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Resistance to Maize Dwarf Mosaic and the Corn Virus Disease Complex in Synthetic Populations of Dent Corn and Sweetcorn

Robert R. Fincher

To the Graduate Council:

I am submitting herewith a thesis written by Robert R. Fincher entitled "Resistance to Maize Dwarf Mosaic and the Corn Virus Disease Complex in Synthetic Populations of Dent Corn and Sweetcorn." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Plant, Soil and Environmental Sciences.

L. M. Josephson, Major Professor

We have read this thesis and recommend its acceptance:

F. L. Allen, V. H. Reich

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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RESISTANCE TO MAIZE DWARF MOSAIC AND THE CORN VIRUS DISEASE COMPLEX IN SYNTHETIC POPULATIONS OF DENT CORN AND SWEET CORN

A Thesis

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Degree

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Robert R. Fincher

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ABSTRACT

Phenotypic recurrent selection for resistance in corn (Zea mays L.) to maize dwarf mosaic (MDM) and the corn virus disease complex was conducted for five cycles in synthetic populations of dent corn and sweet corn. Selection was carried out concurrently at two locations under a natural epiphytotic of the corn virus disease complex of MDMV and maize chlorotic dwarf virus (MCDV) near Waverly, Tennessee and under an artificially induced epiphytotic near Knoxville, Tennessee created by mechanical inoculation with MDMV and transplanting of infected host plants. Resistant plants were selected and interpollinated concurrently and only apparently symptomless plants were harvested. It was of interest to determine the effect of successive cycles of selection as well as the effect of selection under different disease conditions at two locations.

Each cycle of selection at both locations in both synthetics was evaluated for virus reaction by determining the number of diseased plants and the severity of infection of the diseased plants. Host reaction to virus infection is largely quantitative, and genotypes with the same percentage of diseased plants may still vary in resistance because of differences in the severity of infection.

Evaluation of the dent populations showed no improvement for virus reaction from C0 to C4 at either location. The Waverly selections had significantly fewer diseased plants than the Knoxville selections at an early rating representing MDMV infection.

Evaluation of 100 random S_1 selections from the C0 and C3 dent populations showed greater variability for virus reaction in C3. Because hybrid vigor seems to enhance virus tolerance in susceptible and resistant genotypes, it may be that the variability of C3 was due to increasing the number of resistant selections and to greater expression of virus reaction in the susceptible selections due to inbreeding depression.

Selection in the sweet corn synthetic resulted in reduction in the number and severity of diseased plants at both locations when evaluated at Waverly. The Waverly selections were more resistant than the Knoxville selections.

Lack of response to selection in the dent synthetic may have been due to reduction in genetic variability for resistance, inbreeding depression, changes in disease pressure during cycles of selection, or to the inability to identify S_0 plants with high gene frequencies for resistance because of the confounding effects of hybrid vigor and virus resistance in heterozygous plants. Selection among S_0 individuals may have favored heterozygous genotypes and maintained undesirable alleles at higher frequencies than expected.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

A virus disease of corn (Zea mays L.) was first reported in Tennessee in 1964 (14). The disease has caused serious damage in certain corn producing areas of the state but damage has been most severe in river-bottom areas where johnsongrass (Sorghum halapense L., Pers.), the main overwintering host, thrives (23).

The causal agent was initially identified as maize dwarf mosaic virus (MDMV), a disease of corn first reported in Ohio in 1962 (17). More recently maize chlorotic dwarf virus (MCDV) has been identified in stunted corn in Tennessee (11).

Maize dwarf mosaic virus exists as six strains of a filamentous particle that is mechanically transmissible and vectored by aphids in a nonpersistent manner. Strains A, C, D, E, and F infect johnsongrass whereas strain B does not (16, 32). Other hosts for MDMV have been reported but their importance in regards to spreading the pathogen is unknown (35).

Symptoms of maize dwarf mosaic include chlorotic patterns with alternating light and dark green areas producing mosaics, flecks, and rings (9).

Maize chlorotic dwarf virus is an isometric particle vectored in a semipersistent manner by the leafhoppers Graminella nigrifrons (Forbes) and Deltocephalus sonorus (Ball) (10). It is not mechanically transmissible. The principle overwintering host is johnsongrass (10).

The diagnostic symptom of maize chlorotic dwarf is fine chlorotic striping of the tertiary leaf veins. More severe symptoms expressed in the field are yellowing, reddening, plant stunting, marginal leaf chlorosis, chlorosis at the base of the leaf whorls, and leaf tearing (9).

Maize dwarf mosaic virus and maize chlorotic dwarf virus occur together in the southern U.S. and diseased corn may be infected with both pathogens (10). Assay of diseased corn from Tennessee showed that MCDV and strains A and B of MDMV exist in Tennessee (11). It is speculated that the serious damage done to susceptible corn in Tennessee is due to a complex of MDMV and MCDV (33).

Where the corn virus disease is prevalant in Tennessee, corn yields are inversely related to disease and plants with only mild symptoms have also shown reduced yields (13, 23, 26). As a consequence research workers began intensive screening for resistance which was found in domestic and introduced germplasm (29). As the disease spread and became more severe, better sources of resistance were needed. Breeding work to develop resistant inbred lines and hybrids and genetic studies to determine the inheritance of resistance were begun.

Resistance to MDMV in the field seems to involve plant escape because genotypes that exhibit resistance to natural infection are often infected when mechanically inoculated in the field or greenhouse. Nearly all genotypes become infected with MCDV but the "resistant" genotypes exhibit a tolerance expressed by mild symptoms compared to susceptible genotypes (9).

Studies on the inheritance of resistance to MDM have involved crosses between susceptible and resistant inbreds and diallel analysis (8).

Josephson et al. (25), Loesch and Zuber (30), Josephson and Hilty (24), Dollinger et al. (3), and Josephson and Naidu (28) reported that resistance or tolerance to MDM is dominant to partially dominant and controlled by a few major genes. Josephson et al. (25) indicated that additive effects are also important and heritabilities ranged from 0.02 to 0.86. Josephson and Hilty (24), studying F_2 and backcross generations of crosses between susceptible and resistant inbred lines, found heritabilities ranging from 0.120 to 0.916 in four crosses evaluated at three locations. Josephson and Naidu (28) also indicated that minor genes are necessary for a high degree of tolerance.

Johnson (22) used diallel analysis to determine that reaction to MDMV is controlled by major genes with nearly complete dominance. However, general combining ability (gca) accounted for most of the variation among crosses and was probably due to additive effects of minor genes (22). Josephson and Naidu (28) found general combining ability more important than specific combining ability (sca). Loesch and Zuber (31), using diallel analysis, found both general and specific combining ability to be significant but gca mean squares were substantially larger than sca mean squares. Zuber et al. (47) examined predicted and observed double cross responses using tolerant and susceptible inbred lines. They found a nearly linear response in increased MDM ratings for both predicted and observed double cross performances with each additional substitution of a susceptible inbred line. General combining ability mean squares for MDMV reaction were nearly 40 times greater than sca mean squares. They also suggested that additive gene action conditioned the level of tolerance and nonadditive effects were of little consequence among the inbred lines in the study.

These studies allegedly involved MDMV. Although the etiology of MCDV was not confirmed until the 1970's, circumstantial evidence indicates that MCDV was present in the U.S. in the 1960's (10).

In areas where both MDMV and MCDV exist it is impossible to conduct field studies to examine the effects of either pathogen individually. Field studies with MDMV are possible in areas where MCDV does not exist. However, isolated studies with MCDV on a large scale have not been possible because MCDV is not mechanically transmissible (9).

It is probable that the genetic studies described above involved complexes of maize viruses rather than just MDMV based on the symptom descriptions associated with the studies. Findley et al. (7), Findley et al. (6), and Scott and Nelson (37) reported studies conducted under controlled conditions of MDMV infection. Naidu and Josephson (33) reported an inheritance study under the acknowledged condition of a virus disease complex.

Findley et al. (7) reported results of inheritance studies with isolates of MDMV. Using susceptible and resistant inbred lines and aphid and mechanical inoculation, they examined the segregation ratios for F_1, F_2, backcross, and selfed backcross generations. In general the results indicate that single dominant genes control resistance to isolates of MDMV.

Findley et al. (6) used reciprocal translocations to identify major genes for resistance to MDM in inbred line Oh07 associated with both arms of chromosomes 6 and 10 and the short arm of chromosomes 3, 7, and 8. Associations were also found with the long arm of chromosomes 1 and 2. Similar associations were found with inbred Mo22 with the exception of the short arm of chromosome 10.

Scott and Nelson (37) found resistance to MDM in inbred GA209 to be associated with both arms of chromosome 6.

Naidu and Josephson (33) used diallel analysis to study the inheritance of resistance to the corn virus disease complex in Tennessee. This complex is believed to be comprised of MDMV and MCDV. They evaluated the crosses under natural disease conditions and under an artificially induced epiphytotic created by mechanical inoculation with MDMV and by transplanting infected johnsongrass and corn in the field. Disease reaction was evaluated just prior to tasseling and later at full symptom expression. They found high and highly significant positive correlations for disease reaction at both dates and between naturally and artificially induced epiphytotics. They concluded that evaluation can be made concurrent with pollination to facilitate breeding programs. Early and late evaluation of disease reaction may also be a means of determining reactions to MDMV as well as the complex especially when plants are mechanically inoculated (33). Results from their diallel analysis showed highly significant gca and sca effects but gca was much greater. As many as four major genes with some degree of dominance for resistance were indicated to be present in the parental lines. Virus resistance appeared to be largely an additive type of gene action. Host reaction and the nature of genetic variation of resistance were similar at both dates of rating indicating that inbreds in this study react similarly to MDMV and the complex.

Naidu and Josephson (33) and Loesch and Zuber (31) suggested that hybrid vigor may have a confounding effect on disease reaction in that crosses of resistant by susceptible inbred lines were sometimes more resistant than expected on the basis of inbred line performance per se and that inbred lines are more subject to environmental stresses and to competition from johnsongrass.

In general, studies of inheritance of resistance indicate that gca effects are important so that a recurrent selection procedure would be effective in improving breeding populations for virus tolerance (22, 28, 33).

Recurrent selection is essentially the interpollinating of selected plants. Breeding schemes similar to recurrent selection were first described by Hayes and Garber (12) and East and Jones (4). However, these suggestions did not lead to widespread use of the method. Jenkins (18) provided the first detailed description of recurrent selection, and Hull (15) provided the name "recurrent selection" in his description of breeding for specific combining ability.

Recurrent selection is a method of population improvement designed to increase the frequency of desirable alleles for the selected character, release genetic variability for that character by breaking up linkage groups and maintain genetic variability for characters not under selection.

Selection with continued selfing is often unsuccessful in increasing the frequency of desired genes because the ceiling is set by the most favorable foundation plant. Selfing leads to rapid fixation of alleles and the chance of random loss of desirable alleles is substantial. In recurrent selection the ceiling is fixed by the most favorable combination of alleles and intercrossing allows for recombination between favorable alleles (1).

Inbreeding can occur in recurrent selection due to sampling variation caused by small population size. Inbreeding is a function of the effective population size which may be much smaller than the breeding population. According to Falconer (5) effective population size is the number of individuals that give rise to sampling variation or rate of inbreeding. In small populations chance can dominate changes in gene frequency thus making selection ineffective. Effective population size can be estimated from the number of breeding individuals, numbers of males and females, and variation in family size (5). These estimates can be used to calculate inbreeding so that an effective population size can be chosen to minimize inbreeding in a recurrent selection program.

According to Allard (1) there are three phenotypically discernible responses to recurrent selection. They are: (1) a change in the proportion of previously existing genotypes accompanied by a shift in the population mean, (2) the appearance of new genotypes, and (3) changes in variance.

Populations resulting from recurrent selection can be used as improved varieties and syntheties per se or they can be used as sources of inbred lines.

Methods of recurrent selection differ in the use of progeny testing and types of testers used. Simple phenotypic recurrent selection involves no test crossing or progeny testing and is limited to characters accurately identifiable with high heritability. Plants are usually self-pollinated, selected, and recombined. However, if selection can be made concurrently with pollination, plants may be interpollinated without being selfed.

Sprague and Brimhall (40) first demonstrated the effectiveness of phenotypic recurrent selection in corn when they compared two cycles of recurrent selection with five generations of selfing and selection for oil content in the corn kernel. Recurrent selection was found to be 2.6 times more efficient and the relative efficiency of recurrent selection is expected to increase in later generations due to maintenance of genetic variability. They suggested recurrent selection for European corn borer (Ostrinia nubilalis, Hübner) resistance by making selections concurrent with interpollination. Sprague et al. (41) continued to compare recurrent selection and selfing sleection for kernel oil content in five populations of corn. They found recurrent selection 1.3 to 3 times more effective and suggested at least one generation of random mating after intercrossing to maintain genetic variability.

Recurrent selection for characters of low heritability such as yield usually involve S_1 evaluation or test cross evaluation. However, with characters such as disease and insect resistance, which often have high heritabilities, simple phenotypic recurrent selection may be practiced although S_1 evaluation is sometimes used.

Jenkins et al. (19) reported successful use of phenotypic recurrent selection for improving populations of corn for resistance to northern corn leaf blight (Helminthosporium turcicum Pass.). They were able to increase resistance through three cycles of selecting and interpollinating resistant plants concurrently.

Penny et al. (34) practiced recurrent selection for resistance to European corn borer. They used nonreplicated S_1 rows to make selection before recombination. Three cycles of recurrent selection produced essentially borer resistant populations.

Jinahyon and Russell (20) evaluated three cycles of recurrent selection for stalk rot resistance in populations of corn derived from the Lancaster variety. Selections were based on the performance of replicated S_1 progeny rows. Selection was successful in improving resistance, and genetic variability still existed in the third cycle.

Widstrom et al. (45) reported progress from recurrent selection based on test cross performance for corn earworm (Heliothis zea Boddie) resistance.

Scott and Rosenkranz (38) compared three methods of recurrent selection for resistance to corn stunt. They compared selecting the best plant in the best ten S_1 progeny rows, selecting the best S_3 progeny, and selecting the best ten S_1 progenies based on replicated S_1 progeny row tests. Each method was effective and selection based on replicated S_1 progeny rows was most efficient.

Findley et al. (7) reported results from recurrent selection in corn for resistance to a complex of MDMV and MCDV in Ohio. Full-sib or

S_1 progenies or half-sib parents were selected for virus resistance and tested for yield and resistance to root and stalk lodging, European corn borer, and northern corn leaf blight. Three cycles of selection in two synthethic populations were evaluated. All three cycles in Oh(MDM)S1 were from sib matings of selected selfed plants. Cycle one of Oh(MDM)S2 was from four generations of sib mating selected plants, and cycles two and three were from sib mating selected selfed plants. In Oh(MDM)S1 percent MCD infected plants decreased from 74% in C0 to 43% in C3. Percent MDM infected plants decreased from 36% in C0 to 34% in C3. Percent healthy plants changed from 18% in C0 to 14% in C1 to 30% in C2 and was unchanged from C2 to C3. In Oh(MDM)S2 percent MCD infected plants decreased from 60% in C0 to 26% in C3. Percent MDM infected plants decreased from 22% in C0 to 10% in C3. Percent healthy plants increased from 28% to 59%.

Changes in characters other than those being selected can occur from recurrent selection. Such changes must be due to linkage, pleiotropy, inbreeding, or indirect selection (36).

Russell et al. (36) evaluated the C0 and C3 generations for changes in agronomic characters due to recurrent selection for European corn borer resistance by Penny et al. (34). They found differences in the populations per se or their test cross progeny for days to pollen shed, plant and ear height, ear-row number, ear length, weight/300 kernels, and grain yield. They determined whether changes in these characters were due to changes in gene frequency or inbreeding due to assortative mating by comparing population performance per se with test cross performance. Changes in weight/300 kernels and grain yield resulted from inbreeding caused by assortative mating. Since these changes were not changes in gene frequency they should only be important if the improved populations are used commercially per se. The changes would be unimportant if the populations are used as sources of inbred lines (36).

Jinahyon and Russell (21) found changes in plant and ear height, days to silk, mechanical stalk strength, crushing strength, rind thickness, internode weight, natural stalk rot, stalk lodging, grain moisture, and grain yield associated with successive cycles of selection for resistance to stalk rot in corn.

In addition to selection for disease and insect resistance, phenotypic recurrent selection has been reported in corn for lower ear placement (27, 44), early flowering (43), and stalk quality (2, 42, 46). In each case improvement was made for the character selected and associated changes occurred in some other agronomic characters other than the one selected.

The objective of this study was to determine the effect of phenotypic recurrent selection for resistance to maize dwarf mosaic and the corn virus disease complex under naturally and artificially induced epiphytotics in synthetic populations of dent corn and sweet corn.

Specificially, this study was designed to determine if selection under conditions of artificial inoculation with MDMV at Knoxville also conferred resistance to the virus disease complex when grown at Waverly and if selection for resistance to the virus disease complex at Waverly conferred resistance to MDM when inoculated at Knoxville or evaluated at an early season rating representing MDMV infection at Waverly.

CHAPTER II

MATERIALS AND METHODS

Development of Synthetics

The dent corn and sweetcorn synthetics used to initiate selection in this study were developed by Dr. L. M. Josephson at The University of Tennessee, Knoxville, Tennessee. Two synthetics involving virus tolerant inbred lines of dent corn and sweet corn were started in 1971.

The dent synthetic was begun by crossing the following single crosses as A × B, B × C, C × D, D × E, E × F, F × G, G × H, H × I, and I × J:

A = GA209 × Ky226.

B = H.751w × Mo18W.

C = GA209 × Ky61-2335.

D = SC155 × Mo12Y.

E = Ky66-2500 × CI.45.

F = Oh514 × T222.

G = T232 × T×601.

H = T222 × E663.T111.

I = Mo18W × E199.

J = T61WC × GA209.

These nine double crosses were crossed in all combinations plus reciprocals in 1972.

The sweet corn synthetic was created by crossing in all combinations 10 single crosses derived from 15 inbred lines. In 1972 seed composited from all crosses were planted in ten rows with each row representing a composite of seed from the crosses to one single cross. These ten rows were crossed in all combinations, and reciprocally.

In 1973, two composites of seed from each of the 36 dent corn crosses and reciprocals and the 45 sweet corn crosses and reciprocals were used to begin selection for virus resistance at two locations. Composites of dent corn seed and sweet corn seed were used to initiate selection while being grown on the Owens Brothers Farm near Waverly, Tennessee under heavy natural virus infection. The other composites were used to initiate selection at the Plant Science Field Laboratory, The University of Tennessee, Knoxville, Tennessee under an artificially induced epiphytotic.

At Waverly, the natural infestation of johnsongrass was allowed to grow until infection had occurred. The johnsongrass was then removed by hand hoeing. At Knoxville, corn plants were mechanically inoculated with MDMV extracted from infected johnsongrass, and infected johnsongrass plants were transplanted throughout the breeding nursery. These conditions were maintained for each breeding season.

Recurrent Selection Procedure

The method of selection was to intercross visually selected resistant plants of each synthetic each year. To avoid selfing, the plants of each synthetic were divided into two equal groups. Bulk pollen of resistant plants of one group was used to pollinate resistant plants of the other group, and reciprocally. At full symptom expression plants were rated for virus resistance and only apparently disease free plants were harvested. Mild selection was practiced for agronomically desirable plants. Each year a balanced composite of these seed was planted and the procedure repeated until five cycles of selection were completed. This procedure of phenotypic recurrent selection was practiced for both the dent and sweet corn synthetics at both locations each year.

Approximately 200 plants were grown of both synthetics at both locations in 1973. In the dent synthetic, 19% were selected at Waverly and 29% were selected at Knoxville. In the sweet corn synthetic, 7% were selected at Waverly and 12% were selected at Knoxville. The harvested seed constituted the cycle 0 (C0) generation. They are the progeny of the first cycle of recombination although selection was practiced.

Approximately 250 plants were grown of both synthetics at both locations in 1974, 1975, and 1976. Approximately 20% were selected in the dent synthetics and 15 to 20% were selected in the sweet corn synthetics each year. The harvested seed constituted the C1, C2, and C3 generations, respectively.

In 1977 approximately 500 plants of both synthetics were grown at Knoxville and approximately 300 plants of both synthetics were grown at Waverly. In the dent synthetics, 14% were selected at Waverly and 17% were selected at Knoxville. In the sweet corn synthetics, 10% were selected at Waverly and 11% were selected at Knoxville. The harvested seed constituted the C4 generation which was the last cycle of selection.

During each year of selection virus ratings were made on individual plants when maximum symptoms were expressed on a scale of 1 to 9 as follows:

1 = No apparent symptoms.

2 = Top two or three leaves mottled; no stunting.

3 = Entire plant above the ear mottled and/or discolored; no evident stunting.

4 = Chlorosis and/or discoloration above the ear; some stunting.

5 = Plant above the ear discolored; plants stunted and ear reduced in size.

6 = Upper three-fourths of plant chlorotic and/or discolored; plant stunted and ear reduced in size.

7 = Entire plant discolored and stunted; small ear.

8 = Entire plant discolored and stunted; no ear produced.

9 = Plant completely collapsed; no ear.

This rating scale closely parallels the reduction in yield of plants with increasing disease severity (26). In addition to percent plants infected, a severity index (SI) was determined for the diseased plants by multiplying the number of plants in each rating class, except class 1, by the rating value, and the sum of these was divided by the total number of diseased plants. This information on the severity of symptom expression is needed in addition to the number of diseased plants because plant reaction to the virus disease is variable. Two genotypes with the same number of diseased plants are not equal in virus resistance if one genotype has a low SI and the other has a high SI. A mean severity index (MSI) was calculated likewise by including the healthy plants of class 1 in the calculation. MSI provides an overall rating of a genotype that takes into account the number of disease free plants and the severity of infection of the diseased plants.

Phenotypic variances were estimated among the individual plants each year at both locations to determine changes in variability for virus reaction.

Inbreeding, F, due to sampling variance in small populations was calculated for each cycle of selection, t, referred to C0 with an arbitrary inbreeding coefficient of 0 by the following formula provided by Falconer (5):

$$F_t = 1 - \left(1 - \frac{1}{2N_e}\right)^t$$

with N_e being the effective population size. Inbreeding is expressed as a percent of 1.0, fixation.

Evaluation of Selection

Testing procedure. In 1978 progress from phenotypic recurrent selection under naturally and artificially induced epiphytotics was evaluated by three experiments duplicated at Waverly and Knoxville.

The Waverly test site, on the Owens Brothers Farm, was partially in a corn virus test and partially in soybean production the previous year. A fertilizer application of 252 kilograms per hectare of 8-24-24 was applied in the row at planting on 23 May. A side dressing of anhydrous ammonia at the rate of 90 kg/ha of N was applied during the seedling stage. Atrazine was applied over the rows. The test site was uniformly infested with johnsongrass which was allowed to grow until infection occurred. Hand hoeing was used to control the johnsongrass and other weeds threafter.

The Knoxville test site, at the Plant Science Field Laboratory, was in soybeans in 1977 and was in a corn virus test from 1969 through 1976. A fertilizer application of 1077 kg/ha of 6-12-12 was applied before planting. The experiments were planted on 29 May. Atrazine was applied on 29 May. A side dressing of ammonium nitrate was applied at the rate of 90 kg/ha of N on 28 June. Infected johnsongrass and sorghum (Sorghum bicolor L., Moench) plants were transplanted uniformly throughout the field on 7 June. From 12 June through 14 June all plants were mechanically inoculated with MDMV extracted from infected johnsongrass and sorghum.

Remnant seed from C0 through C4 of the Waverly and Knoxville selected dent synthetics constituted 10 entries grown in a 12-replicate, randomized complete block design yield test with 2-row plots of 15 plants per row. Plant spacing at Waverly was 20 cm within the rows and rows were spaced 97 cm apart for a plant population of 50,947 plants per hectare. Plant spacing at Knoxville was 20 cm within the rows and rows were spaced 102 cm apart for a plant population of 48,400 plants per hectare.

Remnant seed from C0 through C4 from Knoxville and Waverly selected sweet corn synthetics constituted 10 entries grown in an eight-replicate, randomized complete block design with single row plots of 25 plants per plot.

The ten entries derived from ten dent and sweet corn synthetics are defined as ten populations.

Remnant seed of C0 and C3 from Waverly and Knoxville selected dent synthetics were grown at Homestead, Florida during the winter of 1977-1978. One-hundred plants of each cycle and location of selection were randomly selected and self-pollinated. Seed from each ear were used to plant S_1 ear-rows with Waverly and Knoxville selections planted in separate two-replicate, randomized complete block designs with single row plots of 25 plants per plot. The entries in one design were 100 S_1 ear-rows each of Waverly selected C0 and C3 plants and the entries in the other design were 100 S_1 ear-rows each of Knoxville selected C0 and C3 plants.

Collection of data. Percent diseased plants was determined by counting the number of diseased plants per plot approximately six weeks after planting and again approximately three weeks after pollination. The early disease count, made during early plant growth, is expected to represent infection from MDMV. The late count, made at full symptom expression, is expected to represent infection from the virus disease complex (33).

Severity index and mean severity index were calculated for each entry in each experiment based on severity ratings made on each plant in each plot at full symptom expression as described in the discussion of the recurrent selection procedure.

In addition to virus reaction, data were obtained on grain yield and agronomic characters for the dent synthetic tests at Waverly and Knoxville.

Percent stalk lodging was obtained for all replications by recording the total number of stalks broken below the first ear-node at harvest. Lodging was severe at Knoxville.

All plots were hand harvested. Yield was determined by weighing the ear-corn produced per plot. All ear-corn weights were adjusted to shelled grain yield at 15.5% moisture. Pounds per plot were converted to quintals per hectare.

Percent moisture at harvest was measured from shelled grain samples from four replications.

Plant and ear height measurements were obtained on ten randomly selected plants for all replications at Waverly. Ear height was defined as the distance from the base of the plant to the top ear-node attachment. Plant height was measured from the base of the plant to the base of the tassel.

Statistical analyses. An epiphytotic did not develop at Knoxville so that all data on disease reaction for the Knoxville test were excluded from analyses. Grain yield and percent stalk lodging are reported for the dent synthetic test at Knoxville.

For both dent synthetic yield tests and the sweet corn synthetic test at Waverly, analysis of variance was computed for all characters measured. The nine degrees of freedom for populations were partitioned into an independent orthogonal contrast of Waverly verses Knoxville selection and orthogonal polynomial regression for cycles of selection with appropriate interactions. F tests were made using the population x replication mean square as the error term as described by Snedecor and Cochran (39). If interaction between location of selection and regression on cycles of selection was significant, the degrees of freedom were partitioned separately for Waverly and Knoxville selections.

Entry means were calculated for each character for each cycle of selection at both locations and overall means for Waverly and Knoxville selections were also calculated.

Plant and ear height data from the Waverly dent synthetic test were also used to estimate variances for each entry based on the 120 measured plants per entry rather than plot means.

Linear correlation coefficients between various disease and agronomic characters were estimated from the dent and sweet corn synthetic tests. It was of interest to determine if there was any linear association between the number of diseased plants and the severity of infection, the number of diseased plants and changes in agronomic characters, and the severity of infection and changes in agronomic characters.

Entry mean data from the S_1 ear-row dent synthetic test at Waverly were used to plot frequency distribution curves for percent diseased plants, severity index, and mean severity index to allow for comparisons between C0 and C3 and between Waverly and Knoxville selections.

Variability was estimated for C0 and C3 of Waverly and Knoxville selections from the S_1 ear-row test at Waverly by determining variance components from the analysis of variance (39) for early and late percent diseased plants, severity index, and mean severity index.

CHAPTER III

RESULTS AND DISCUSSION

Evaluation of Selection in the Dent Synthetic

Evaluation in Selection Cycles

Percent diseased plants, severity index (SI) of diseased plants, mean severity index (MSI), and variability among plants for SI and MSI during selection at Waverly and Knoxville are shown in Table 1. Successful selection should direct gene frequencies for resistance toward 1.0. An increase in resistance accompanied by a decrease in variability for resistance indicates that gene frequencies have been directed from intermediate levels toward 1.0. Overall, the number of diseased plants, the severity of infection, and variability for virus reaction decreased with successive breeding cycles at both Waverly and Knoxville.

Proportion selected and cumulative inbreeding for each cycle of selection at both locations are shown in Table 2. The inbreeding coefficients, expressed as a percent of 1.0, are based on estimates of effective population size. Inbreeding did occur with successive cycles of selection.

Evaluation of Cycles of Selection in Yield Trials

Virus reaction. Means of virus reaction of each cycle of selection from both locations evaluated at Waverly are shown in Table 3. Percent diseased plants at the early rating is expected to represent infection from MDMV whereas percent diseased plants at the late rating is expected to represent infection from the complex of MDMV and MCDV. Statistical

Table 1. Means and phenotypic variances for virus reaction of the dent synthetics estimated from actual years of selection.

Year	Means			$\hat{\sigma}^2$	
	Percent Diseased Plants	Severity Index	Mean Severity Index	Severity Index	Mean Severity Index
			Waverly Selection		
1973	41.7	4.0	2.3	3.58	3.70
1974	---†	---	---	---	---
1975	---	---	---	---	---
1976	5.1	2.9	1.1	0.07	0.19
1977	35.1	2.9	1.7	0.62	1.04
			Knoxville Selection		
1973	10.7	2.3	1.1	2.68	0.43
1974	28.4	3.2	1.6	1.45	1.41
1975	18.6	2.7	1.3	1.00	0.63
1976	4.6	2.7	1.1	0.24	0.13
1977	2.0	3.1	1.0	0.11	0.09

†Data not available for Waverly, 1974 and 1975.

Table 2. Proportion selected and inbreeding estimates for cycles of selection in the dent synthetic.

Cycle	Waverly Selections		Knoxville Selections	
	Proportion Selected†	F	Proportion Selected	F
	%	%	%	%
C0	19	0	29	0
C1	--	1.4	25	0.9
C2	--	2.3	19	1.9
C3	22	3.1	20	2.9
C4	14	4.2	17	3.5

†Data not available for Waverly C1 and C2.

Table 3. Means of virus reaction for the dent populations evaluated at Waverly, 1978.

Cycle	Diseased Plants: Early Rating %	Diseased Plants: Late Rating %	Severity Index	Mean Severity Index
		Waverly Selections		
C0	13.5	5.5	2.6	1.1
C1	16.9	7.3	2.5	1.1
C2	18.0	4.4	2.9	1.4
C3	16.0	7.9	2.4	1.1
C4	12.1	7.9	2.6	1.3
Mean	15.3	6.6	2.6	1.2
		Knoxville Selections		
C0	19.3	8.3	2.1	1.1
C1	19.5	8.3	2.9	1.2
C2	20.3	7.5	2.3	1.1
C3	19.4	7.9	2.1	1.1
C4	20.3	6.6	2.3	1.1
Mean	19.8	7.7	2.3	1.1

significance of mean differences can be determined by examining the analysis of variance in Table 4. Trends in increasing or decreasing virus resistance are indicated by significant mean squares for regression of virus reaction on cycles of selection. Differences in performance between Waverly and Knoxville selections are indicated by significant mean squares for location of selection. When neither deviations from linear regression or location x deviations mean squares are significant, interpretations are straightforward concerning response to selection from C0 to C4 and differences between the two locations of selection. When location x regression interaction is significant, response to selection should be examined separately for the two locations of selection. If interaction is not significant then it can be inferred that response to selection from C0 to C4 was the same at both locations.

No linear trend of increasing resistance from C0 to C4 is indicated. The Waverly selections had significantly fewer diseased plants at the early rating than the Knoxville selections when evaluated at Waverly indicating that selection while recombining to create C0 at Waverly was more effective than at Knoxville. This was expected because of greater disease pressure at Waverly resulting in fewer disease escaped plants being selected.

Agronomic characters. Means of grain yield and other agronomic characters that may be changed by selection or influenced by the level of resistance under disease pressure are shown in Table 5. The analysis of variance in Table 6 indicates that the Waverly selections had less stalk lodging than the Knoxville selections when evaluated under disease

Table 4. Analyses of variance of virus reaction of the dent population evaluated at Waverly, 1978.

Source	df	Mean Squares: Diseased Plants: Early Rating %	Mean Squares: Diseased Plants: Late Rating %	Severity Index	Mean Severity Index
Replications	11	340.24**	81.46*	0.43	0.06
Populations	9	---	---	---	---
Location of Selection	1	529.30**	35.75	2.20	0.18
Cycles of Selection	4	---	---	---	---
Linear	1	2.65	1.96	0.19	0.03
Deviations	3	48.98	19.07	0.77	0.08
Location x Cycles	4	---	---	---	---
Location x Linear	1	19.38	53.30	0.07	0.13
Location x Deviations	3	43.80	10.50	1.19	0.07
Error	99	59.75	35.84	0.83	0.12
C.V.,%		44.1	83.8	36.9	29.5

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 5. Means of grain yield and agronomic characters for the dent populations evaluated at Waverly, 1978.

Cycle	Grain Yield	Stalk Lodging	Plant Height	Ear Height	Grain Moisture
	q/ha	%	cm	cm	%
			Waverly Selections		
C0	46.5	11.5	222	120	21.3
C1	45.6	8.8	220	115	22.4
C2	45.9	12.1	218	114	21.5
C3	49.3	11.2	217	107	21.5
C4	49.0	8.7	219	111	22.1
Mean	47.3	10.5	219	113	21.8
			Knoxville Selections		
C0	41.1	13.9	224	122	22.6
C1	43.2	15.4	216	114	21.8
C2	48.8	11.7	220	114	21.2
C3	45.0	14.2	216	105	22.1
C4	43.7	17.2	218	109	21.4
Mean	44.2	14.5	219	113	21.8

Table 6. Analyses of variance of yield and agronomic characters of the dent populations evaluated at Waverly, 1978.

Source	df	Mean Squares: Grain Yield	Stalk Lodging	Plant Height	Ear Height	Grain Moisture
		q/ha	%	cm	cm	%
Replications	11	133.01**	89.94	260.97*	50.39	0.81
Populations	9	---	---	---	---	---
Location of Selection	1	278.75**	485.21**	8.97	8.26	0.02
Cycles of Selection	4	---	---	---	---	---
Linear	1	172.49*	2.54	246.71	2232.77**	0.33
Deviations	3	35.36	5.25	95.23	216.58	0.60
Location x Cycles	4	---	---	---	---	---
Location x Linear	1	0.03	43.60	4.71	56.90	1.83
Location x Deviations	3	103.05*	83.83	58.06	6.39	1.47
Error	99	33.08	58.31	132.06	89.29	0.63
C.V.,%		12.6	61.3	5.3	8.4	3.6

*,**Significant at the 0.05 and 0.01 levels, respectively.

pressure at Waverly. The location x deviations mean square for grain yield is significant, thus requiring partitioning of degrees of freedom separately for Waverly and Knoxville selections. Such partitioning revealed no significant change in yield with succeeding cycles of selection at Waverly. Selection at Knoxville resulted in no significant linear change but a quadratic response was significant at the 0.05 level of probability. Examination of the means of the Knoxville selections in Table 5 shows that grain yield increased and then decreased with five cycles of selection. A significant reduction in ear height occurred with successive cycles of selection at both locations without a corresponding reduction in plant height.

Linear correlation coefficients between disease and agronomic characters estimated from the ten populations evaluated at Waverly are shown in Table 7. Highly significant positive correlations occurred between the number of diseased plants at the late rating and SI and MSI. There was a highly significant negative correlation between the number of diseased plants at the early rating and grain yield but not between the number of diseased plants at the late rating and grain yield.

Variability among the ten populations was estimated by the phenotypic variances for plant and ear height as determined from ten randomly selected plants from each replication (Table 8). Ear height variability decreased from C0 to C4 with selection at both locations. The reduction in variability may be associated, in part, with inbreeding.

Means of grain yield and percent stalk lodging for the ten populations evaluated at Knoxville in the absence of an epiphytotic

Table 7. Linear correlation coefficients between various disease and agronomic characters estimated from the dent populations evaluated at Waverly, 1978.

Character	Diseased Plants (Late Rating)	Severity Index	Mean Severity Index	Grain Yield	Stalk Lodging
Diseased Plants (Early Rating)	0.23*†	0.12	0.03	-0.29**	0.05
Diseased Plants (Late Rating)		0.47**	0.25**	-0.12	0.02
Severity Index			0.33**	-0.10	-0.03
Mean Severity Index				-0.08	0.04
Grain Yield					-0.25**

*,**Significant at the 0.05 and 0.01 levels, respectively.
†Degrees of freedom = 119.

Table 8. Phenotypic variances for plant and ear height estimated from 120 randomly selected plants of the dent populations evaluated at Waverly, 1978.

Cycle	Plant Height	Ear Height
	cm	cm
	Waverly Selections	
C0	126.53	59.59
C1	114.51	59.05
C2	133.31	63.67
C3	78.06	26.88
C4	118.85	38.80
	Knoxville Selections	
C0	115.52	61.56
C1	132.82	60.46
C2	109.38	51.41
C3	96.03	37.07
C4	107.39	40.95

are shown in Table 9. None of the populations differed significantly for either character.

Evaluation of Random S_1 Selections

The relative resistance of the C0 and C3 populations selected at Waverly and Knoxville is compared in frequency distributions with the performance of plants within an S_1 row plotted on the x-axis and the number of S_1 rows with that performance plotted on the y-axis. Such distributions present changes in means, changes in the frequency of observations at the mean, and changes in the proportion of plants in the resistant and susceptible tails of the distributions. Interpretations can be made concerning the improvement of the synthetic due to selection and the potential for selecting resistant lines from the improved population by having a larger proportion of plants in the resistant tail. Evaluating mean performance of S_1 ear-rows should overcome the problem of S_0 plants escaping infection.

The frequency distribution for infected plants at the early rating (Fig. 1.) is believed to represent MDMV infection. The Waverly selected C3 population had a higher mean percent diseased plants than the Waverly selected C0 population. The proportion of plants in the resistant tail of the distribution is about the same for C0 and C3 selected at Waverly. There is a higher proportion of plants in the susceptible tail of C3. Essentially no change can be determined from the distribution of the Knoxville selections except that there are more disease free S_1 rows in C3 than C0. The Knoxville C3 selections had a lower mean than the Waverly C3 selections.

Table 9. Means of yield and stalk lodging for the dent populations evaluated at Knoxville, 1978.

Cycle	Grain Yield	Stalk Lodging
	q/ha	%
	Waverly Selections	
C0	69.0	24.6
C1	62.1	23.7
C2	68.4	23.2
C3	68.4	18.7
C4	67.1	20.0
Mean	67.1	22.1
	Knoxville Selections	
C0	63.3	20.9
C1	64.6	21.5
C2	67.1	30.0
C3	67.7	24.4
C4	66.5	20.6
Mean	65.9	23.5

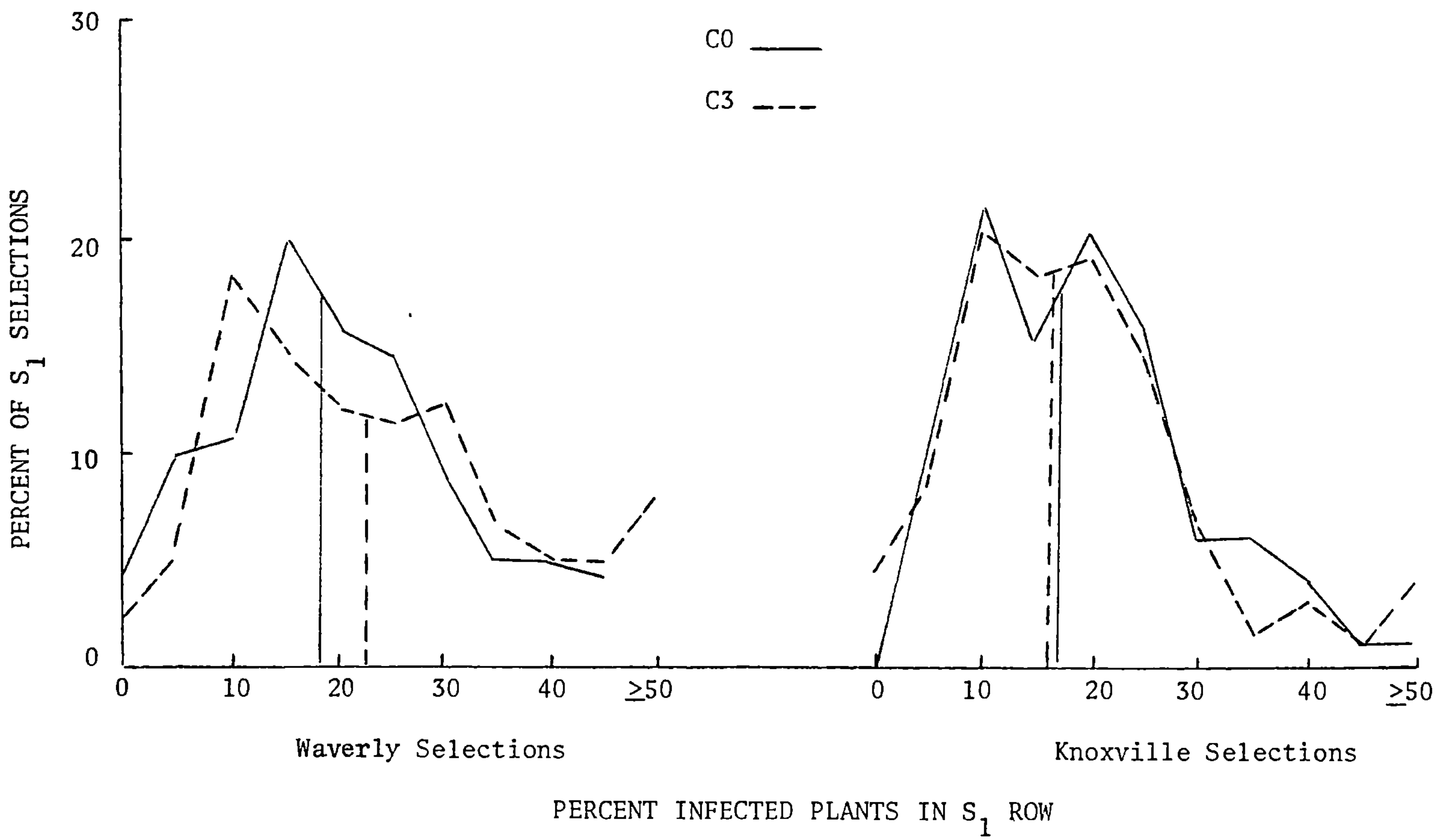

Fig. 1. Frequency distribution for infected plants at early rating in 100 selections of C0 and C3 dent populations evaluated at Waverly, 1978.

The frequency distribution for infected plants at the late rating (Fig. 2.) is believed to represent infection from the virus disease complex of MDMV and MCDV. Selection at Waverly did not substantially change the mean virus reaction from C0 to C3. Waverly C3 had a higher proportion of plants in both tails than Waverly C0. Selection at Knoxville resulted in little change except for a higher proportion of plants in the susceptible tail of C3. The mean of Knoxville selected C3 is lower than the mean of Waverly selected C3.

The frequency distribution for severity index (Fig. 3.) represents the degree of symptom expression of diseased plants at the late rating. Selection at Waverly resulted in no change in the mean from C0 to C3 but C3 had a higher proportion of plants in both ends of the distribution. Selection at Knoxville resulted in no change in the mean from C0 to C3 but C3 had a higher proportion of plants in both ends of the distribution. Knoxville C3 had a lower mean than Waverly C3 and a higher proportion of plants in classes 1 and 2.

The frequency distribution for mean severity index (Fig. 4.) represents the degree of symptom expression of all plants at the late rating. Selection at Waverly did not change the mean from C0 to C3 but C3 had a higher proportion of plants in both ends of the distribution. Selection at Knoxville did not change the mean from C0 to C3 but C3 had a higher proportion of plants in both ends of the distribution. Knoxville C3 had a lower mean than Waverly C3 and a higher proportion of plants in classes 1 and 2.

In general, selection did little to change the mean virus reaction from C0 to C3, but selection resulted in a higher proportion of plants

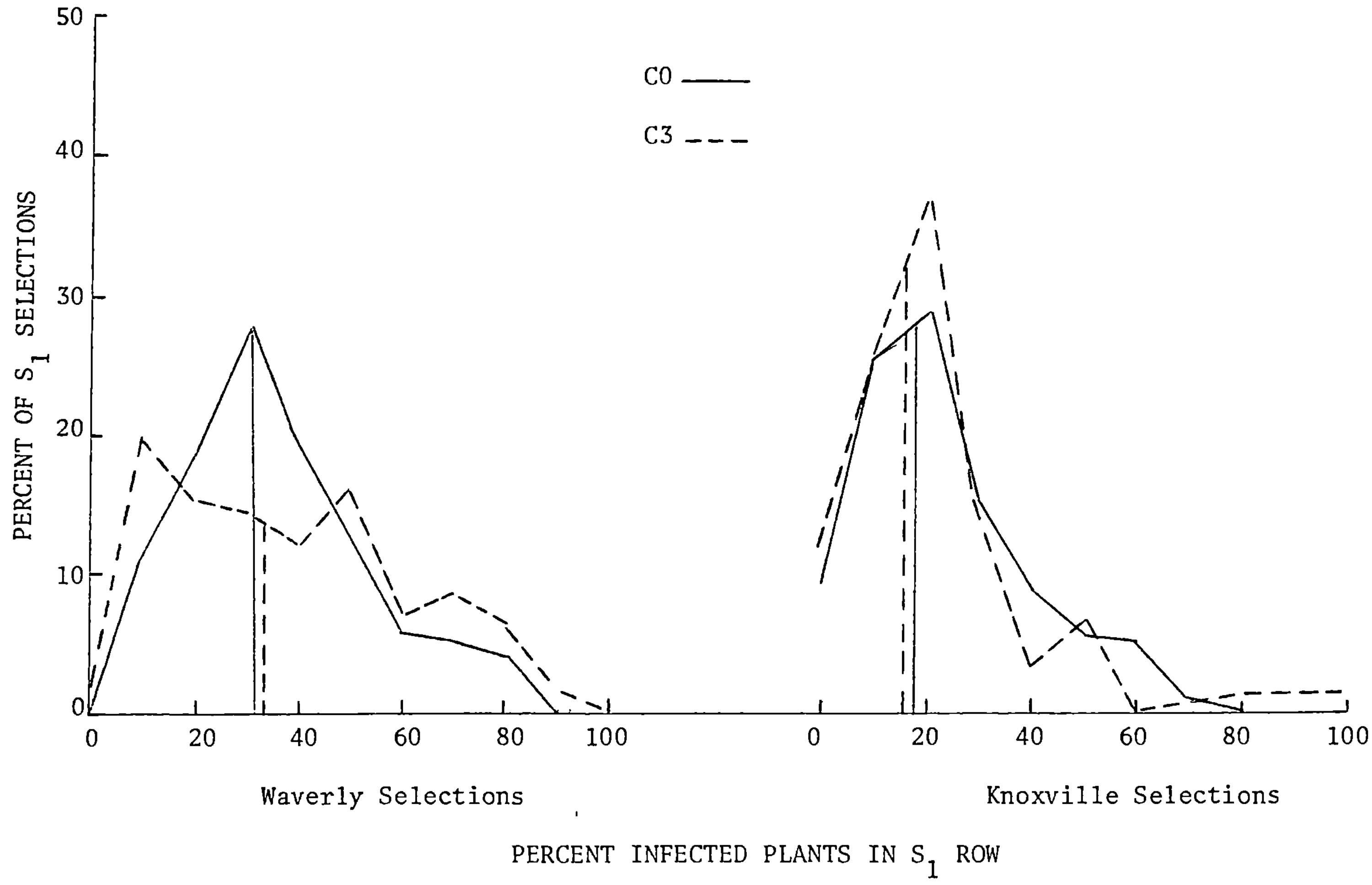

Fig. 2. Frequency distribution for infected plants at late rating in 100 selections of C0 and C3 dent populations evaluated at Waverly, 1978.

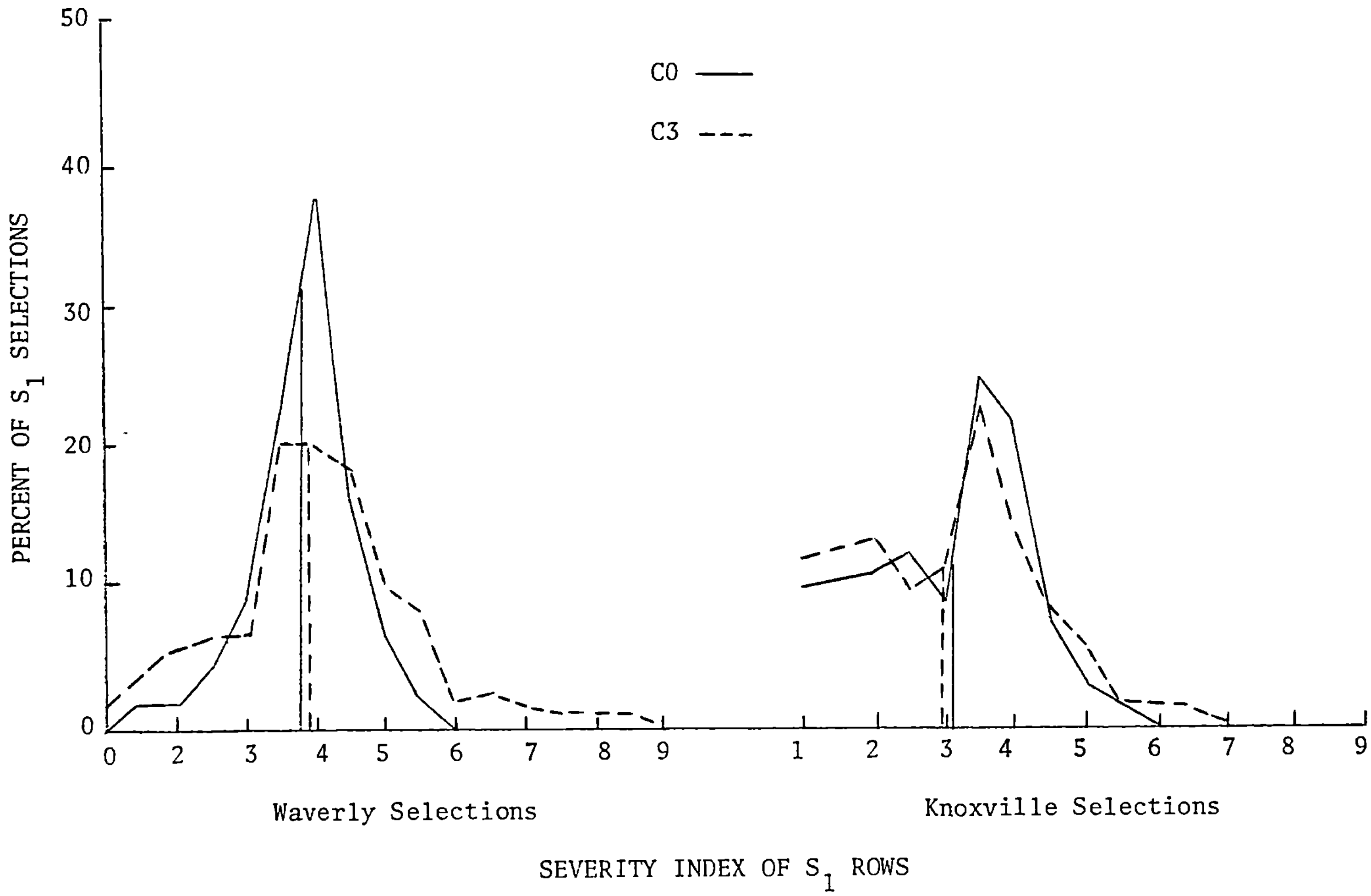

Fig. 3. Frequency distribution for severity index in 100 selections of C0 and C3 dent populations evaluated at Waverly, 1978.

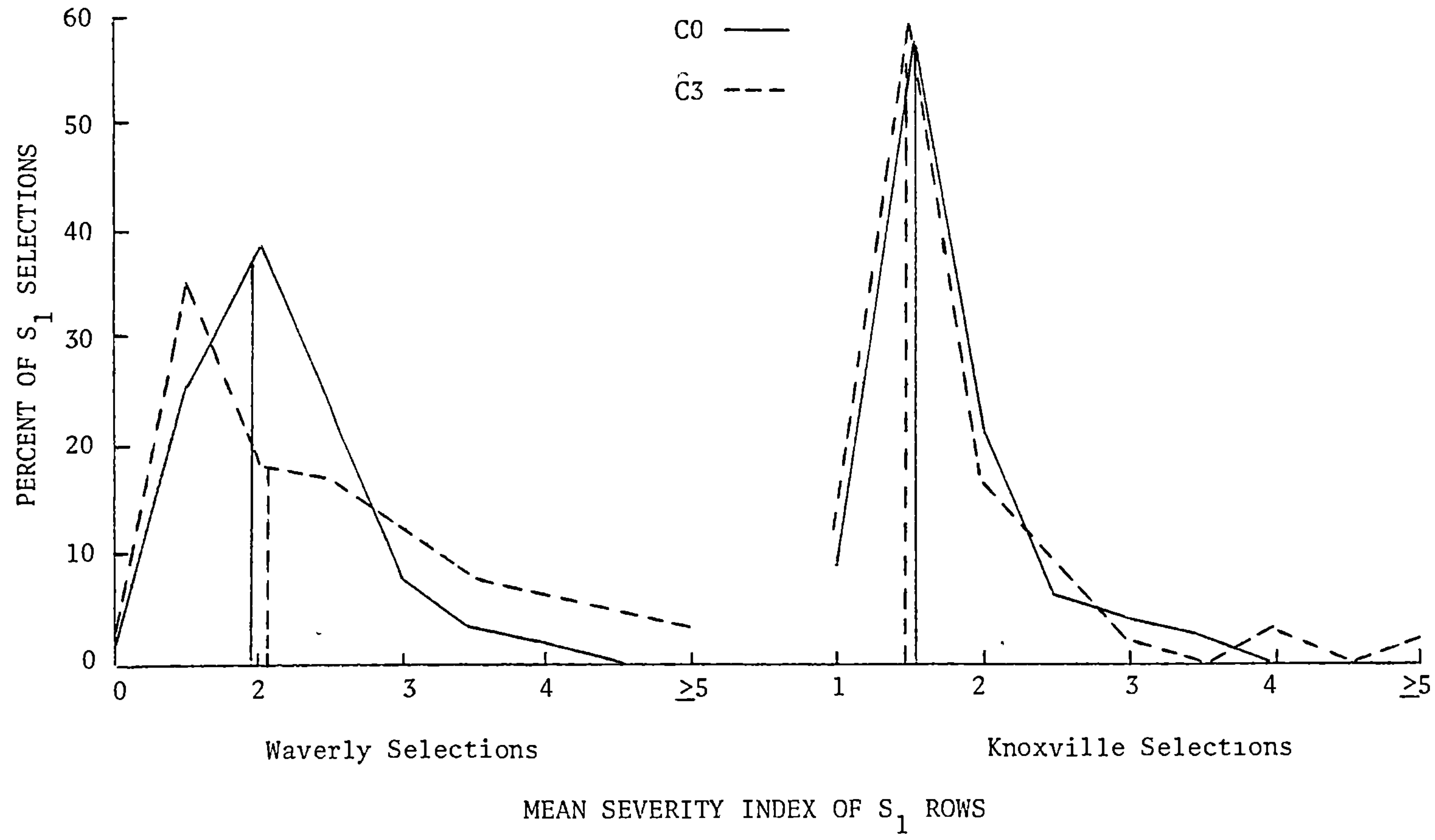

Fig. 4. Frequency distribution for mean severity index in 100 selections of C0 and C3 dent populations evaluated at Waverly, 1978.

in the resistant and susceptible tails of the distributions. This indicates greater variability for virus reaction in C3 than C0. This is confirmed by examining the variance components for variation among 100 S1 rows of C0 and C3 selected at Waverly and Knoxville (Table 10). In each case variability was greater in C3. Recurrent selection theoretically reduces variability for the selected character as gene frequencies move from intermediate levels toward 1.0. Variability will increase as gene frequencies move from low levels toward 0.5, but the level of resistance in the C0 populations and in the inbreds used to create the synthetic indicate relatively high gene frequencies. The apparent discrepancy may perhaps be explained by the confounding effect of hybrid vigor on virus reaction. Hybrid vigor seems to enhance virus tolerance in genetically resistant and susceptible genotypes. It is possible that the effectiveness of selection among vigorous plants is reduced because of this confounding of tolerance and resistance. Susceptible genotypes generally express greater symptom severity when they become inbred. The population of plants used to create C0 consisted of F_1 progeny of crosses between different double cross hybrids. Although C0 is a product of some recombination, it is not a product of random recombination under the conditions of an idealized population which reaches equilibrium in one generation of random mating. The C3 population had a high distribution of resistant plants in one tail presumably due to selection. A high distribution of infected plants in the other tail indicates that these infected plants may be more susceptible than expected when compared to C0 because of inbreeding depression relative

Table 10. Variance components for C0 and C3 dent populations estimated from 100 S_1 rows evaluated at Waverly, 1978.

Cycle	Diseased Plants: Early Rating %	Diseased Plants: Late Rating %	Severity Index	Mean Severity Index
		Waverly Selections		
C0	58.00	163.88	0.05	0.16
C3	180.28	398.72	0.82	0.69
		Knoxville Selections		
C0	46.25	181.90	0.48	0.17
C3	67.46	223.48	0.72	0.34

All variance components are significant at the 0.5 level.

to C0. Thus selection has directed the population into two more distinct subgroups in C3.

Selection for resistance by choosing symptomless plants at maximum symptom expression resulted in little difference in performance when rated for MDMV reaction early in the season and the virus complex reaction later.

The apparent superiority of Knoxville C3 over Waverly C3 in terms of lower means and higher proportion of plants in the resistant tail of the distributions is difficult to explain. This is in contrast to the results based on performance of the S_0 populations (Table 3, p. 24, Table 4, p. 26), which showed the Waverly selections superior in the early rating and no difference for the other characters.

Evaluation of Selection in the Sweet Corn Synthetic

Evaluation in Selection Cycles

Percent diseased plants, SI of diseased plants, MSI, and variability among plants for SI and MSI during selection at Waverly and Knoxville are shown in Table 11. Overall, the number of diseased plants and the severity of infection decreased with successive cycles of selection in both locations. At Waverly, variability for virus reaction decreased from 1973 to 1977. At Knoxville, variability increased from 1973 to 1974 and decreased thereafter.

Proportion selected and cumulative inbreeding for each cycle of selection at both locations are shown in Table 12. Inbreeding did occur with successive cycles of selection.

Table 11. Means and phenotypic variances for virus reaction of the sweet corn synthetics estimated from actual years of selection.

Year	Means: Percent Diseased Plants	Means: Severity Index	Means: Mean Severity Index	$\hat{\sigma}^2$: Severity Index	$\hat{\sigma}^2$: Mean Severity Index
			Waverly Selection		
1973	80.2	5.8	4.9	4.42	7.28
1974	---†	---	---	---	---
1975	---	---	---	---	---
1976	54.7	4.9	3.1	3.05	5.39
1977	58.0	3.8	2.6	2.57	3.37
			Knoxville Selection		
1973	71.4	4.2	3.3	2.85	4.20
1974	72.3	5.0	3.9	5.25	7.00
1975	63.8	3.4	2.6	2.07	2.71
1976	33.0	3.0	1.7	1.16	1.29
1977	22.6	3.4	1.5	2.37	1.55

†Data not available for Waverly for 1974 and 1975.

Table 12. Proportion selected and inbreeding estimates for cycles of selection in the sweet corn synthetic.

Cycle	Waverly Selections: Proportion Selected†	Waverly Selections: F	Knoxville Selections: Proportion Selected	Knoxville Selections: F
	%	%	%	%
C0	7	0	12	0
C1	--	2.5	14	1.7
C2	--	3.6	21	2.7
C3	15	4.9	19	3.8
C4	10	6.7	11	4.7

†Data not available for Waverly C1 and C2.

Evaluation of Sweetcorn Populations

Means of virus reaction for each cycle of selection from both locations are shown in Table 13. Statistical significance of mean differences can be determined by examining the analyses of variance in Table 14. A highly significant linear reduction in SI occurred with successive cycles of selection at both locations.

A significant mean square for deviations from linear regression for percent diseased plants at the early rating requires examination of the quadratic response which revealed significant location x quadratic interaction thus requiring partitioning of degrees of freedom separately for Waverly and Knoxville selections (Table 15). Significant location x deviations mean squares for percent diseased plants at the late rating and MSI also require separate partitioning of degrees of freedom for both locations of selection and examination of quadratic responses (Table 15). In the Waverly selections, no significant response to cycles of selection was detected for percent diseased plants at the early rating and for MSI. A highly significant quadratic response for percent diseased plants at the late rating occurred. Examination of the means in Table 13 revealed that the number of diseased plants increased through C2 and then decreased through C4. C0 had 57.1% diseased plants and C4 had 49.4% diseased plants. In the Knoxville selections significant linear and quadratic responses were obtained for cycles of selection for percent diseased plants at the early rating, percent diseased plants at the late rating, and MSI. Examination of the means of the Waverly selections (Table 13) shows that percent diseased

Table 13. Means of virus reaction for the sweet corn populations evaluated at Waverly, 1978.

Cycle	Diseased Plants Early Rating %	Diseased Plants Late Rating %	Severity Index	Mean Severity Index
		Waverly Selections		
C0	33.6	57.1	5.2	3.4
C1	27.2	67.6	4.8	3.5
C2	30.8	68.7	4.7	3.5
C3	32.9	63.4	4.8	3.3
C4	23.0	49.4	4.2	2.6
Mean	29.9	61.2	4.7	3.3
		Knoxville Selections		
C0	49.7	74.5	5.7	4.5
C1	26.8	66.2	4.8	3.6
C2	30.4	54.3	5.0	3.4
C3	33.1	59.6	4.7	3.2
C4	32.5	61.5	5.0	3.5
Mean	34.5	63.2	5.0	3.6

Table 14. Analyses of variance of virus reaction of the sweet corn populations evaluated at Waverly, 1978.

Source	df	Mean Squares: Diseased Plants: Early Rating %	Diseased Plants: Late Rating %	Severity Index	Mean Severity Index
Replications	7	1173.50**	293.71	3.72**	1.86**
Populations	9	---	---	---	---
Location of Selection	1	424.58	78.80	2.15	3.00*
Cycles of Selection	4	---	---	---	---
Linear	1	908.69*	1099.35*	5.26**	6.68**
Deviations	3	544.12*	71.12	0.58	0.17
Location x Cycles	4	---	---	---	---
Location x Linear	1	30.02	68.38	0.18	0.23
Location x Deviations	3	236.30	848.25**	0.63	1.87*
Error	63	133.98	173.85	0.56	0.60
C.V.,%		36.0	21.2	15.3	22.4

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 15. Analyses of variance of virus reaction with degrees of freedom partitioned separately for Waverly and Knoxville selected sweet corn populations evaluated at Waverly, 1978.

		Mean Squares		
		Diseased Plants		Mean
		Early Rating	Late Rating	Severity
Source	df	%	%	Index
Waverly Selections	4	---	---	---
Linear	1	304.20	309.68	2.21
Quadratic	1	12.76	1749.06**	1.98
Deviations	2	229.62	1.68	0.13
Knoxville Selections	4	---	---	---
Linear	1	634.50*	858.05*	4.70**
Quadratic	1	1086.89**	810.01*	3.64*
Deviations	2	391.19	97.85	0.12

*,**Significant at the 0.05 and 0.01 levels, respectively.

plants at the early rating decreased significantly from C0 to C1 and increased slightly from C1 to C4. C0 had 49.7% diseased plants and C4 had 32.5% diseased plants. Percent diseased plants at the late rating decreased significantly from C0 to C2 and then increased from C2 to C4. However, C0 was 74.5% diseased whereas C4 was 61.5% diseased. MSI decreased significantly from C0 to C3 and increased from C3 to C4. However, C0 had a MSI of 4.5 whereas C4 had a MSI of 3.5.

In general, selection at both locations reduced the amount and severity of disease significantly in the sweet corn synthetic. There was a greater response to selection from C0 to C4 at Knoxville. However, the Waverly selected C0 population had fewer diseased plants and a lower severity of infection than the Knoxville selected C0 population. This indicates that selection while recombining to create C0 at Waverly was more effective than at Knoxville. Despite the greater response to selection at Knoxville after creation of C0, the Waverly selected C4 population had fewer diseased plants at both ratings and less severity of infection than the Knoxville selected C4 population.

Negative response to selection in the later generations may suggest the effect of inbreeding depression in that improvement for virus resistance was made in the early generations but inbreeding caused greater expression of severity of infection in susceptible plants that exhibited a tolerance when they were more vigorous due to heterozygosity.

Linear correlation coefficients were estimated from the sweet corn population test at Waverly (degrees of freedom = 79). There was a highly significant correlation of 0.68 between the number of diseased plants at the early rating and the severity index at the late rating. A lower correlation of 0.27 between the number of diseased plants at the late rating and the severity index at the late rating was significant. The higher correlation between the number of diseased plants at the early rating and SI indicates that the plants infected with MDMV early in the season may have greater symptom expression at the late rating. The correlation between the number of diseased plants at the early and late ratings was 0.10 and not significant. This does not indicate a relationship between plant response to MDMV at the early rating and the virus disease complex at the late rating.

CHAPTER IV

CONCLUSIONS

The objective of this study was to determine the effect of phenotypic recurrent selection for resistance to MDM and the virus disease complex in synthetic populations of dent corn and sweet corn under naturally and artificially induced epiphytotics. It was of particular interest to determine if selection at Knoxville under mechanical inoculation with MDMV resulted in resistance in the virus disease complex when evaluated at Waverly, and if selection for resistance to the complex at Waverly resulted in improved resistance to MDM as expressed in the early disease rating.

Each cycle of selection at both locations in both synthetics was evaluated for virus reaction by determining the number of diseased plants and the severity of infection of the diseased plants. Host reaction to virus infection is largely quantitative, and genotypes with the same number of diseased plants may still vary in resistance because of differences in the severity of infection.

Evaluation of the dent populations showed no improvement for virus reaction from C0 to C4 at either location. The Waverly selections had significantly fewer diseased plants at the early rating than the Knoxville selections when evaluated at Waverly. This indicates that selection at Waverly while recombining to create C0 was more effective than at Knoxville. This would presumably be due to the greater disease pressure at Waverly resulting in selection of fewer escaped plants.

Evaluation of the frequency distributions for virus reaction at Waverly among 100 S_1 ear-rows from 100 random selections in the C0 and C3 dent populations showed no substantial changes in means from C0 to C3. The C3 distributions showed greater variability for virus reaction with a higher proportion of plants in the resistant and susceptible tails of the distribution. Since heterozygous plants seem to tolerate virus infection better than partially inbred plants, there is a confounding effect of hybrid vigor and virus reaction. Selection may have directed the synthetic into two more distinct subgroups in C3 with selection increasing the frequency of resistant selections but inbreeding depression causing greater expression of disease severity in the susceptible plants.

The frequency distributions indicate that the Knoxville selected C3 population is superior to the Waverly selected C3 population in terms of lower mean virus reaction and a higher proportion of plants in the resistant tail of the distributions. This is in contrast to the performance of the S_0 populations which showed little difference between Waverly and Knoxville selected C3 populations.

Selection in the sweet corn synthetic resulted in reduction in the number and severity of diseased plants at both locations when evaluated at Waverly. In general, selection improved resistance in the first cycles but response leveled off or reversed in the later cycles presumably due to inbreeding depression and reduction in variability for virus reaction. However, the C4 populations were superior to the C0 populations. Response to selection after C0 was greater at Knoxville than at Waverly. However, the Waverly selected C0 population was more resistant than the Knoxville selected C0 population. This indicates that selection while recombining to create the C0 populations was more effective at Waverly than at Knoxville.

Positive response to selection from C0 to C4 in the sweet corn synthetic as compared to little or no response from C0 to C4 in the dent corn synthetic may be a result of differences in genetic variability for resistance between the two synthetics. The level of resistance in the dent populations is much higher than in the sweet corn populations. Such differences may be due to differences in vigor, but differences in gene frequencies for resistance should be important. The high level of resistance in the dent populations should be a result of high gene frequencies. The lower level of resistance in the sweet corn populations should be a result of low or intermediate gene frequencies. Genetic variability is low at low gene frequencies and increases as gene frequencies approach 0.5. Response to selection is partly a function of heritability and heritability is maximum when genetic variance is maximum.

Theoretically, recurrent selection should be effective in increasing virus resistance in a genetically variable population. Lack of response to selection from C0 to C4 in the dent synthetic may be due to inbreeding depression, reduction in genetic variability for resistance, and changes in disease pressure from season to season resulting in susceptible disease escaped plants being selected. However, because selection for resistance and mild selection for agronomically desirable plants was conducted among S_0 plants, selection may have favored vigorous heterozygous plants rather than just the plants with high gene frequencies for resistance. If such was the case then the undesirable alleles would have been maintained at higher frequencies than expected.

Selection based on evaluation of S_1 progeny rows may have provided for better discrimination among S_0 genotypes. This should allow identification of susceptible genotypes that either escaped inoculation or were tolerant to virus infection due to hybrid vigor.

Since response to selection is a function of heritability and selection intensity, response can be improved by increasing selection intensity when heritability is low. Growing approximately 250 plants per generation and selecting the best 10% based on S_1 performance would allow for a high selection intensity with a low rate of inbreeding.

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LITERATURE CITED

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