INHERITANCE OF RESISTANCE OF CORN TO DOWNY MILDEW CAUSED BY *Peronosclerospora philippinensis* (Weston) SHAW

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ABSTRACT

Evaluation of 36 entries for downy mildew reaction revealed significant differences due to location and genotype components; genotype-environment interaction was also detected. The interactions of general and specific combining ability components with locations were highly significant. The presence of partial or incomplete dominance governing the resistance of corn to downy mildew was detected using the variance/covariance graphic analysis. Estimation of genetic parameter detected major contribution of additive gene action in downy mildew resistance. The average degree of dominance as measured by $(H1/D)^{\frac{1}{2}}$ was partial. Broad and narrow sense heritability estimates were 45.67 and 39.23%, respectively.

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KEY WORDS: Corn. *Zea mays.* Downy mildew. *Perenosclerospora philippinensis.* Inheritance. Variance/Covariance analysis. Incomplete dominance. Genetic parameters. Broad sense heritability. Narrow sense heritability. General combining ability. Specific combining ability.

INTRODUCTION

Downy mildew of corn caused by *Peronosclerospora philippinensis* (Weston) Shaw is considered as the most destructive disease of corn in the Philippines (Exconde, 1974). Thus, considerable efforts have been devoted for its effective control. Carangal, Claudio and Sumayao (1970) recommended roguing infected plants but this practice cannot always be followed because of limitations in labor and implements. A fungicide, Ridomil (Ciba-Geigy), was found to be effective in controlling corn downy mildew from emergence until harvest (Exconde and Molina, 1978). However, it is possible for the downy mildew fungus to develop tolerance to the chemical. Another method of disease control considered most efficient and economical is through the use of resistant varieties.

A suitable breeding program for developing downy mildew resistant varieties and hybrids should start with the knowledge of genetic mechanism of disease resistance. Likewise, it is also desirable to know the nature of gene action and the relative amount of additive and dominance portions of gene action responsible for resistance. Such information would provide the breeder some bases for making sound decisions on the method of developing resistant populations.

This study presents the mode of inheritance of downy mildew resistance in corn.

MATERIALS AND METHODS

Four Philippine inbred lines resistant to downy mildew and four susceptible inbred lines from the United States were used as parents in making the diallel crosses (Table 1).

Half-diallel crosses among the eight parental inbred lines were generated. The eight parental inbred lines and the 28 single crosses were evaluated for downy mildew reaction at two locations. One was conducted at the Central Experiment Station, College of Agriculture, University of the Philippines at Los Baños, College, Laguna and the other at the Central Mindanao University at Musuan, Bukidnon. A randomized complete block design with 3 replications was used in each location. Each replication consisted of 36 entries (28 F1's and 8 parents). The experimental unit was a row 5 m in length, 1 m in diameter planted with 42 seeds. Fertilizer was applied at the rate of 45-60-30 kg/ha (N, P205, K20) at planting time.

A susceptible variety (UPCA Var 1) was planted in border rows and along alleyways three weeks before planting the entries to serve as source of inoculum. The spreader

Table 1. Description of the eight corn inbred lines used in the study.

	Code	Pedigree	Origin	Reaction to Disease*
Phil. Inbred No. 2	1	Ph 102-28 Phil. DMR Comp. 2-22-1-2-1-1	Philippines	R
Phil. Inbred No. 3	2	Ph 102-38 Phil. DMR Comp. 2-85-1-1-1-2-6	Philippines	R
Phil. Inbred No. 13	3	Ph 110-14 Medium Early DMR Comp. 2-78-1-1-1-2-2	Philippines	R
Phil. Inbred No. 14	4	Ph 110-26 Medium Early DMR Comp. 2-78-1-1-1-5-1	Philippines	R
AFR B_{73}	5		U.S.A.	S
BFR Mo_{17}	6		U.S.A.	S
EH 98-652-B-1	7		U.S.A.	S
KR R 619 60 SWI	8		U.S.A.	S

*R- Resistant
S - Susceptible

rows were inoculated with conidial suspension four days after seedling emergence.

Data on test materials of the number of plants infected were taken on the 2nd and 4th week after emergence. Infection percentages were calculated following the formula:

$$\% \text{ infection} = \frac{\text{No. of plants infected}}{\text{Total no. of plants}} \times 100$$

The data were transformed into arc sin using the transformation table of Gomez and Gomes (1976). The transformed values were used in the statistical analysis. Combining ability analysis over locations was performed following the procedure proposed by Singh (1973). Genetic components (D, H_1, H_2 and F) were estimated following the procedures of Hayman (1954) and Aksel and Johnson (1963).

The statistics used to estimate the components of variation are the following: D (Additive effects of genes), H_1 (dominance effect of genes), H_2 (proportion of positive and negative genes in the parents), F (covariance of additive and dominance effects) and E (environmental component of variation). The components of variation provided the estimates of the following ratios:

$(H1/D)^{\frac{1}{2}}$ = mean degree of dominance over all loci

$(H_2/4H_1)$ = shows whether or not positive and negative alleles are present in equal proportions

K = the ratio of reflecting the number of gene groups controlling the character calculated by:

$$\frac{(\text{Overall progeny mean - parental mean})^2}{1/4\,H_2}$$

Heritability values were estimated by the formula proposed by Mather and Jinks (1971) with modifications, that is:

$$\text{Heritability (Narrow sense)} = \frac{1/2\,D + 1/2\,H_1 - 1/2\,H_2 - 1/2\,F}{1/2\,D + 1/2\,H_1 - 1/4\,H_2 - 1/2\,F + E + GE}$$

$$\text{Heritability (Broad sense)} = \frac{1/2\,D + 1/2\,H_1 - 1/4\,H_2 - 1/2\,F}{1/2\,D + 1/2\,H_1 - 1/4\,H_2 - 1/2\,F + E + GE}$$

where:

E = environmental component of variation

GE = genotype x environmental component of variation

D =
H_1 & H_2 = as defined above
F =

RESULTS AND DISCUSSION

Downy Mildew Incidence.

The mean percentage infection

Table 2. Mean values of parents (underlined) and F1 hybrids in an eight-parent diallel cross for percentage of downy mildew infection at UPLB.

Inbred Line	Phil. Inbred No. 2	Phil. Inbred No. 3	Phil. Inbred No. 13	Phil. Inbred No. 14	AFR B 73	BFR Mo17	EH 98 652 B-1	KR R 619 60 SWI
Phil. Inbred No. 2	9.00	7.32	16.50	12.70	41.85	30.84	34.06	33.83
Phil. Inbred No. 3		20.66	19.01	15.40	28.10	40.06	29.06	32.00
Phil. Inbred No. 13			25.99	13.37	38.23	25.31	31.07	49.38
Phil. Inbred No. 14				17.48	32.60	38.30	53.44	40.17
AFR B73					60.48	68.80	61.20	71.08
BFR Mo17						82.70	71.85	50.97
EH 98-652-B-1							76.17	62.09
KR R 619 60 SWI								69.36

of downy mildew of the parents and hybrids at UPLB and CMU is shown in Tables 2 and 3. At UPLB, percentage infection ranged from 9.00 to 82.70 with a mean of 45.23 in the parents and from 7.32 to 71.85 with a mean of 37.45 in the hybrids. Percentage infection at CMU ranged from 13.14 to 73.99 with a mean of 43.27 in the parents and from 15.41 to 83.69 with a mean of 42.92 in the hybrids.

Higher percentages of infection were observed in CMU, Musuan, Bukidnon than in UPLB, College, Laguna (Tables 2 and 3). This results may be attributed to the varying environmental conditions in which the different genotypes were exposed. Although no record was taken on the amount and frequency of rainfall in both locations, it was believed that rainfall is more evenly distributed at CMU than UPLB. Since larger areas are devoted to corn production at CMU, the corn plants could continuously serve as potential sources of inoculum for

Table 3. Mean values of parents (underlined) and F1 hybrids in an eight-parent diallel cross for percentage of downy mildew infection at CMU.

Inbred Line	Phil. Inbred No. 2	Phil. Inbred No. 3	Phil. Inbred No. 13	Phil. Inbred No. 14	AFR B73	BFR Mo 17	EH 98 652 B-1	KR R 619 60-SWI
Phil. Inbred No. 2	13.14	17.00	15.55	15.41	38.44	53.13	50.07	44.18
Phil. Inbred No. 3		26.12	19.09	22.21	42.45	36.78	47.92	45.16
Phil. Inbred No. 13			17.44	18.90	43.23	19.80	39.28	34.06
Phil. Inbred No. 14				24.47	43.07	41.43	43.43	49.93
AFR B73					61.13	64.35	68.02	83.69
BFR Mo17						66.45	66.17	69.02
EH 98-652-B-1							73.99	69.90
KR R 619-60-SWI								66.13

downy mildew infection. Barredo and Exconde (1973) pointed out that the disease epiphytotics are greatly affected by environmental factors. Exconde (1974) reported that downy mildew infection was dependent on sunshine duration, temperature, nutrition and age of host plants.

Carangal, Claudio and Sumayao (1970) stated that Philippine areas most severely affected by downy mildew are in Mindanao and the Cagayan Valley representing 62% of the total corn production with an even distribution of rainfall. It is possible that the overall environmental conditions at CMU favored downy mildew infection at the time of the experiment. In addition, it is likewise possible that higher percentages of downy mildew infection at CMU may be related to the prevalence of more virulent races of *P. philippinensis.* Results of the investigation of Josue and Exconde (1979) and Titatarn and Exconde (1974) indicated the possibility of the existence of physiologic races and showed the Bukidnon isolates to be the most virulent group.

Results revealed that the percentage downy mildew infection values of four parental Philippine inbred lines were very much lower than these introduced US inbred lines. Single cross hybrids between resistant inbred lines had the lowest infection whereas the single crosses between resistant x susceptible inbred lines had intermediate and high downy mildew infection in most of the observations in both locations. High percentage infections were observed between susceptible x susceptible inbred lines in either location. These results seemed to indicate partial dominance to downy mildew resistance among the genotypes evaluated.

Combined Analysis.

Results revealed significant differences due to location (Table 4). Higher percentages of infection were observed at CMU than at UPLB and this may be attributed to favorable environmental conditions like evenly distributed rainfall and constant source of inoculum attributed by large areas devoted to corn production which hastened disease development and also by the possible presence of more virulent races.

Genetic differences existed among the genotypes for downy mildew reaction as reflected by highly significant genotype effect. It was also noted that the effects due to general and specific combining abilities were highly significant indicating the presence of additive and non-additive types of gene action although the additive type had a higher magnitude. Thus, the additive type of gene action had the predominance in the downy mildew resistance of corn.

Highly significant G x E interaction indicates that the genotypes reacted with the prevailing environmental conditions in which they were exposed. Varieties that showed resistance in a particular locality should be recommended for that kind of area to ensure that they will

Table 4. Combined analysis of variance for percentage downy mildew infection (transformed data) in an eight-parent diallel cross grown at UPLB and CMU.

Source of Variation	Degrees of Freedom	Mean Squares
Location (E)	1	335.37*
Replication/Loc (R/E)	4	216.79*
Genotype (G)	(35)	1023.76**
General combining ability (GCA)	7	1727.72**
Specific combining ability (SCA)	28	847.78**
Genotype x Location (G x E)	(35)	129.78**
GCA x E	7	234.59**
SCA x E	28	103.58*
Error	140	66.20
C. V. (%)		20.55

*Significant at 5% level of probability.
**Significant at 1% level of probability.

not easily succumb to the disease. It is of practical significance to note the existence of physiologic races of *P. philippinensis.* Hence, it is highly probable that resistant varieties developed in one locality may lose their resistance in other localities with virulent races.

Graphical Analysis.

In both locations, the observed regression line cuts the ordinate well above the point of origin, indicating that dominance was incomplete or partial (Figs. 1 and 2).

The arrays are mostly located along the actual regression line suggesting no wide genetic variation. At UPLB, the order of dominance was line 3 > 2 > 4 > 1 > 8 > 5 > 7 > 6 and of parental performance, line 1 > 4 > 2 > 3 > 5 > 8 > 7 > 6. The distribution of parent points indicates that parents 3, 2, 8 and 4 possess an excess of dominant alleles while parents 5 and 1 possess more or less equal proportions of dominant and recessive alleles. However, parents 7 and 6 possess an excess of recessive alleles.

At CMU, the order of dominance was line 3 > 2 > 7 > 4 > 5 > 6 > 8 > 1 and the parental performance was line 1 > 3 > 4 > 2 > 5 > 8 > 6 > 7. The distribution of parent points indicated that parents 3, 2, 7 possess an excess of dominant alleles whereas parents 4, 5 and 6 possess more or less equal proportions of dominant and recessive alleles. On the other hand, parent 1 possesses an excess of recessive alleles. It was reflected from the distribution of parents that parents 2 and 3 from the Philippines possess an excess of dominant alleles. The inconsistency of dominant behavior with regard to downy mildew resistance in most of the parents was also noticeable from the distribution of parent points in both locations.

Estimates of Genetic Components of Variation.

Highly significant differences were obtained in all the components (Table 5). The component D, which measures additive gene action, was greatly higher than the dominant components (H_1 and H_2) indicating the predominance of additive genes conditioning downy mildew resistance. However, the presence of incomplete dominance was also detected as exemplified by the ratio of $(H_1/D)^{\frac{1}{2}}$ which had value less than unity.

Estimated values for narrow and broad sense heritability were 39.23 and 45.67%, respectively. The heritability values are low indicating that the heritable variation is comparatively smaller than the difference due to environmental variation. Therefore, it is clear that environmental conditions had a profound effect on the resistance of corn to downy mildew. Since heritability is an attribute of the population and environmental conditions to which they had been exposed, the heritability estimates would provide the basis for selection only for the population and range of infection

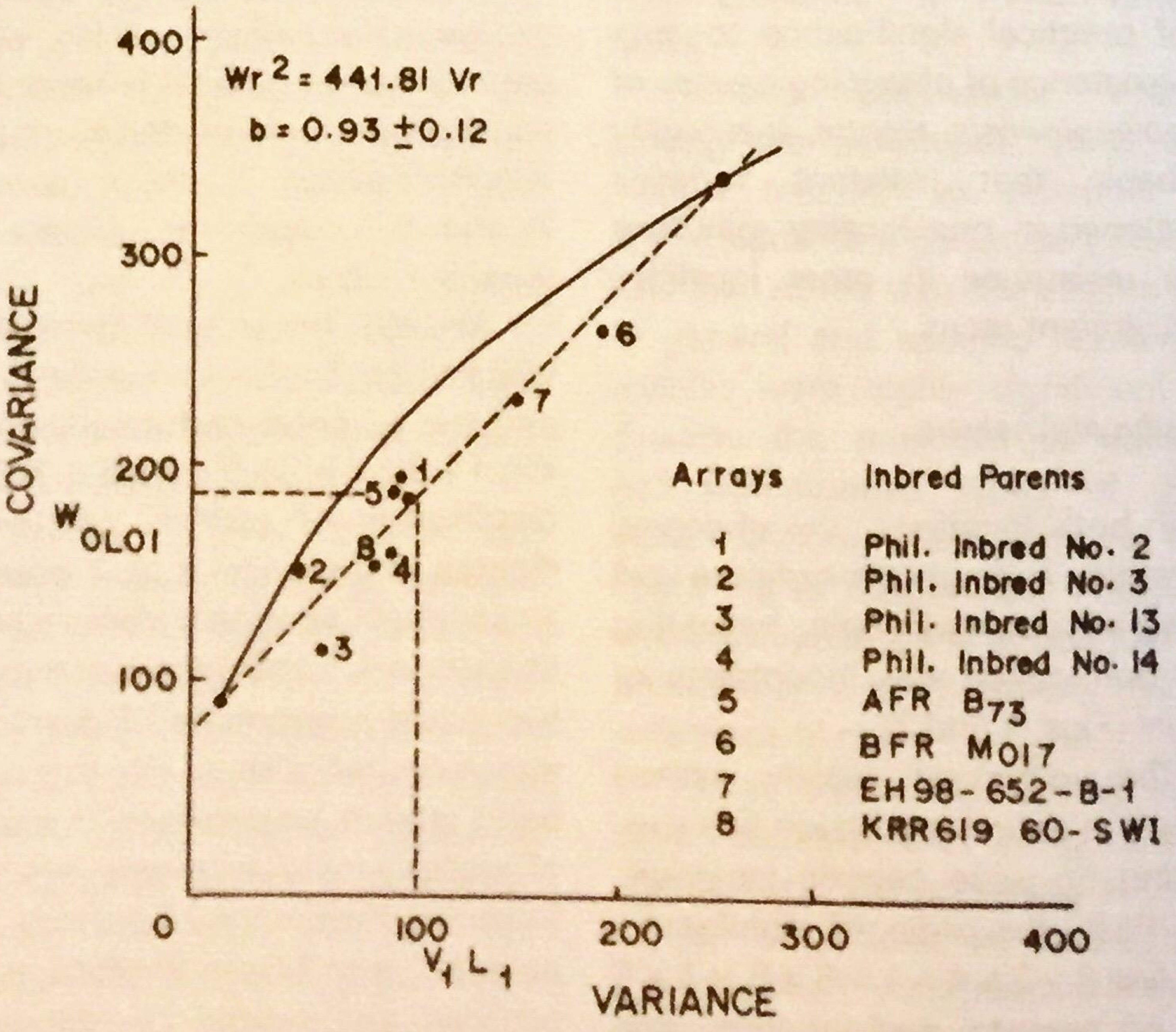

Fig. 1. Variance/Covariance (Vr/Wr) analysis for downy mildew infection at UPLB, College, Laguna, Philippines.

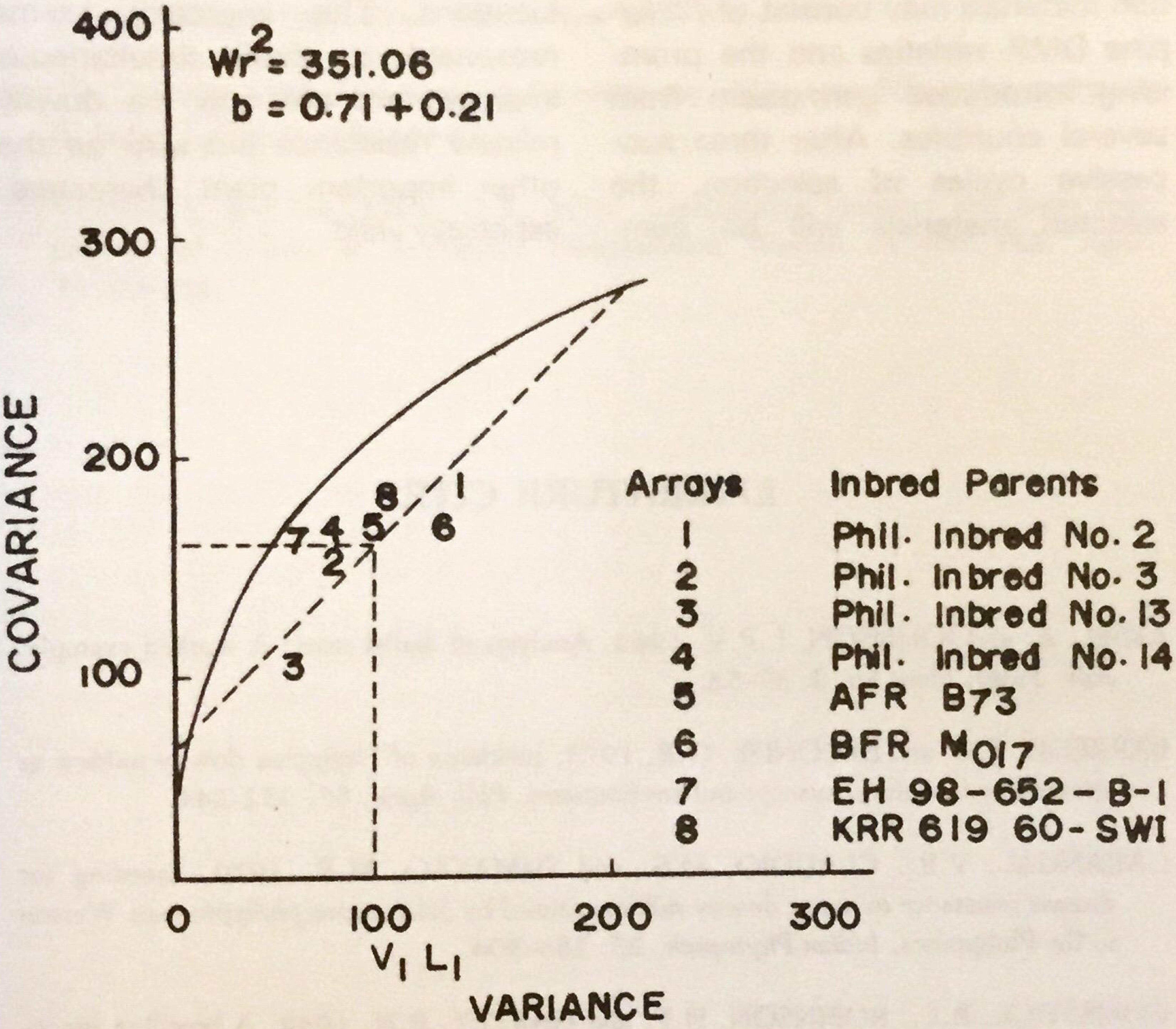

Fig. 2. Variance/Covariance (Vr/Wr) analysis for downy mildew infection at CMU, Musuan, Bukidnon, Philippines.

Table 5. Estimates of the components of genetic variance of downy mildew infection in an eight-parent diallel cross grown at UPLB and CMU.

Components of Variation	Estimated Value
D	672.75 ± 15.94**
H1	426.07 ± 36.33**
H2	220.28 ± 31.95**
F	207.50 ± 37.74**

**Significant at 1% level of probability.

observed in this particular study.

Both additive and non-additive types of gene action were responsible for conveying resistance of corn to *Peronosclerospora philippinensis* with the non-additive type providing more prominent influence. The use of reciprocal recurrent selection proposed by Comstock, Robinson and Harvey (1949) would appear to be one of the effective selection schemes in concentrating genes for resistance since additive and non-additive types of gene action governed the resistance of corn to downy mildew. The foundation materials may consist of Philippine DMR varieties and the promising introduced germplasm from several countries. After three successive cycles of selection, the selected materials will be composited and evaluated at several locations. This approach seems reasonable to obtain simultaneous improvement not only on downy mildew resistance but also on the other important plant characters, especially yield.

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