Technical Papers

Disease Resistance and Early Testing of Maize[1]

C. C. Wernham

Department of Botany, The Pennsylvania State College School of Agriculture, State College

The writer has been engaged in devising a program for isolating disease-resistant lines of corn since 1944. Methods and techniques used in this program have been published (*1, 2*). Until recently the output of resistant material was so limited as to present little difficulty in the strictly agronomic phases of yield-testing. Work conducted at this station, in addition to projects at Beltsville and Purdue, has furnished a nucleus of material of diverse origin which makes the production of large numbers of resistant inbred lines relatively easy.

Resistance to *Helminthosporium turcicum* is rare. A nursery population of 20,000 F_2 plants of a cross (very resistant × very susceptible) usually yields less than 20 plants of a rating 0.5–1.0 and about 40–60 plants of an acceptable rating of 2.0 (*3*). This selected residue yields such abundance of acceptable sublines that a major problem arises in conducting the proper experiments in yield-testing. If each original selection were represented by only two sublines in F_3 or F_4, yield-testing is experimentally unmanageable.

The solution would appear to be early testing of the original 60 or so F_2 families, a number rather easily fitted into experimental design. Two arguments are presented against the procedure: (*a*) nonuniformity in maturity of such material makes it difficult to outcross, and (*b*) a second top cross at a later date is required to sort out segregates within family progenies.

In a total disease program, corn and certain maize pathogens are planted in cold wet soil. Emergence is delayed because of differentials in seedling reaction to microorganisms and/or physiological tolerance to the environment. Experience has shown that maturity dates of surviving plants from a disease nursery represent a greater spread than do similar data under normal conditions of planting. A ten-day difference in the disease nursery often shrinks to a three- or four-day difference when corn is planted in warm soil. It may well be advisable to observe the original selections for one season under normal conditions so that their functional maturity range and general agronomic characters may be observed prior to top-crossing. An alternative procedure would be to top-cross as many as fitted the pollen-shedding range of successive plantings of the male tester, and at the same time noting the maturity of those that did not fit, so that they could be tested the following season. In the meantime other lots of S_0 or F_2 material could be processed in the disease nursery.

The objection to an additional top-cross test at a later date (*4*) is not so easily disposed of. Several authors (*4–7*) have shown that significant segregation for yield occurs at later stages of inbreeding. All agree that the better segregates were visually undetectable. Yet all are at a loss to explain the segregation. It seems inconsistent with genetic theory.

If we consider genes for yield prepotency to have small effects, and yield-testing to be a sorting device for selecting plants with the largest blocks of favorable genes (*8*), the material presented in Table 1 may serve as a basis for further comment. The following postulates should be kept in mind:

TABLE 1

CHANGES (ACCORDING TO GENETIC THEORY) IN COMPOSITION THROUGH FOUR GENERATIONS OF SELFING OF FIVE S_0 CORN PLANTS CARRYING 200 "FAVORABLE" GENE PAIRS WHICH ARE PRESENT IN EACH S_0 PLANT IN A DIFFERENT PROPORTION OF HOMOZYGOUS TO HETEROZYGOUS COMPOSITION

Plant No.	S_0		S_1		S_2		S_3		S_4		Total favorable gene pairs
	A*	B†	A	B	A	B	A	B	A	B	
1	150	50	162.5‡	25	168	12	171	6	172	3	175
2	100	100	225	50	137	25	143	12	146	6	152
3	75	125	106	62	121	31	129	15	132	7	139
4	50	150	84	75	103	38	112	19	117	10	127
5	25	175	69	88	91	44	102	22	107	11	118

* A, homozygous pairs.
† B, heterozygous pairs.
‡ Hereafter figures are given in whole numbers.

a) Genetic theory requires that heterozygosity decrease by one half with each additional generation of self-pollination. The data of Jenkins (*9*) and Sprague (*4*) support this theory.

b) Half the homozygotes accumulated will be of the dominant, or *plus*, type, since dominants and recessives accumulate in equal numbers. (It is assumed that genes favorable for yield and vigor are of the dominant-recessive, or plus-zero, type. Therefore homozygotes will have more influence on yield of top crosses than heterozygotes.)

c) Genes in the homozygous condition may be discarded but cannot be lost by inbreeding. *They can only be added to.*

d) Selection practices are typical of the corn breeding procedures (i.e., a small number of ears are chosen to perpetuate each line selected and sister lines are discarded by visual evaluation).

From Table 1 it is apparent that no advantage has accrued through the accumulation of favorable genes by selfing plants 1–5. They maintain their relative position with respect to blocks of favorable genes in the homozygous condition. Although plant 5 accumu-

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lates favorable genes in larger amounts, it never quite catches up (through S_1 to S_4) with plant 4, which had more favorable gene pairs in the homozygous condition to begin with.

Then if we accept, as a basis for separation, a top-cross test after S_3 or S_4 as a valid procedure, we must perforce assume that a similar test at S_0 level is equally valid, since the different S_0 plants maintain their relative positions in S_3 or S_4.

The data of Sprague and Bryan (*7*), Payne and Hayes (*6*), and Lonnquist (*5*) clearly contradict the theory.

Segregation of genes with small effects does not seem to be an adequate answer. Ten such genes in heterozygous condition would produce 1024 possible combinations of gametes, of which 66% are in the modal classes. The distribution being normal, any random sampling of the gametes would cancel advantages or disadvantages of selection outside the mode. It is doubtful if segregation of less than ten genes (with small effects) could be detected in top crosses. There appear to be two alternate assumptions.

a) The sample size used in test-crosses is inadequate for accurate appraisal of genetic theory. The author frankly admits his academic inability to evaluate the validity of the practices in use, except to point out that general adoption of a technique does not guarantee its adequacy. Sprague and Bryan (*7*) present data to indicate that segregation for top-cross combining ability was not significant in 1938 but was significant for 1939 and combined 1938–39 data.

b) A relatively few genes affect yield out of all proportion to their number. In some families these occur initially in the heterozygous state, and because of their small number their genetic distribution in a nursery row of 30–35 plants is fairly common. Thus some sublines would be selected which carried these genes in the homozygous (dominant or recessive) or heterozygous state.

It is unlikely that the effect of these postulated genes is concerned with vigor; otherwise they would be discarded visually. The effect is probably more in the realm of conditioning of vital processes which affect weight and moisture content of grain. Any investigator familiar with the light chaffy ears of stalk-rotted plants could well imagine the impact of a bad stalk-rot season on the yield of susceptible top crosses (*10*). Sprague and Bryan (*7*) report segregation for lodging (erect plants) and disease resistance (kernel damage) in addition to yield differences. There is little evidence, however, of a significant positive correlation between high-yielding sublines and low lodging or few damaged kernels.

A program for the production of disease-resistant corn envisages and employs pathological techniques which sort out resistant material in a breeding nursery from the onset of the breeding program. Its purpose is not unlike, nor unrelated to, early testing for combining ability in the same lot of material. The low gene frequency of certain types of resistance demands that screening for disease reaction be carried out first. The techniques for selecting disease-resistant corn are available. It is no more possible to select resistant corn plants without presence of disease than it is possible to select high-yielding lines without yield-testing.

There is a rapidly accumulating stockpile of resistant inbred material of a wide range of maturity which may serve as starting points in a breeding program. It is becoming increasingly apparent that native open-pollinated varieties are fertile sources of resistant material, although the gene frequency for resistance to *H. turcicum* is rather low.

Early testing for total disease is a sound program insofar as techniques are available. Segregation will occur in later generations. Early testing for yield is gaining in usage. Segregation in later generations has been demonstrated, but whether this reported segregation is permanent, as might be shown by progeny testing, or intermittent, because of unknown fluctuating environmental factors, has not been proved.

A delayed test involving S_1 or F_3 material is recommended for a combined program involving disease resistance. If genetic theory and the generally postulated effect of genes for yield in maize are correct, an additional top-cross test following further inbreeding is unnecessary.

References

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Chemical Constitution and Biological Activity of some Organophosphorus Compounds

D. Ramaswami,[1] E. R. Kirch, and Elizabeth H. Jenney

Department of Chemistry, and
Department of Pharmacology,
Chicago Professional Colleges,
University of Illinois, Chicago

The relationship of the chemical constitution of a substance to its biological activity has been the subject of investigation since Brown and Frazer (*1*) attempted a generalization connecting the physiological action of a substance with its chemical structure. Many specific relationships have since been elucidated,

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