half-sib family selection (hollow symbols) and mass selection (solid symbols) for resistance to *Albugo candida* race 2 in *Brassica campestris*. Gain per cycle for each procedure was determined from least-squares regression.

RESULTS

Experiment I. Significant differences were observed between selection cycle populations in the uniform evaluation of disease reaction (Table 1). Populations accounted for more than 80% of the total variation in the model. Linear contrasts across the four selection cycle populations within both of the selection procedures were highly significant, and quadratic (curvilinear) contrasts were nonsignificant, indicating that the responses to selection from both selection procedures were predominantly linear. Main effects of inoculation blocks and disease-rating evaluators were nonsignificant, as was the interaction between inoculation and population. All evaluator interactions were nonsignificant and were pooled to produce the error C term. Least-squares regressions indicated linear changes of -1.12 ± 0.17 per cycle of mass selection and -0.94 ± 0.19 per cycle of half-sib family selection (Fig. 2). Slopes of regression lines for the two selection procedures were not significantly different. Mean sporulating ratings declined from 4.2 in the unselected base population to 1.3 in cycle 3 of half-sib family selection and to 0.95 in cycle 3 of mass selection. The realized heritability of the sporulation ratings was determined to be 0.40. In addition to reducing the quantity of host sporulation, selection appeared to influence disease expression, increasing the incidence of hypersensitive lesions and the chlorosis of infection sites.

Experiment II. Distributions of S_1 family means from the most resistant individuals of the base population, cycle 3 of half-sib family selection, and cycle 3 of mass selection are shown in Figure 3. The S_1 families were significantly variable within each of the three populations, indicating the presence of genetic variation for disease rating even among a sample of plants with sporulation ratings of 0. Mean sporulation ratings of many S_1 families from

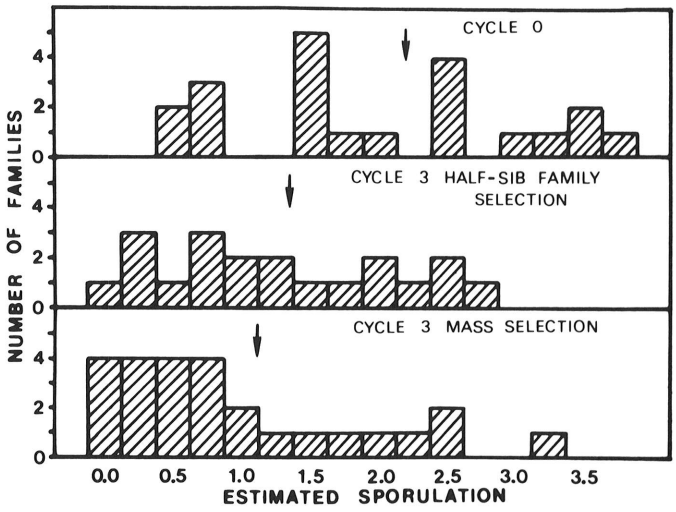

Fig. 3. Distributions of mean estimated sporulation ratings of *Brassica campestris* S_1 families derived from the most resistant individuals in each of cycle 0, cycle 3 of half-sib family selection, and cycle 3 of mass selection for resistance to *Albugo candida* race 2. Means across families within each selection cycle population are designated by arrows.

cycle 3 of half-sib family selection and cycle 3 of mass selection transgressed beyond the lowest values observed among S_1 families from the base population. Selection, therefore, appeared to increase the degree of resistance of individual plants, as well as the frequency of resistant individuals in the population.

Analysis of variance of testcross family disease ratings also revealed that families were a significant source of variation (not presented). Mean disease ratings of testcross families were significantly correlated ($r = 0.67$) with corresponding resistant S_1 family means (Fig. 4). The mean sporulation ratings of S_1 progeny from the highly susceptible testcross parent were 6.6 and 7.4 in the F_1 and S_1 evaluations, respectively. The S_1 progeny from resistant S_0 parents exhibited a mean sporulation rating of 1.0. Resistant × susceptible F_1 progeny exhibited a mean rating of 2.23.

The distribution of sporulation values of 489 F_2 individuals across all 18 resistant × susceptible F_2 families was positively skewed with a mean rating of 2.78 (Fig. 5). Analysis of variance (not presented) indicated that F_2 families were significantly variable. Their means ranged from 0.64 to 5.62. Distributions of individuals within each F_2 family are presented in Figure 6, with families ranked according to the mean sporulation rating. Although the numbers of individuals within each family are small, there is no apparent segregation into simple Mendelian ratios. The discontinuities within each distribution exist at different sporulation rating values. Thus, no single genes influencing host resistance are evident based on F_2 segregation patterns of any of the 18 families.

DISCUSSION

The rapid response to selection for resistance to *A. candida* from the susceptible base population reflects a high degree of genetic control of the observed variation in estimated sporulation ratings.

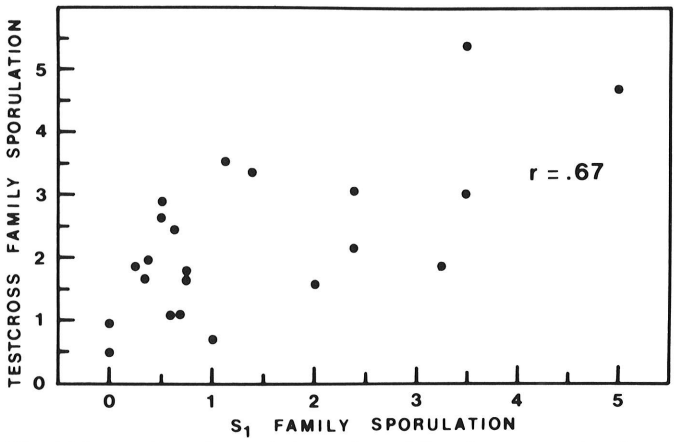

Fig. 4. Mean estimated sporulation ratings of *Brassica campestris* resistant × susceptible F_1 families plotted against corresponding values of S_1 progeny from the respective resistant parents, after inoculation with *Albugo candida* race 2.

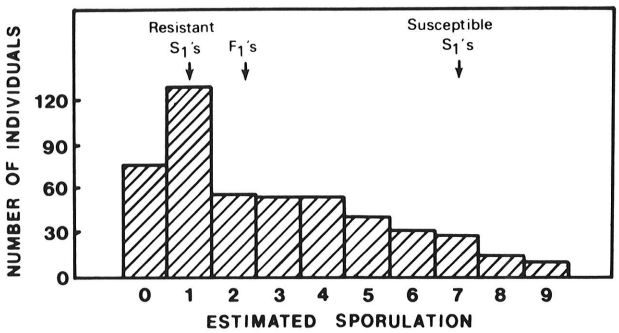

Fig. 5. Distribution of estimated sporulation ratings of *Brassica campestris* F_2 individuals across 18 resistant × susceptible testcross families, after inoculation with *Albugo candida* race 2.

The nonsignificance of evaluator effects and interactions in the uniform evaluation suggest that although the sporulation ratings are subjective, they are consistent measures of sporulation intensity. The effectiveness of these subjective ratings is fortunate because it would be prohibitive to actually quantify pathogen sporulation for the thousands of host plants involved in selection schemes such as those employed here. The moderately high heritability of sporulation ratings might be attributable, in part, to the careful control of inoculation and incubation procedures, which minimized these experimental sources of variation.

A range of host-pathogen interactions were observed in the advanced selection cycles, including some that were not evident in the base population. Most notable among these were localized necrotic flecking and general chlorosis of the inoculation sites. We hoped that some of these reactions would segregate in a simple Mendelian fashion in the resistant × susceptible F_2 families, elucidating simple genetic components of the accumulated resistance. This was not observed, perhaps indicating that each of these apparently distinctive phenotypes are, themselves, polygenically determined. Distinct physiologic bases for these phenotypes might be elucidated, however, as in the host reaction of barley, *Hordeum vulgare* L., to *Puccinia hordei* Otth. (12).

The two selection schemes that were used appeared equally effective through the first three selection cycles. However, mass selection was considerably easier to conduct because it did not require the maintenance of a pedigree structure and separate harvesting of seeds from each selected plant. Half-sib family selection may have been perpetuating the selection response more effectively than mass selection in the advanced cycles (see means for cycles 2 and 3 in Fig. 2). The confidence intervals for these means do not allow confirmation of this hypothesis. However, this trend would be expected to occur as a greater frequency of the population fails to support sporulation of *Albugo*, resulting in an unavoidable decrease in the selection intensity that can be imposed with continued mass selection. It is possible, then, that mass selection might be the preferred method early in the selection procedure, later followed by some form of selection among replicated progeny.

The subjective scale used for the sporulation ratings was arbitrary and may not represent the underlying biological scale in which gene effects are exerted. Even if sporulation had been quantified, the researcher would be left with the problem of establishing an appropriate scale for measuring gene effects. The scale of measurement is inconsequential to the effectiveness of selection, but it is important in making inferences regarding gene action and estimates of the numbers of genes involved in the selection response. The skewedness of the resistant × susceptible F_2 and the nonintermediacy of F_1 values relative to parental values (Fig. 5) may be merely functions of an inappropriate scale of measurement (2). Transformation of individual sporulation ratings to square roots produces a more nearly intermediate F_1 value of 1.99 (vs. 0.63 and 2.65 for the resistant and susceptible S_1 means, respectively) and a less skewed F_2 distribution. A predominantly linear selection response is obtained in either measurement scale, thus providing little basis for discriminating between these two possibilities. The degree of dominance characteristic of this polygenic resistance, therefore, is not evident.

Likewise, the choice of scale may influence estimates of gene numbers involved in quantitative trait expression (9). Substantially underestimated gene numbers may also result from dominant gene action, nonequivalence of gene effects, absence of complete association of like alleles in the parents, and linkage (9,10). Gene number estimates were very different when original sporulation ratings were used than when ratings were square-root-transformed. Gene number estimates using original sporulation ratings were 4.0 and 4.5 for the two trials in which the resistant and susceptible parental S_1s were evaluated. Corresponding values for square-root-transformed ratings were 77 and 90 genes, respectively. The large differences between estimates in the two scales was due primarily to the small difference between the variance of F_1 and F_2 generations when sporulation values were transformed to square roots. These results indicate the magnitude

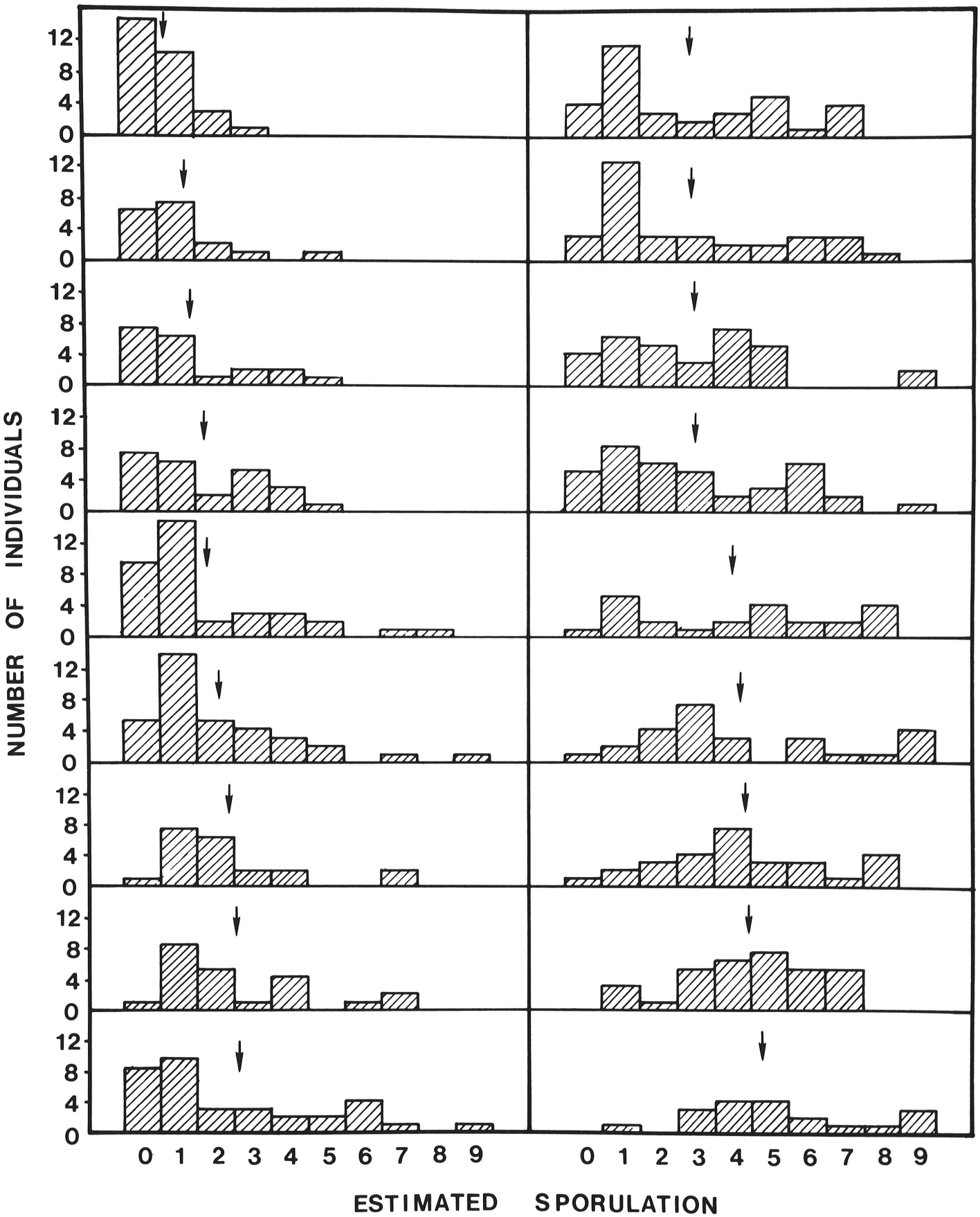

Fig. 6. Distributions of estimated sporulation ratings of *Brassica campestris* F_2 individuals from each of 18 resistant × susceptible testcross families, after inoculation with *Albugo candida* race 2. Families are ranked by family mean values (indicated by arrows).

of bias in gene number estimates that may arise solely from scaling influences and suggest that the procedure has little merit in this circumstance, where a reasonable biological scale is not evident.

The response to selection for minor gene resistance in this pathosystem has been surprisingly rapid. The transfer of genes accumulated in these selection procedures to other populations of *B. campestris* via backcrossing might be expected to be difficult. However, it seems likely that similar procedures might be effective for horticulturally or agronomically useful populations of *Brassica*. Pound and Williams (15) reported a high degree of heterogeneity in host response to *A. candida* races 1 and 2 among 115 cultivars of 10 *Brassica* species, suggesting that polygenic variation was prevalent among cultivated forms. Aside from the usefulness of this investigation as an empirical model for the accumulation of polygenic resistance from a susceptible base population, we hope that this pathosystem will be of value in investigating the behavior and mechanisms of polygenic resistance. Many different terms have been extended to describe quantitative pathosystems including durable resistance, horizontal resistance, rate-reducing resistance, partial resistance, etc. Many of these terms imply that certain behavioral features are characteristic of polygenic resistance, when, in fact, little empirical information is available regarding many aspects of quantitative pathosystems. Further empirical investigations are needed to understand the range of behaviors and mechanisms that characterize polygenic resistance. Seed of the rapid cycling original stock and each generation of mass selection are available through the Crucifer Genetics Cooperative as stocks CrGC-1 (original, rapid cycling population), CrGC-62 (cycle 0), CrGC-16 (cycle 1), CrGC-17 (cycle 2), and CrGC-18 (cycle 3).

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