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Selection for corn rootworm tolerance in maize

by

John Charles Owens

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INTRODUCTION

Resistance of crops to insect pests is highly desirable but not easily achieved. It is generally concluded that resistant varieties offer distinct advantages over insect control devoted exclusively to chemical and cultural methods. Resistant varieties normally would allow for gains in yield while lowering the increased production costs inherent with pesticide purchase and application. The widespread use of such varieties should alleviate the everincreasing emergence of insect strains resistant to insecticides which have previously controlled them. Potentially, even a low level of crop resistance would allow insecticide users an alternative to the blanket applications which so often have been employed by necessity. Cultural methods of insect control, including crop rotation, barriers, and trap crops, are becoming more restricted in modern agriculture where their value must be carefully assessed in relation to economic return. In light of such features, resistance should not be regarded as a panacea in the host-pest relationship, but rather a method of insect control which performs at its best in a well-integrated abatement effort.

R. H. Painter (1951, p. 27) produced the definitive work on insect resistance in crop plants and classified the mechanisms of resistance on three interrelated bases: nonpreference, antibiosis, and tolerance. Tolerance was

defined as

> ". . .a basis of resistance in which the plant
> shows an ability to grow and reproduce itself
> or to repair injury to a marked degree in
> spite of supporting a population approximately
> equal to that damaging a susceptible host."

Historically, recovery or tolerance to the corn rootworm

has been considered an important factor in the resistance

observed in strains of maize.

The corn rootworm complex [Diabrotica virgifera

LeConte, western corn rootworm; D. longicornis (Say),

northern corn rootworm; and D. undecimpunctata howardi

Barber, southern corn rootworm] has long been known as a

serious pest of corn. Rootworm larval feeding has not only

caused the lodging of entire corn fields, but also has

provided infection courts for disease organisms. The

feeding of even a small number of larvae has been noted to

inhibit the capacity of the infested plants to assimilate

water and nutrients (Ortman and Fitzgerald 1964). Dif-

ferential reactions of some strains of corn to rootworm

feedings were observed as early as the late 1920's (Bigger

et al. 1938). Subsequent investigations have revealed

certain lines to be superior in rootworm resistance, and

resistance has also been shown to be heritable (Bigger

1941 and Bigger, Snelling, and Blanchard 1941). There is

a continuing need for evaluation of the actual prospect of

forming populations with tolerance to rootworms.

With these guidelines in mind, the major objectives of this study have been (1) to screen populations of corn grown under natural rootworm infestations for tolerance to corn rootworms; (2) to construct indicators of heritable variation of desired characters in these populations; (3) to examine the genotypic and phenotypic correlations of important characters associated with rootworm tolerance; and (4) to select efficiently for maximum rootworm tolerance in a given population.

REVIEW OF LITERATURE

Plant Resistance to Insects

An intensified search for new and improved sources of resistance was suggested by Painter (1968) and he recommended that such resistance be incorporated into acceptable plant varieties. Earlier, Painter (1951) implied that, when plant breeders have raised varieties to "upper limits" of production, yields might be increased past such plateaus if insect resistance were included in the genetic make-up of the crop. The primary utility of such a concept would occur in situations where the insect is a known limiting factor in crop production. Luginbill (1969) reasoned that, if nature were completely undisturbed by man, through natural selection, plant species would have evolved with some resistance to insects. He suggested that a lack of built-in resistance to specific insects is the result of differences in emphasis. Primary importance necessarily has been on agronomic characters with less concentration on plant resistance to insects. Luginbill couples a review of successful breeding programs with the urgency of finding, identifying, and transferring resistance into commercial varieties.

Resistance, in a practical sense, is all the heritable characters of a plant which lessen insect damage even though plants of the same species and environment receive greater damage. Resistance is not necessarily a clear-cut phenom-

enon in that its expression in some plants may appear as a lesser degree of susceptibility while in other plants it may be strongly expressed. As mentioned in the Introduction, Painter (1951) divided plant resistance mechanisms into three main categories: (1) antibiosis: in which the plant is resistant by exerting an adverse effect on the biology of the insect; (2) preference and nonpreference: where, through plant characters and insect responses, resistance is displayed through a leading away of the insect from a partic- ular plant or variety; and (3) tolerance: in which plants exhibit no loss of vigor or yield despite infestations which would damage more susceptible plants. Chesnokov (1962) indicated that tolerance is expressed in an ability of damaged plants to react in a certain way to the specific action of a given insect species and to show no decrease in yield or economic value. These divisions of resistance were primarily derived in terms of their agricultural implications, i.e., economic damage was fundamentally important, and certain workers have not been in complete agreement on this importance. S. D. Beck (1965), in an excellent review of plant resistance to insects, admitted tolerance to be an important plant characteristic, but did not include it in his interpretation of resistance. He approached resistance with major emphasis on the biological relationships involved and, believing tolerance implied a

different relationship, could not fit it into his particular scheme. Regardless, for the purpose of this study tolerance was considered as a full component of resistance.

Rootworm Studies

The vast majority of rootworm resistance found in corn has been classified as tolerance; that is, some lines are able to develop new roots above the feeding points of the larvae almost as fast as the larvae destroy the roots. This tolerance permits the plant to remain upright while providing new root growth which allows adequate nutrient uptake. Fitzgerald and Ortman (1964) suggested that tolerance of corn to rootworm infestations was due to a naturally well-developed root system, the ability of the plant to generate new roots, insect attack in relation to the developmental stage of the plant, and various environmental conditions.

The history and importance of corn as well as the impact of corn rootworms are well documented in the litera-ture, and it is not the purpose of this study to dwell on these facts. The life cycles of the species and the feeding of both the larvae and adults were adequately reported by Metcalf, Flint, and Metcalf (1962) and Ortman and Fitzgerald (1964). Corn rootworm resistance studies have been the subject of two major literature reviews: Painter (1951) searched the earlier literature, while Eiben (1967) reported on subsequent investigations. Considering the

scope of these pursuits, it was the purpose of this review
to establish only the baselines of fundamental rootworm
resistance studies.

In the late 1930's a great deal of lodging was observed
in corn fields throughout the Corn Belt. At that time it
had not been possible to secure an acceptable degree of
rootworm control through the use of insecticides or cultural
practices. Attempts were made to resolve the situation with
the hope of using resistant strains of corn as the ultimate
answer to the control problem. Bigger et al. (1941) measured
the resistance of several corn strains to rootworm larvae
attack by the ability of the strains to withstand lodging
on naturally infested soil. This study not only revealed
that some lines differed in the degree of lodging after
rootworm feeding, but also it detected a differential
response of certain plants to adult feeding activity. These
research workers determined that resistance to rootworm
feeding was heritable and concluded that resistant strains
were the only practical means available to reduce rootworm
damage.

The Illinois corn harvest of 1941 was conducted in
very wet fields and the problems associated with such
conditions were compounded by the fact that corn, lodged
as a direct result of corn rootworm feeding, clogged much
of the harvest machinery (Cooper et al. 1942). It was

observed in many cases that over 50% of the corn in a field would be lodged, a condition which resulted because many of the commonly used hybrids of the day were totally inadequate in resistance to rootworm feeding. Such heavy rootworm populations allowed these investigators to determine that several hybrids were consistently superior in their ability to tolerate rootworm feeding.

An Iowa study (Eiben and Peters 1962) revealed the existence of differential responses to rootworm feeding on seven inbreds evaluated at two locations; 75% of the root-worm damage occurred on the first three root nodes below the soil which seemed to indicate that these roots are preferred by the insect. As an alternative to the insect's overt preference for these roots, it is possible that the concentration of damage is a function of the insect attack coinciding with that particular developmental stage of the plant.

Coon and Huber (1946) determined that many hybrids which had previously been considered outstanding showed tendencies toward excessive lodging after rootworm feeding. The authors pointed out that breeders are often limited in selections because, even though a substantial root system is quite desirable in a hybrid, there are other characters which are equally important, and these too must be considered.

Huber et al. (1948) reached the prevailing conclusion

that the best control of rootworms would be through the use
of hybrids including inbred lines resistant to attacks of
the insect (antibiosis) or having root systems which would
tolerate such attacks. An evaluation of 25 inbreds resulted
in the selection of seven as having "good" resistance to
rootworm feeding.

Bigger (1941) pointed out that a natural resistance to
insects probably has developed through the hundreds of years
that corn has been used as a food for man and animals.
Researchers have reasoned that, if such natural resistance
has occurred throughout the years, an excellent beginning
point in the search for resistance would be a locality which
long has had high populations of both the insect and the
host plant. Such thoughts closely parallel the concept of
Vavilov (1951) that the greatest diversity of a crop will
be found in the region where that crop originated. An
extensive study was undertaken by Melhus, Painter, and
Smith (1954) who selected Guatemala as a natural place for
a search since evidence showed that Guatemalan corn has
been a host of several species of Diabrotica for approxi-
mately 5000 years. A total of 310 varieties of Central
American corn were screened for rootworm resistance during
a five-year period. Ten varieties expressed some degree
of resistance. Inbreds developed from the most promising
of these resistant varieties were as resistant as the

parent variety; the resistance was heritable in testcross combinations. A susceptible U.S. single cross was used as testcross parent.

Fitzgerald and Ortman (1965) evaluated 150 Corn Belt inbreds in South Dakota for rootworm resistance; 38 inbreds had varying degrees of resistance. Twelve of the 38 inbreds indicated a good degree of resistance the following year. The authors suggested a continued search for germ plasm with a high level of tolerance or antibiosis. Eiben and Peters (1965) evaluated several lines under heavy to moderately heavy rootworm infestations in Iowa. Their results indicated that three lines snowed tolerance to rootworms, but that lines which performed well under moderate infestations may not perform equally well under severe infestations.

Recognizing the need for standard methods to be used in evaluating corn for rootworm resistance, Eiben (1967) made an intensive study of several methods which seemed to be applicable to such evaluations. Plant ratings on each of the lines included root size, root damage, pounds-pull, lodging percentage, root angle, and secondary roots. Eiben found that digging and washing the root systems prior to rating for resistance gave the most reliable information of the methods studied. He indicated that rootworm damage was independent of maturity, but stressed

that size comparisons between lines be made within close maturity ranges. Results of his experiments revealed that a combination of root damage ratings and root size ratings would be the most effective method of evaluating lines for resistance to corn rootworms.

Walter (1965) evaluated several lines of sweet corn for rootworm resistance and found large differences between closely related lines. This study indicated that two types of resistance were present: in the first type only a scarring of the root surface was detectable, while in the second type a tolerance of the root enabled it to survive and produce an abundance of side roots despite severe tunneling by the larvae. The study indicated that a direct examination of the root systems is the most efficient estimator of resistance and such findings are in accord with the root rating system of size and damage proposed by Eiben (1967).

Shank et al. (1965) were enthusiastic about the possibilities of the inbred SD10, a short, early maturing line. This inbred was developed from a cross of the inbreds Iowa B8 and Ohio 56A. During development of the line, selection was made for standability, plant type, and seed quality. SD10 was presented as a superior breeding line which has shown a high potential for root regeneration and the ability to transmit this character to its hybrids.

Heritability

Sprague (1966) revealed that population improvement in terms of genetic expectation or experimental results from selection is often considered from the standpoint of a single attribute. He indicated that in actual practice the breeder may wish to modify several attributes simultaneously or change a single attribute with no change in other desired characters. Estimates of heritability are useful in the attainment of such goals.

Heritability was defined by Baker et al. (1968, p. 725) as

> "a measure of that portion of the selection differential which is expected to show up as a response to selection."

Such a definition agrees with that of Lush (1949) who stated that heritability "is the portion of the observed variance for which difference in heredity is responsible." Another definition was offered by Johnson et al. (1955a) as "the fraction of variance in phenotypic expression that arises from genetic effects." Heritability was perhaps best summarized by these same workers who explained it to be an indicator of the effectiveness with which selection of genotypes can be based on phenotypic performance. Thus, a heritability estimate of 100% would mean that phenotypic performance would be a perfect indicator of genotypic value.

Heritability, in its simplest conceptual form, was portrayed by Sprague (1966) as:

$$H = \frac{S_g^2}{S_g^2 + S_e^2}$$

where

S_g^2 = total genetic variance,

S_e^2 = environmental variance.

He noted that this expression may often be inadequate and he reviewed an alternate form which utilizes only the additive genetic component of variance in the numerator. Sprague emphasized that while the distinction between the two forms is of much theoretical importance, in practice it is of limited value because of the large standard errors associated with the estimates.

Genotypic and Phenotypic Correlations

Selection for superior genotypes is the concern of the plant breeder but, of necessity, he must take his selections on the basis of phenotypic performance. Most characters of importance are complex in inheritance and may involve several related characters. Such complexity necessitates the calculation of estimates of the degree of genotypic and phenotypic correlations of the related characters. To obtain these correlations it is necessary to have not only the variances for the characters, but

also their genotypic and phenotypic covariances (Robinson et al. 1951). These authors mentioned that in addition to being of theoretical value, such correlations are of practical value since selection is usually concerned with changing two or more traits at the same time. Correlations between important and unimportant characters were utilized by Johnson et al. (1955b) to determine if characters of lesser importance had value as indicators of the more important ones. In the same manner, the authors used correlations as aids in identifying characters of little or no importance in a selection program. They estimated gentic and phenotypic correlations of 24 characters associated with soybean yield and determined that correlations between 13 traits were low, inconsistent, and of little value as indicators of yield. Selection for highly correlated characters resulted in gains as effective as selection for yield by itself. Robinson et al. (1951) evaluated selection in corn and reasoned that selection for a single trait such as yield may not be satisfactory since other plant characters (lodging, ear height, and husk characteristics) are of great importance. The authors point out that positive correlations of yield with ear number and ear height serve as warnings that improper selection for these characters will contribute to the genetic improvement of yield but eventually will develop objectionably taller material

with small ears.

Caldwell (1963) and El-Rouby (1965) reviewed the literature concerning genotypic and phenotypic correlations. Caldwell indicated that selection for a character may be possible through "correlated selection" which he defined as selection for a character highly correlated with a character of interest, but which is not so sensitive to environmental variation. El-Rouby reasoned that genetic correlation in maize could be due to pleiotropy or linkage. He noted that large variances of genetic correlations often make it difficult to determine associations between characters.

Index Selection

Objectivity in selection is of utmost importance when it is considered that selection determines the potential of a given breeding program. Since characters are often considered simultaneously, subjective judgments of relative value for many single characters may confound selection so as to preclude the consistent choice of superior material. Index selection has been demonstrated to be the most effective method of improving several traits simultaneously (Pesek and Baker 1969).

Smith (1936) proposed the concept of utilizing a "discriminant function" as the best indicator of the genetic value of a plant or line of wheat. His method

evolved into what is now known as index selection and has been used by both plant and animal breeders. Manning (1956) suggested that the object of index selection is to maximize net genotypic worth of a population. Harris (1963) discussed the theory of index selection and stated that a value for net worth (H) exists for each individual in a given population. Since the H value for an individual will not be known he suggests the use of index selection as an approximation. Pesek and Baker (1970) explained genetic worth as the overall value of a particular line or individual and defined it as consisting of "the sum products of the genotypic values of the measured characters and their respective 'economic weights'." Economic weights are determined by the researcher when constructing the index and they place the various characters in the proper ratio for maximum progress from selection.

Pesek and Baker (1970) report that assignment of economic weights for the improvement of a single character by the incorporation of other related characters is much more feasible than assigning weights for the simultaneous improvement of more than one character. They note that when improving a single character, called the "primary trait," the economic values of related characters, known as "secondary traits," may be set at zero and that of the primary trait at one. They further suggest that it is

often impossible to assign economic weights when simultaneous improvements of several characters is desired. As an option the authors formulated the concept of "desired genetic gains" which is said to remove the need for assigning relative economic weights and substitutes desired gains in the calculation of indexes (Pesek and Baker 1969).

Henderson (1963) gave a theoretical discussion of index selection for both single and multiple traits. He indicated that the unsolved problems of index selection included the consequence of nonnormality on index efficiency, the consequence of not using parameter values, and how to construct indexes when normality and known parameters do not hold.

Index selection has been the subject of several studies and has been adequately reviewed by recent authors including: Pesek and Baker (1970), Manning (1956), Caldwell (1963), and El-Rouby (1965). A current review of available literature revealed no reported work on the use of index selection in host-plant resistance studies.

MATERIALS AND METHODS

Experimental Material

The experimental material which was screened for root-worm tolerance consisted of selfed, full sib, and S_1 lines developed by corn breeders at Iowa State University. This material was developed from the synthetic variety of maize known as 'Stiff Stalk Synthetic' which has been used extensively throughout the Corn Belt. It is characterized by superior stalks and high general combining ability and has been widely used as a source of commercial inbred lines.

Stiff Stalk Synthetic is a 16-line synthetic variety developed in the early 1930's at Arlington, Virginia and Ames, Iowa (Penny 1968). The strains from the synthetic used in this study were: 221 random inbred lines developed by seven generations of selfing, having an expected homozygosity of 99+ % and hereafter referred to as the selfed lines; 239 random inbred lines developed from the same material as the selfed lines by six generations of full sibbing and two generations of selfing, having an expected homozygosity of 92%, and hereafter referred to as full sib lines; and 172 S_1 lines selected on the basis of general plant vigor, having an expected homozygosity of 50%, and hereafter referred to as the S_1 lines. This material was developed by five cycles of reciprocal recurrent selection for yield, the lines were selfed, and

172 ears were selected at harvest.

Field Plots

The study was conducted at three locations over three growing seasons (1968-1970). The breeding material was screened initially for rootworm tolerance and superior lines were selected for re-evaluation at a different location in the following year. Initial screening of the selfed lines was conducted in 1968 at the Iowa State University Ankeny Research Farm near Ankeny, Iowa. Re-testing of superior lines from this experiment was conducted in 1969 at the Iowa State University Allee Research Farm located near Newell, Iowa. The full sibs and the S_1 lines were originally screened at the Allee Farm in 1969 and were retested in 1970 at the Damman Farm east of Sanborn, Iowa.

Locations were chosen as to the likelihood of high rootworm populations which were enhanced by planting corn in the desired plot area late in the growing season of the year prior to planting the actual experiment. Such late planted corn tends to serve as a trap crop in that it attracts adult rootworms from surrounding areas to feed on the green silks produced late in the season. In theory, the trap crop serves as an excellent oviposition site for adult female beetles feeding in the field since the majority of the surrounding fields are more mature and thought to be less appealing.

All lines were hand planted in single-row plots ranging from 13 to 17 hills; two seeds were planted in each hill, and number of hills was consistent for a given experiment. Hill spacing was 10-inches and row spacing was 30-inches. Approximately four weeks after plant emergence the plots were thinned to one plant per hill. Plant pairs at each end of the plots were not thinned. After peak pollen shedding, three plants per replication were selected at random (end plants were excluded from consideration), tagged for identification, and dug from the soil. Eiben (1967) described methods for selecting, tagging, and digging plants and his techniques were followed in this study. After digging, the root systems were soaked in tubs of water then washed with pressurized spray to remove the remaining soil. Washed roots were rated for rootworm feeding damage, degree of secondary root development, and size of root system.

Rating Systems

Root ratings were essentially those described by Eiben (1967) and locally known as the Iowa State University rootworm rating system. Six categories were used for damage and their numerical equivalents were as follows: 1--no visible damage or with only minor feeding scars; 2--definite feeding scars, but no roots eaten off to within 1-1/2 inches of the plant; 3--several roots eaten off to

within 1-1/2 inches of the plant, but never the equivalent of an entire node of roots destroyed; 4--one node or the equivalent completely destroyed; 5--two nodes of roots destroyed; and 6--three or more nodes of roots destroyed.

Size ratings were made relative to the size of other root systems within a given experiment. Representative roots were selected prior to rating the experiment and the remaining roots were rated in comparison to these standards. Six categories were used for the size ratings and a rating of 1 represented roots in the range of the smallest root system in an experiment while a rating of 6 was reserved for the largest and most vigorous roots. The remaining ratings fell between these two extremes.

Secondary root development was rated on a 1 to 6 scale where the different categories were: 1--a system in which there is no development of secondary roots; 2--a system in which a small amount of secondary root growth is evident; 3--a system having a moderate amount of secondary root growth; 4--above average secondary root development; 5--extremely profuse growth of secondary roots and characterized by trapped soil and difficulty in separating crown roots when cut from the plant; and 6--exceptional system even more profuse in secondary roots than category 5.

Lodging data were recorded for each plot and expressed as a percentage of plants that were lodged 30° or more from

the vertical. Whenever possible, lodging observations were made prior to digging a given experiment. In certain cases lodging did not occur until after digging and in these situations lodged plants located next to excavations were not included in the lodging counts.

Maturity data were recorded as 50% pollen shedding date or 50% silking date of the individual plots. The experimental fields were located a considerable distance from the university, making it difficult to obtain daily maturity information. Thus, maturation notes accurately identified only the range of development for lines within an experiment.

Roots from the original population of S_1 lines were rated only for rootworm damage and secondary root development. Preliminary results from the initial screening of the selfed lines in 1968 indicated that phenotypic and genotypic correlations between secondary roots and root size were relatively high. On this basis it was decided to select in the S_1 lines only for secondary root development and to expect the achievement of correlated selection for root size. The secondary root rating for this experiment was modified from the original. A rating of 0 was reserved for those roots with no appreciable secondary root development, a rating of 1 for those roots with a small amount of secondary root growth, and a rating

of 8 for those root systems with extensive secondary
development. The ratings 2 through 7 fell equidistance
between ratings 1 and 8. This adjustment in the secondary
root rating scheme was made in an attempt to gain a more
sensitive rating of total root development in the absence
of a specific size rating.

The process of collecting and washing the dug roots
is both laborious and time-consuming and usually is a major
limiting factor in the amount of material which can be
evaluated in a season. Approximately half of the S_1 roots
were rated in the field immediately after digging. It was
not possible to rate the better roots of the material in
this manner because as secondary roots increased the amount
of trapped soil also increased and made accurate observa-
tions difficult. Those systems with larger amounts of
secondary roots were washed in the conventional manner
before rating. The retest population of this experiment
was washed and rated in the conventional manner since the
number of entries for retesting was greatly reduced.

Experimental Designs

The experimental design for all initial screenings
was the randomized complete block with four replications
for the selfed and full sib material and three replications
for the S_1 lines. Retests of the 50 superior selfs also
utilized a randomized complete block design with four

replications. Balanced lattice designs with four replica-
tions were employed for the retest of both the superior

sibs and the S_1 lines. Combined analyses of variance and

covariance were performed on the data from the original

populations. Mean squares for each character and mean

cross products for each pair of characters were obtained

from the sources of variation. Genotypic and phenotypic

variance and covariance as well as genotypic and phenotypic

correlations were estimated from this information. Analyses

of variance were also performed on the data from the retest

populations.

Variances, Covariances, and Heritability

Genotypic and phenotypic variances and covariances and

correlations were calculated from components of variance

and covariance according to methods described by Kempthorne

(1957) and Falconer (1960). Using treatment A (root damage)

and treatment B (secondary root development) as examples,

the specific formulae employed in these estimates are

presented in the following sections.

Genotypic and phenotypic variances and covariances

Genotypic Variance (V_g)

$$V_g = \frac{M.S._t - \sigma^2}{No.\ replications}$$

Genotypic Covariance (Cov_g)

$$Cov_{gA,B} = \frac{M.C.P._{tA,B} - M.C.P._{eA,B}}{No.\ replications}$$

Phenotypic Variance (V_p)

$$V_p = \frac{M.S._{tA}}{No.\ replications}$$

Phenotypic Covariance (Cov_p)

$$Cov_{pA,B} = \frac{M.C.P._{tA,B}}{No.\ replications}$$

Genotypic, phenotypic, and error correlations

Genetic Correlation (r_g)

$$r_{gA,B} = \frac{Cov_{gA,B}}{\sqrt{V_g\ t\ A\ X\ V_g\ t\ B}}$$

Phenotypic Correlation (r_p)

$$r_{pA,B} = \frac{M.C.P._{tA,B}}{\sqrt{M.S._{tA}\ X\ M.S._{tB}}}$$

Error Correlation (r_e)

$$r_{eA,B} = \frac{M.C.P._{eA,B}}{\sqrt{\sigma^2_A\ X\ \sigma^2_B}}$$

where the definitions are:

$M.S._t$ is the treatment mean square term obtained from the analysis of variance.

σ^2 is the true variance or error mean square term taken from the analysis of variance.

$M.C.P._t$ is the mean cross product term for treatments and is obtained from the analysis of co-variance.

$M.C.P._e$ is the mean cross product term for error and is obtained from the analysis of covariance.

No. replications is the number of replications used in the experiment.

Heritability on plot and mean bases

Two heritability estimates were made to provide an indication of the influence of replication on the various characters. Heritability claculated on a plot basis does not utilize replications in the denominator while heritability on a mean basis does.

Plot Heritability (h^2)

$$h^2 = \frac{V_g}{\sigma^2 + V_g}$$

Mean Heritability (h^2)

$$h^2 = \frac{V_g}{\frac{\sigma^2}{\text{No. replications}} + V_g}$$

where

the same definitions apply.

Selection

Selection within original populations for retesting of superior individuals was based on rootworm damage, size of root system, secondary root development, percent lodging, and relative maturity. Equal weight was placed

on each of the four primary characteristics. Since maturity data were not completely accurate they were used only to eliminate obviously late-maturing entries. Each entry was evaluated on the four primary characters and the ratings for each character were arranged from most to least desirable. Selection was made first in the upper 10% of each category. Those entries which achieved ratings in the upper 10% of all four categories were chosen first. Selection was next made for those entries with superior qualities in three categories followed by selection of those in two categories. Reference was always made to each category which was not in the upper percentiles so that obviously inferior material could be eliminated. Selection proceeded as described until 50 entries of each population were chosen for possible retest. This method of selection tended to be somewhat subjective, laborious, and perhaps inadequate in those situations where roots were superior in one or two traits but less desirable in the remaining traits.

During the terminal phase of this study a specific selection index was constructed for the original population of sib lines. This index was developed to obtain a comparison of entries chosen by the original selection process with entries indicated as superior by the index. In theory, index selection maximizes objectivity by giving

proper weight to each of the root characters under con-
sideration and could provide a single "root tolerance
index" for each entry in a population. Genotypic and
phenotypic correlations provided the bases for construction
of the index. An index is of the general form:

$$I = \sum_{i=1}^{n} b_i X_i$$

where I is the index and X_i is the phenotypic value of an
individual for the ith trait and there are n traits of
interest. The index coefficient for the ith character is
represented by b_i. These index coefficients are the optimum
weights to be given to the characters on which phenotypic
data have been taken. They are functions of the genetic
and phenotypic variances and covariances of the traits
under consideration as well as functions of the relative
contributions of the traits to phenotypic net worth
(Manning 1956). Each phenotypic value (X_i) is considered
to be made up of genetic contributions of the individual
entries plus contributions due to environmental influences.
Expanded into the selection index employed in this study
it becomes:

Root Tolerance Index $= b_1 X_1 + b_2 X_2 - b_3 X_3 - b_4 X_4$

where, for the mean total value of the three roots dug
for each entry, X_1 = secondary root rating, X_2 = root size

rating, X_3 = rootworm damage rating, and X_4 = mean lodging percentage for that entry. The corresponding index coefficients are represented by b_1 through b_4. The positive values assigned to characters X_1 and X_2 result in selection for a desired increase in number of secondary roots and root size while the negative signs of X_3 and X_4 result in selection for decrease in both rootworm damage and lodging of the plant.

Construction of selection indexes under conventional index theory requires that "relative economic weights" be assigned to the traits under consideration. Elaborating on the material presented in the Review of Literature, economic weights are often difficult to assign, even to obviously economic characters. Such weights are virtually impossible to assign to the less well known root characters considered in this study. The "desired gains" of Pesek and Baker (1969) are in reality economic weights and not necessarily applicable to all situations. The four primary characters employed in this study were interrelated and not easily separated, thus their economic weights were set at unity to give equal emphasis to the traits. Since the root characters in the original selection for retest were considered equal, it was desirable to retain this same equality in the index.

The b values are obtained by solving the set of

simultaneous equations, and in the matrix notation similar
to that of El-Rouby (1965) the solution becomes:

$$
\underset{\text{Phenotypic matrix}}{\begin{bmatrix} V_{11} & C_{12} & \cdots & C_{1n} \\ C_{21} & V_{22} & \cdots & C_{2n} \\ \cdot \\ \cdot \\ \cdot \\ C_{n1} & C_{n2} & \cdots & V_{nn} \end{bmatrix}}
\underset{\text{Betas}}{\begin{bmatrix} b_1 \\ b_2 \\ \cdot \\ \cdot \\ \cdot \\ b_n \end{bmatrix}}
\underset{\text{Genotypic matrix}}{\begin{bmatrix} V_{11} & C_{12} & \cdots & C_{1n} \\ C_{21} & V_{22} & \cdots & C_{2n} \\ \cdot \\ \cdot \\ \cdot \\ C_{n1} & C_{n2} & \cdots & V_{nn} \end{bmatrix}}
\underset{\text{Weights}}{\begin{bmatrix} a_1 \\ a_2 \\ \cdot \\ \cdot \\ \cdot \\ a_n \end{bmatrix}}
$$

The elements of the phenotypic matrix are as follows:

V_{11} an estimate of the phenotypic variance of X_1, etc.;

C_{12} an estimate of the phenotypic covariance of X_1 and X_2, etc.

The beta vector consists of the phenotypic weights for which
the equations are solved. The elements of the genotypic
matrix are:

V_{11} an estimate of the genotypic variance of X_1, etc.;

C_{12} an estimate of the genotypic covariance of X_1 and X_2, etc.

The weight vector consists of the economic weights which
were set at unity.

In the general notation employed by El-Rouby (1965)
this becomes:

$$[P] \ [B] \ = \ [G] \ [A]$$

$$= \ [D] \ .$$

The estimates of the phenotypic weights were obtained by

$$[B] = [C] [D] ;$$

where

[P] = the phenotypic variance and covariance matrix,

[B] = the vector of phenotypic weights which become the index coefficient,

[G] = the genotypic variance and covariance matrix,

[A] = the vector of economic weights, and

[C] = the inverse of matrix P.

RESULTS AND INTERPRETATIONS

Rootworm Infestations

Root size and secondary development are easily influenced by environmental effects, and available soil moisture is a primary component of this influence. The rootworm is affected also by moisture. Explanations of unusually light infestations in trap crop areas may be based on flooding or drouth periods during the immature stages of the pest. Rainfall information for the three study sites is presented in Table 1 as a reference for moisture influence on root systems and the insect. It is apparent that below average rainfall accumulations were recorded in much of the 1968 and 1970 growing seasons. The 1969 season was characterized by below average accumulations during May and August while above average accumulations were recorded during June and July.

Western corn rootworms were the predominant species at all study sites. Slight infestations of northern and only chance occurrences of southern corn rootworms were observed at these locations. Rootworm infestations at Ankeny in 1968 and at Newell in 1969 were considered to be comparable and rather heavy. Early indications were that large numbers of adults would be observed in late August at the Newell plots. This did not occur and heavy rainfalls may have drowned many larvae before they could complete development.

Table 1. Average monthly rainfall accumulations for Ankeny, Iowa, 1968; Newell, Iowa, 1969; and Sanborn, Iowa, 1970

Month	Ankeny, 1968 Actual[a]	Average[b]	Newell, 1969 Actual[c]	Average[d]	Sanborn, 1970 Actual[e]	Average[f]
May	1.66	4.49	1.97	3.98	0.94	3.84
June	4.17	4.54	8.11	4.87	0.36	3.35
July	4.65	4.29	5.26	3.56	0.34	3.67
August	3.15	4.12	2.94	3.54	0.85	3.91

[a]Recorded at United States Department of Agriculture, European Corn Borer Laboratory Weather Station.

[b]Averages of the monthly values for the period 1959 to 1969.

[c]Recorded at Iowa State University, Allee Farm weather station.

[d]No data available. Normal derived from the average monthly precipitation at Pocahontas, Storm Lake, and Rockwell City.

[e]Recorded at the Damman farm, east of Sanborn, Iowa.

[f]Averages from United States Department of Commerce climatological data for Iowa, Sanborn weather station.

Rootworm eggs were extracted from soil samples of the
Sanborn plots in September, 1969 and high egg counts revealed
that infestations should have been heavy. Drouth conditions
at these plots in 1970 were definitely a factor in the low
rootworm infestations encountered.

Field Data and Analyses of Variance

Selfed lines

Analyses of variance for the original population of
selfed lines are presented in Table 2 and for the retest
population in Table 3. Each trait was subjected to analysis
of variance and significant differences were detected for
each trait. The damage ratings of the original population
(Table 2) were significant only at the 5% level of confidence.
The corresponding values for root size, secondary roots, and
lodging were large and highly significant. Examination of
the range and median in Table 2 indicated that lodging was
definitely skewed toward zero and the variance, as expected
with this character, was large. Data in Table 3 are for
the retest population and, as indicated, significance was
detected for each trait at the 1% level of probability.
Again, an examination of the range and median discloses
that lodging remained skewed toward zero. The coefficients
of variation for damage, size, and secondary roots were
found to be lower in the retest population than in the
original population.

Table 2. Analyses of variance for root damage, root size, secondary roots, and percent lodging for 221 inbreds (selfed lines) evaluated in four replications. Ankeny, Iowa, 1968

Source	d.f.	Root damage M.S.	Root size M.S.	Secondary roots M.S.	Percent lodging M.S.
Replications	3	408.61	104.03	15.71	4641.14
Entries	220	6.52*	19.69**	20.84**	1127.42**
Error	660	5.18	5.84	3.97	416.17
Total	883				
Minimum		10.0	4.0	3.8	0.0
Maximum		17.2	16.5	16.8	94.0
Range		7.2	12.5	13.0	94.0
Median		13.8	8.2	10.1	12.0
Mean		13.7	8.5	10.4	17.7
$S_{\bar{x}}$		1.1	1.2	1.0	10.2
$LSD_{(.05)}$		3.1	3.4	2.8	28.3
C.V.		16.6	28.6	19.3	115.4

* = significant at the 5 percent level, ** = significant at the 1 percent level.

Table 3. Analyses of variance for root damage, root size, secondary roots, and percent lodging for 50 superior inbreds (selfed lines) evaluated in four replications. Newell, Iowa, 1969

Source	d.f.	Root damage M.S.	Root size M.S.	Secondary roots M.S.	Percent lodging M.S.
Replications	3	7.41	12.22	15.54	253.85
Entries	49	4.51**	19.92**	32.60**	201.48*
Error	147	1.55	2.58	3.27	95.92
Total	199				
Minimum		11.5	7.8	6.0	0.0
Maximum		16.5	16.8	18.0	37.5
Range		5.0	9.0	12.0	37.5
Median		12.8	12.9	12.8	0.0
Mean		13.0	12.6	12.7	3.3
$S_{\bar{x}}$		0.6	0.8	0.9	4.9
$LSD_{(.05)}$		1.7	2.2	2.5	13.6
C.V.		9.6	12.8	14.3	298.6

** = significant at the 1 percent level.

Analysis and selection were made on average plot performance of an entry rather than on individual plant performance. Thus, a plot damage rating of 12, when divided by the three roots dug in each replication, is equal to a 4 on the individual rating scheme explained on page 21. Data are presented in this manner since ears were not saved from the plants and the seeds for retest were obtained from the original source.

Full sib lines

The original population of full sib lines was evaluated under acceptable rootworm infestations at the Allee farm in 1969. The retest population, however, was screened at the Damman farm under infestations inadequate for distinct expression of differential responses to rootworm feeding. Analyses of variance for the original population of full sib lines are presented in Table 4 and for the retest population in Table 5. Each trait was subjected to analysis of variance and F-tests indicated that each trait was highly significant in both experiments.

Coefficients of variation for the original population (Table 4) ranged from 11% for root damage to 160% for lodging. These coefficients may be considered large when compared with a character such as grain moisture, but the variances and LSD's were found to be acceptable in making comparisons among entries. Coefficients of variation for

Table 4. Analyses of variance for root damage, root size, secondary roots, and percent lodging for 239 inbreds (full sib lines) evaluated in four replications. Newell, Iowa, 1969

Source	d.f.	Root damage M.S.	Root size M.S.	Secondary roots M.S.	Percent lodging M.S.
Replications	3	36.51	26.63	207.95	4492.20
Entries	238	4.01**	10.29**	14.56**	931.94**
Error	714	2.10	3.36	4.46	451.10
Total	955				
Minimum		10.5	6.3	5.0	0.0
Maximum		16.0	15.0	16.8	67.8
Range		5.5	8.8	11.8	67.8
Median		13.0	11.0	11.5	8.3
Mean		13.0	10.9	11.4	13.3
$S_{\bar{x}}$		0.7	0.9	1.1	10.6
LSD$_{(.05)}$		2.0	2.6	2.9	29.4
C.V.		11.2	16.8	18.5	160.3

** = significant at the 1 percent level.

Table 5. Analyses of variance for root damage, root size, and secondary roots for 47 superior inbreds (full sib lines) evaluated in four replications. Sanborn, Iowa, 1970

Source	d.f.	Root damage M.S.	Root size M.S.	Secondary roots M.S.
Replications	3	1.95	16.13	19.48
Entries	46	1.86**	9.02**	25.27**
Error	138	0.78	2.58	3.88
Total	187			
Minimum		5.0	8.0	8.0
Maximum		8.5	14.3	18.0
Range		3.5	6.3	10.0
Median		6.3	11.2	13.3
Mean		6.4	11.1	12.8
$S_{\bar{x}}$		0.4	0.8	1.0
LSD$_{(.05)}$		1.2	2.2	2.7
C.V.		13.8	14.5	15.4

** = significant at the 1 percent level.

the retest population (Table 5) ranged from 14% for root damage to 15% for secondary root development. Damage ratings at the Newell site averaged 13.0 and had a range of 5.5, while those of the retest population at Sanborn averaged only 6.3 but, under the circumstances, had a relatively large range of 3.5. Mean root size and mean secondary root development were increased over the original population even though the retest population was subjected to drouth stress.

S_1 lines

Environmental conditions for the S_1 lines at both the original and retest locations were identical with those of the full sib lines. As previously mentioned, the S_1 lines had an expected homozygosity of 50% which gave this material much greater genetic variability within lines than either the selfed or full sib lines. The differences of years and locations between the original and retest populations essentially had the same effects as described for the full sib lines. Analyses of variance for the original population of S_1 lines are presented in Table 6 and for the retest population in Table 7. Each trait was subjected to analysis of variance and each trait was found to be highly significant.

Coefficients of variation for damage in both populations of S_1 lines were comparable with those for the selfed and

Table 6. Analyses of variance for root damage, secondary roots, and percent lodging for 172 S_1 lines evaluated in three replications. Newell, Iowa, 1969

Source	d.f.	Root damage M.S.	Secondary[a] roots M.S.	Percent lodging M.S.
Replications	2	53.25	19.98	16916.96
Entries	171	3.06**	5.01**	1186.31**
Error	342	2.54	3.17	756.41
Total	515			
Minimum		10.7	0.0	0.0
Maximum		15.7	7.0	100.0
Range		5.0	7.0	100.0
Median		13.2	1.7	30.8
Mean		13.1	1.8	34.4
$S_{\overline{x}}$		0.9	1.0	15.9
LSD$_{(.05)}$		2.6	2.9	44.0
C.V.		12.1	96.8	80.0

[a]Modified rating system described on pages 22 and 23.

** = significant at the 1 percent level.

Table 7. Analyses of variance for root damage, root size, and secondary roots for 50 superior S_1 lines evaluated in four replications. Sanborn, Iowa, 1970

Source	d.f.	Root damage M.S.	Root size M.S.	Secondary roots M.S.
Replications	3	3.31	8.42	12.78
Entries	49	2.68**	3.62**	11.90**
Error	147	1.22	1.38	2.45
Total	199			
Minimum		6.3	8.0	7.0
Maximum		9.8	12.5	15.3
Range		3.5	4.5	8.3
Median		8.0	9.5	10.7
Mean		7.9	9.6	10.6
$S_{\bar{x}}$		0.6	0.6	0.8
LSD(.05)		1.5	1.6	2.2
C.V.		13.9	12.2	14.7

** = significant at the 1 percent level.

full sib lines. The coefficient of variation for secondaries in the original population is extremely high at 97%. The modified secondary rating described on pages 22 and 23 was used for this material. The conventional secondary rating scheme was used for the retest population which had a coefficient of variation of 15%.

Heritability

Heritability for the various characters under consideration were computed for each of the experimental populations. These estimates for the selfed, full sib, and S_1 lines are presented in Table 8. It can be seen that heritability forms two rather distinct groups according to magnitude. Damage comprises the first group and the estimates were low which indicated that selection on the basis of damage alone would tend to be ineffective. Estimates of heritability for damage were higher in the full sib lines than for the other populations, and were considered to be relatively high for such a character. The second group consists of root size, secondary roots, lodging, and maturity for which the estimates were generally high. The values for root size, secondary roots, and lodging indicate that gains could be expected from selection for each of these characters. Data on the S_1 lines indicated that heritability for all characters of this material was relatively low when compared with similar data on the remaining two

Table 8.   Relative heritability (h^2) on a plot and mean basis
for selected characters from three populations of
corn.   221 selfed lines grown at Ankeny, Iowa,
1968; 239 full sib lines and 172 S_1 lines grown at
Newell, Iowa, 1969

Character	h^2 (plot) %	h^2 (mean) %
	Selfed lines	(4 reps)
Root damage	6.1	20.6
Root size	37.2	70.3
Secondary roots	51.5	80.9
Lodging	29.9	63.1
Maturity	80.9	94.4
	Full sib lines	(4 reps)
Root damage	18.5	47.6
Root size	34.0	67.4
Secondary roots	36.2	69.4
Lodging	21.0	51.6
Maturity	41.6	74.0
	S_1 lines	(3 reps)
Root damage	6.3	16.7
Secondary roots	16.2	37.2
Lodging	15.9	36.2
Maturity	14.3	33.3

populations. This is, perhaps, best explained by the fact that the S_1 lines had an expected homozygosity of only 50% and were still segregating. The selfed and full sib lines each had expected homozygosity of over 90% and higher heritability would be expected for material of this type.

Although heritability estimates for damage were low, damage remained as a consideration in selection since it gives the most direct estimate of rootworm influence on the plant. Damage is also the only root character which can be used to detect the presence of either antibiosis or non-preference. Differences in heritability determined in this study indicate that more information is needed on the basis of variation in heritability for the various root characters under consideration.

Correlations

Genotypic, phenotypic, and error correlations between the various characters of the selfed, full sib, and S_1 lines are presented in Tables 9, 10, and 11 respectively. Generally, the correlations between characters appeared to be consistent for the three populations, and the genotypic correlations were slightly higher than the phenotypic. Positive correlations were found for root size with secondary roots and lodging with rootworm damage. As might be expected, negative correlations were found for size with lodging, secondary roots with lodging, damage

Table 9. Genetic (r_G), phenotypic (r_p)*, and error (r_e) correlations among lodging, root damage, root size, secondary roots, and maturity for 221 inbreds (selfed lines) grown in four replications. Ankeny, Iowa, 1968

		Root damage	Root size	Secondary roots	50% silking date
Lodging	r_G	.53	- .48	- .18	- .13
	r_p	.35	- .43	- .17	- .09
	r_e	.30	- .32	- .17	.05
Root damage	r_G		- .69	- .30	- .58
	r_p		- .57	- .15	- .22
	r_e		- .63	- .07	.17
Root size	r_G			.61	- .36
	r_p			.56	.26
	r_e			.41	- .20
Secondary roots	r_G				.26
	r_p				.23
	r_e				- .04

*Five percent level of significance = .14.

Table 10. Genetic (r_G), phenotypic (r_p)*, and error (r_e) correlations among lodging, root damage, root size, secondary roots, and 50% pollen shedding date for 239 full sibs obtained from Stiff Stalk Synthetic grown in four replications. Newell, Iowa, 1969

		Root damage	Root size	Secondary roots	50% pollen shedding date
Lodging	r_G	.31	- .47	- .16	- .02
	r_p	.19	- .30	- .12	- .02
	r_e	.07	- .06	- .06	- .02
Root damage	r_G		- .62	- .76	- .17
	r_p		- .42	- .46	- .14
	r_e		- .15	- .05	- .10
Root size	r_G			.73	- .07
	r_p			.66	- .05
	r_e			.52	- .01
Secondary roots	r_G				- .27
	r_p				- .22
	r_e				- .07

*Five percent level of significance = .14.

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Table 11. Genetic (r_G), phenotypic (r_p)*, and error (r_e) correlations among lodging, root damage, recovery, and 50% pollen shed date for 172 S_1 lines obtained from SSS(R)C_5 grown in three replications. Newell, Iowa, 1969

		Root damage	Secondary roots	50% pollen shedding date
Lodging	r_G	.77	- .86	- .28
	r_p	.35	- .36	- .18
	r_e	.22	- .07	- .12
Root damage	r_G		-1.35	.39
	r_p		- .39	.05
	r_e		- .07	- .06
Secondary roots	r_G			- .04
	r_p			- .03
	r_e			- .02

*Five percent level of significance = .16.

with secondary roots, and damge with root size. An
interesting genetic correlation of -1.35 was found between
damage and root size in the S_1 lines (Table 11). It was
determined that while this value was theoretically
impossible, it was computationally possible when calcu-
lated as described on page 25. Correlations of root
characters with maturity generally were found to be low
and negative.

Correlations between secondary root development and
damage were high and negative which indicated that
correlated selection for superior secondary roots might
result in a corresponding reduction of damage in the
selected material. Similar correlations between root size
and rootworm damage also indicate that correlated selection
for larger root size should reduce rootworm damage. In
addition, high correlations were observed between root size
and secondary root development indicating that selection
for one would also result in selection for the other. The
magnitude of these correlations can be attributed to the
fact that the largest root systems usually have the most
extensive secondary root development. Thus, a size rating
of 6 is almost invariably followed by a secondary rating of
4, 5, or 6. This is not to say that large root systems
with poor secondary development or small systems with
extensive secondary development did not occur because

their presence was noted occasionally in small numbers. Error correlations between root size and secondary roots were found to be positive and much higher than between any other characters. This was considered indicative of the tremendous effect of environment on the ability of the corn plant to produce secondary roots and develop root size potential.

Similar directions and magnitudes of the correlations between various pairs of characters in the three experimental groups indicate that consistent associations among these characters might be expected in other populations of corn. In material with a narrow maturity range it can be considered that maturity is of little or no importance as a direct indicator of rootworm tolerance.

Response to Selection

Selfed lines

Selection was not made on the basis of any single root character, but on an equal combination of rootworm damage, root size, secondary root development, and lodging. Maturity information was used to eliminate extremely late material.

Results from selection for rootworm tolerance are portrayed for the individual characters as follows: damage (Figure 1), size (Figure 2), secondary development (Figure 3), and lodging (Figure 4). A comparison of

frequency distributions for damage is shown in Figure 1,
and the upper population is the original while the lower
is that of the retest of superior plants. As already
mentioned, the retest plants were chosen from the original
population and were grown at a different location the
following year. In each distribution the mean is indicated
by a solid vertical line and the mean of the plants chosen
for retest by the broken vertical line in the upper distri-
bution. The damage rating appears on the abscissa and is
the average plot rating for the entries. Lesser amounts of
damage are on the left of the distributions and greater
damage is to the right. The ordinate is divided into
percentages of entries for both the original and retest
populations.

Rootworm infestations and damage levels at the 1968
Ankeny site of the original population and the 1969 Newell
site of the retest population were considered equal and
gave the best comparisons of damage for any of the materials
under consideration. An examination of Figure 1 reveals that
while damage was not the only consideration in selection,
the retest population was shifted toward lesser degrees of
damage. It is readily apparent that the bulk of the
severely attacked roots was eliminated after selection
for tolerance. The shift in the mean of plants in the
retest population from their mean in the original population

Figure 1.   Frequency distributions for average rootworm
            feeding damage rating of selfed lines.
            Original population, Ankeny, Iowa, 1968.
            Retest population, Newell, Iowa, 1969. In
            each distribution the mean is indicated by a
            solid vertical line, and the mean of superior
            entries chosen for retest by a broken vertical
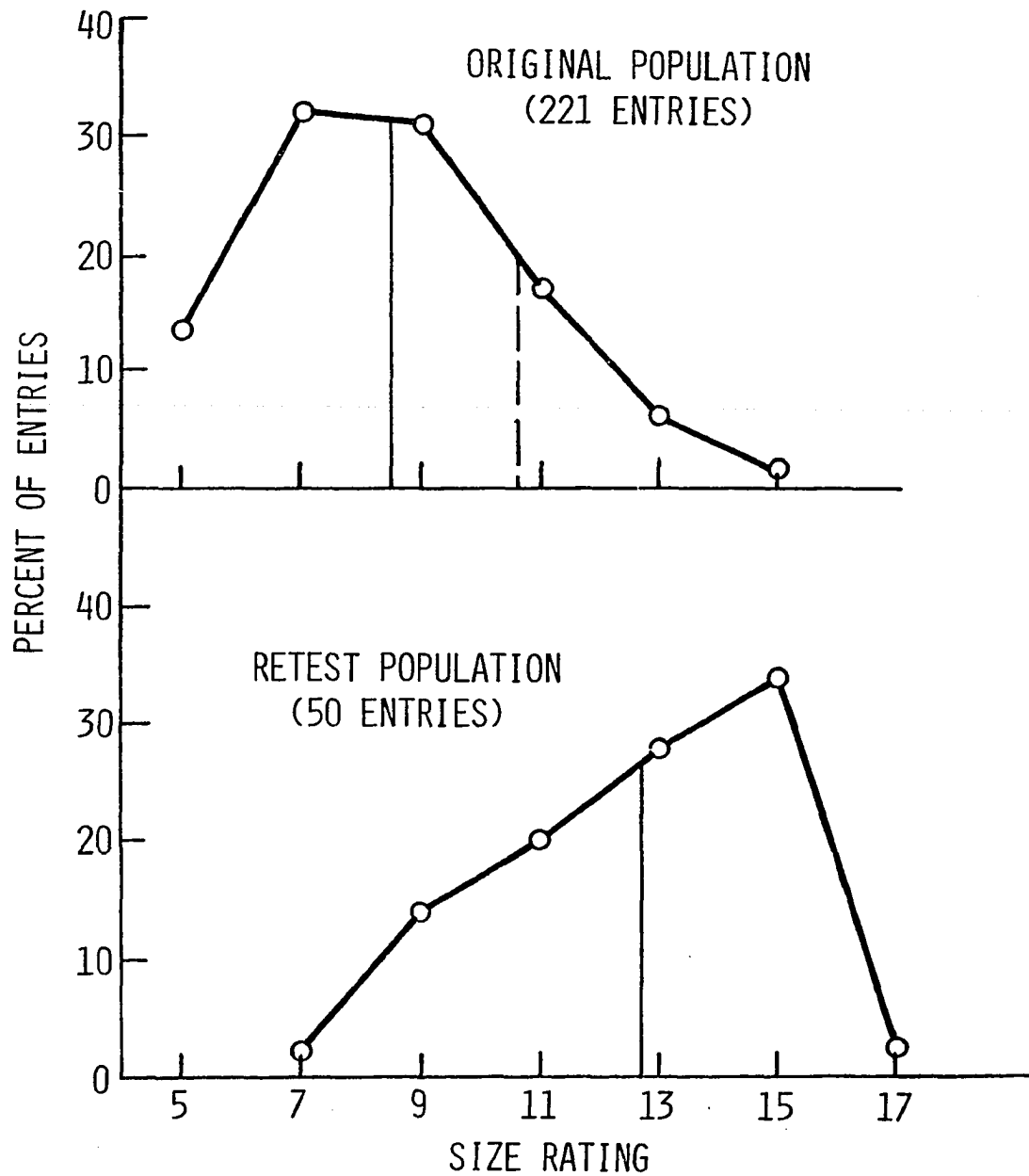   line in the original population
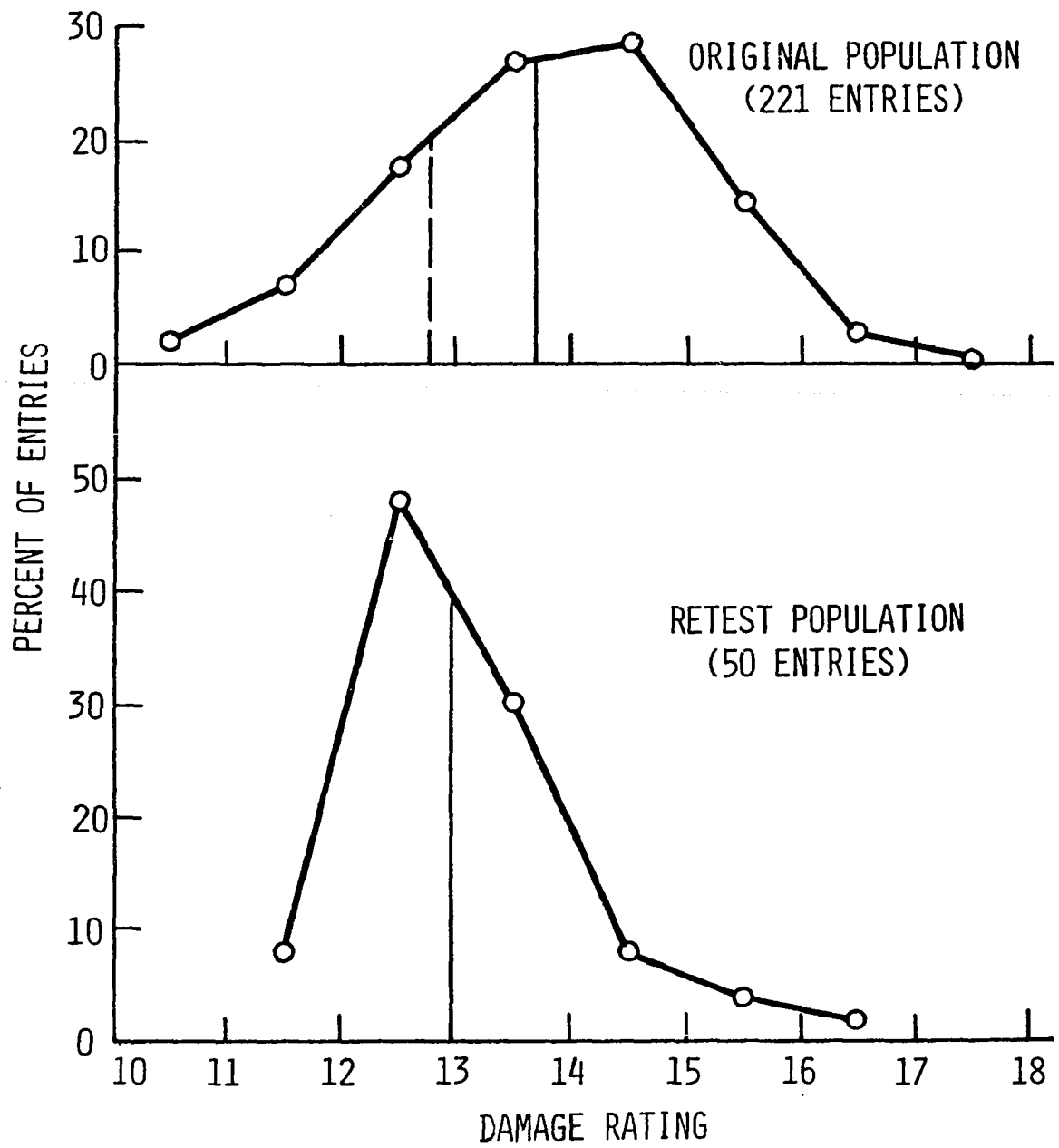
is not particularly significant when it is considered that
the tests were conducted in different years at different
locations.

Frequency distributions for root size of the selfed
lines are presented in Figure 2. The size rating is the
plot average and larger root systems are toward the right.
Again, it is evident that selection for rootworm tolerance
affected a concentration of larger root systems. The mean
of the retest population was shifted beyond its mean in
the original population but such a shift is most likely
attributable to environmental differences between locations
and years.

Frequency distributions for secondary root ratings of
both populations are presented in Figure 3. Superior
secondaries are toward the right of the distribution and
the ratings are the plot averages. Once again, it is
evident that selection for rootworm tolerance resulted in
root systems with superior secondary root development. The
mean for the superior entries in the original population was
found to be almost identical with the mean in the retest
population. These data indicate that environmental effects
on secondary root development were similar in both popula-
tions.

Histograms for percent lodging of the two selfed
populations are displayed in Figure 4. The ordinate is

Figure 2. Frequency distributions for average root size
rating of selfed lines. Original population,
Ankeny, Iowa, 1968. Retest population, Newell,
Iowa, 1969. In each distribution the mean is
indicated by a solid vertical line, and the
mean of superior entries chosen for retest by
a broken vertical line in the original population

ORIGINAL POPULATION
(221 ENTRIES)

RETEST POPULATION
(50 ENTRIES)

PERCENT OF ENTRIES

SIZE RATING

Figure 3. Frequency distributions for average secondary
root rating of selfed lines. Original popula-
tion, Ankeny, Iowa, 1968. Retest population,
Newell, Iowa, 1969. In each distribution the
mean is indicated by a solid vertical line, and
the mean of superior entries chosen for retest
by a broken vertical line in the original popula-
tion
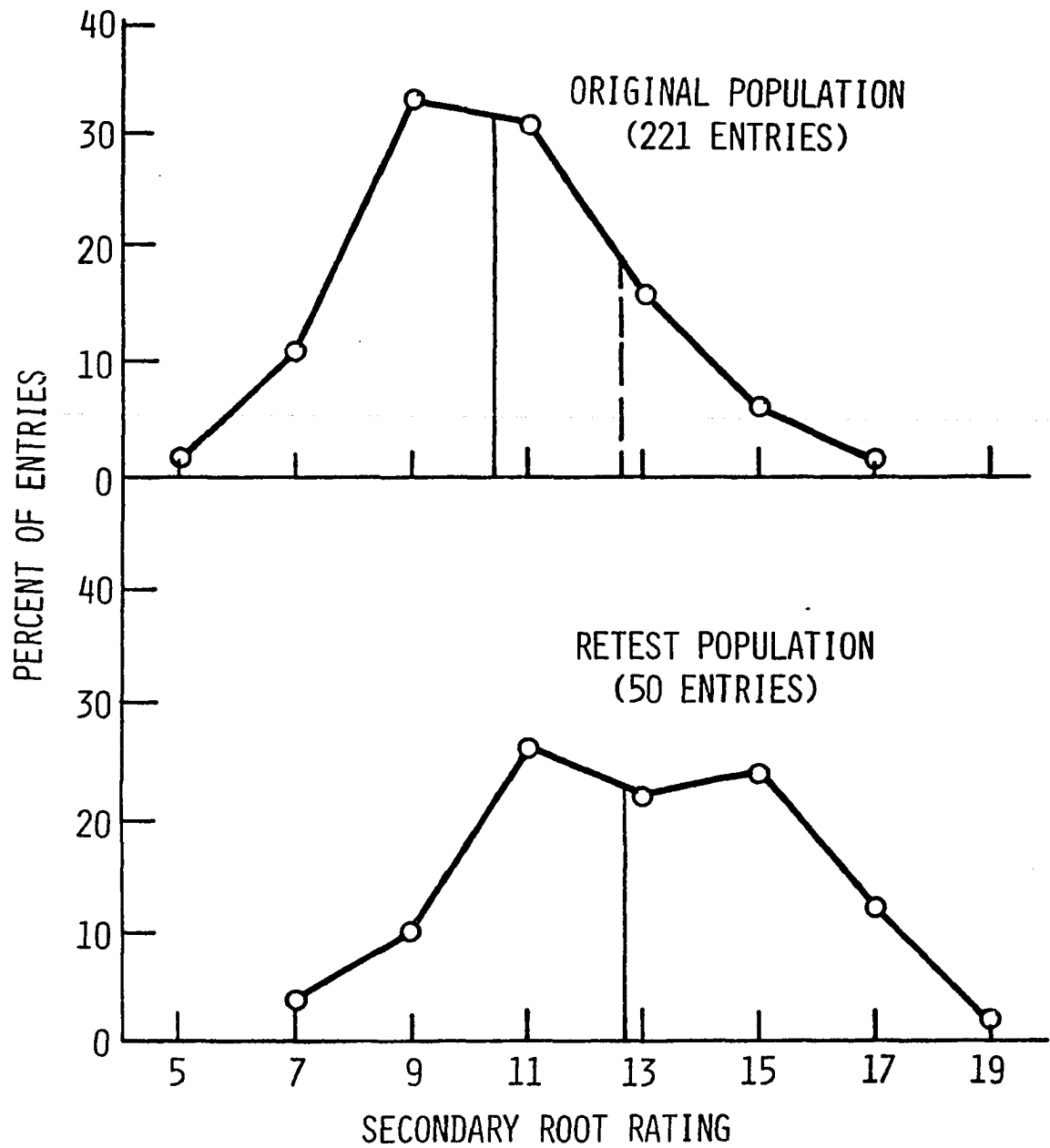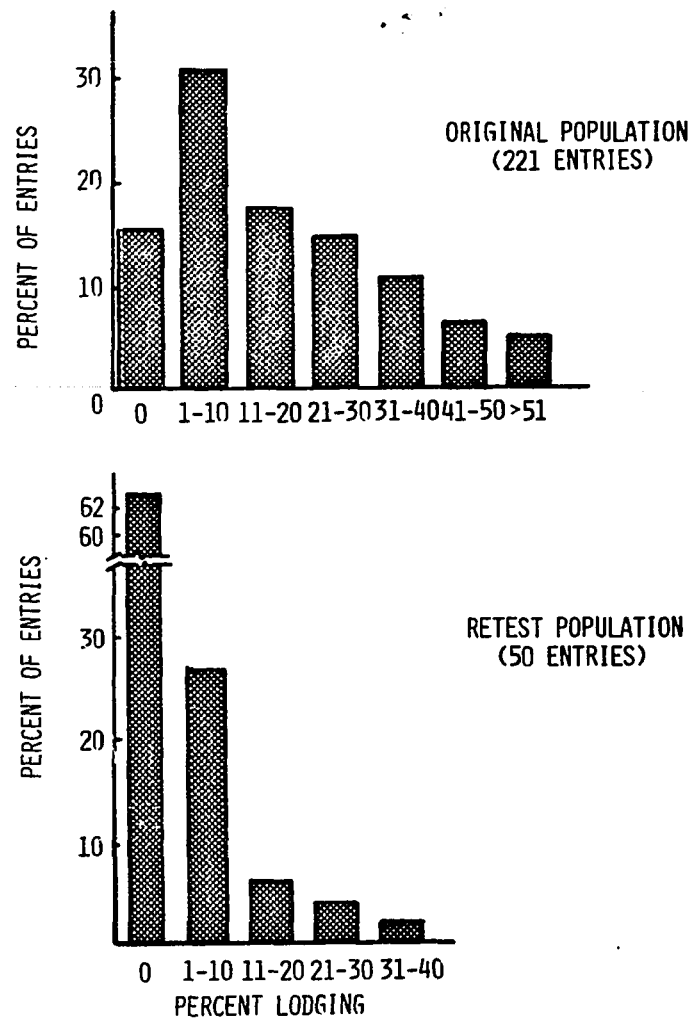
Figure 4. Histograms for average percent lodging of selfed lines. Original population, Ankeny, Iowa, 1968. Retest population, Newell, Iowa, 1969

divided into percentage of entries for both populations.
Classes for percent lodging appear on the abscissa and
lesser lodging is toward the left. It is evident that
lodging is skewed to lesser percentages in both populations
and that percent of entries with zero lodging is much higher
in the retest population. Lodging is a character which is
dependent upon environmental effects and it should not be
assumed that the dramatic decrease in lodging was altogether
a result of selection for rootworm tolerance. However, the
Newell plots were subjected to some severe rain and wind
storms which would lead to the expectation of more lodging
than was actually observed. The only occurrence of lodging
in both the original and retest populations was for these
selfed lines.

Full sib lines

Response of rootworm damage to selection for rootworm
tolerance is displayed by the frequency distributions in
Figure 5. Rootworm infestation in the retest population
was not as great as that of the original which was grown
at the Allee farm in 1969. These distributions are not
directly comparable but they do portray the observed ranges
in damage ratings and give some indication of response to
selection. The inbred lines B67 (rootworm tolerant) and
WF9 (rootworm susceptible) were included in the experimental
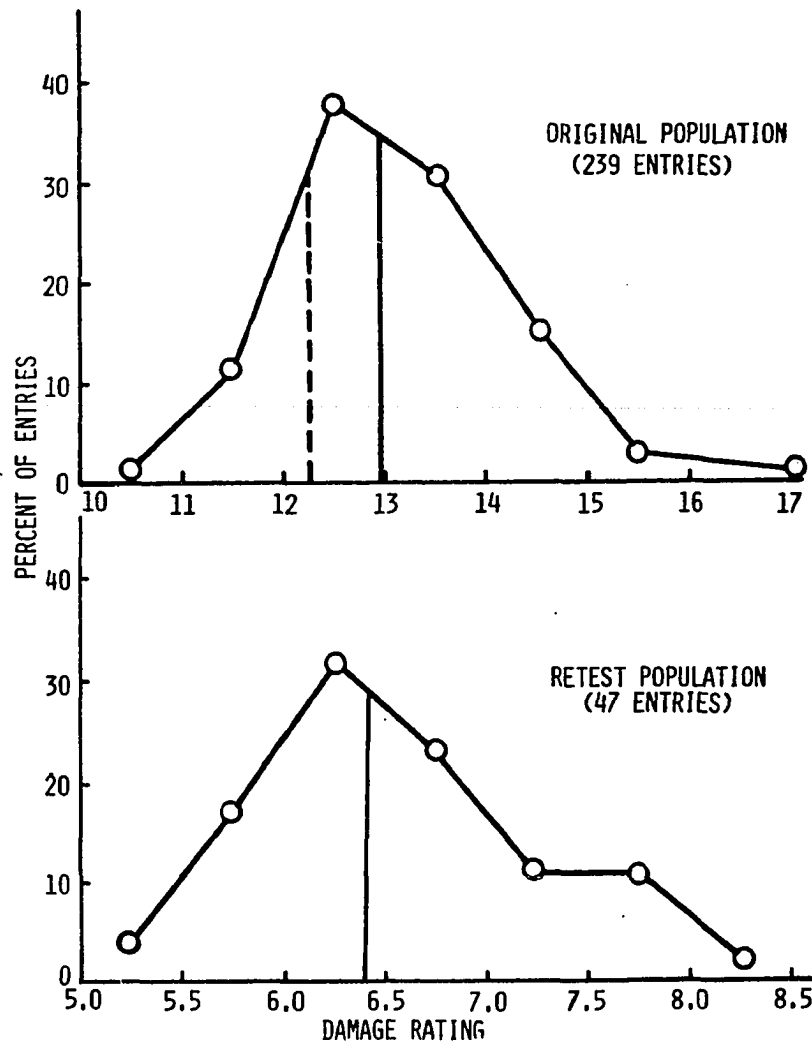design of the retest population at Sanborn. The average

Figure 5. Frequency distributions for average rootworm damage rating of full sib lines. Original population, Newell, Iowa, 1969. Retest population, Sanborn, Iowa, 1970. In each distribution the mean is indicated by a solid vertical line, and the mean of superior entries chosen for retest by a broken vertical line in the original population.

damage rating for the B67 plots was 5.8 which was below the 6.4 mean of the retested sib lines. The sib line with least damage averaged 5.0. The inbred line WF9 achieved a mean plot damage rating of 7.3.

Root size and secondary development are influenced by both rootworms and environmental factors. The original and retest distributions for both root size (Figure 6) and secondary development (Figure 7) were considered to be more equivalent than the corresponding distributions for damage. Selection for rootworm tolerance resulted in acceptable gain for root size when the differences in rainfall for the two years are considered (Table 1). The shift in the mean of the retest population from that of superior plants in the original population may be considered a direct result of the drouth conditions encountered in 1970. An examination of the distributions for secondary development (Figure 7) reveals that drouth did not affect this character to the extent that it affected root size. It is evident that selection for rootworm tolerance eliminated those entries with poor secondary root development. It can be assumed that under equal environments for the original and retest populations, the distributions for root size would have been similar to those observed for size in the selfed lines (Figure 2).

Figure 6. Frequency distributions for average root size
rating of full sib lines. Original population,
Newell, Iowa, 1969. Retest population, Sanborn,
Iowa, 1970. In each distribution the mean is
indicated by a solid vertical line, and the
mean of superior entries chosen for retest by
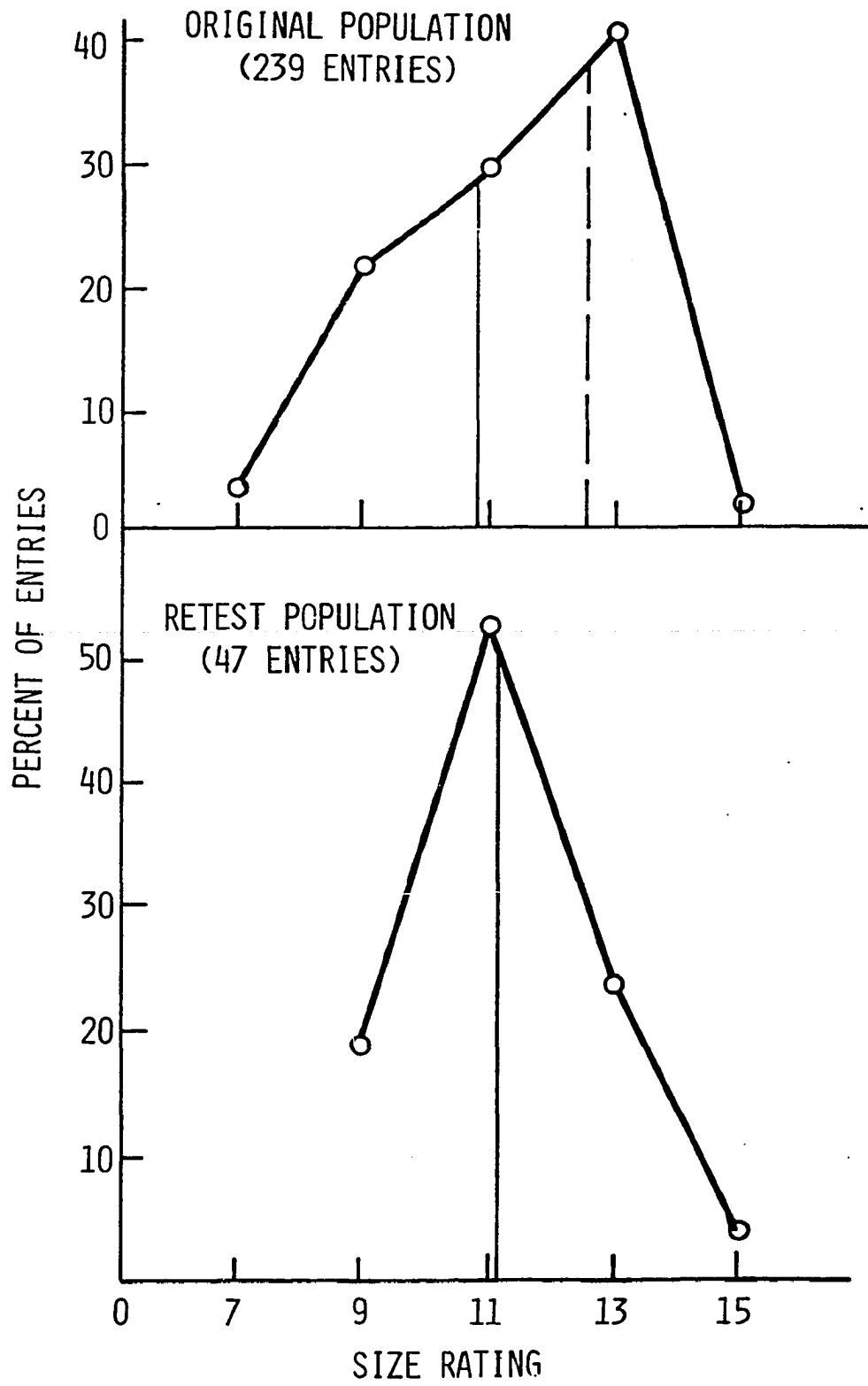a broken vertical line in the original population

Figure 7. Frequency distributions for average secondary
root rating of full sib lines. Original
population, Newell, Iowa, 1969. Retest
population, Sanborn, Iowa, 1970. In each
distribution the mean is indicated by a solid
vertical line, and the mean of superior entries
chosen for retest by a broken vertical line in
the original population
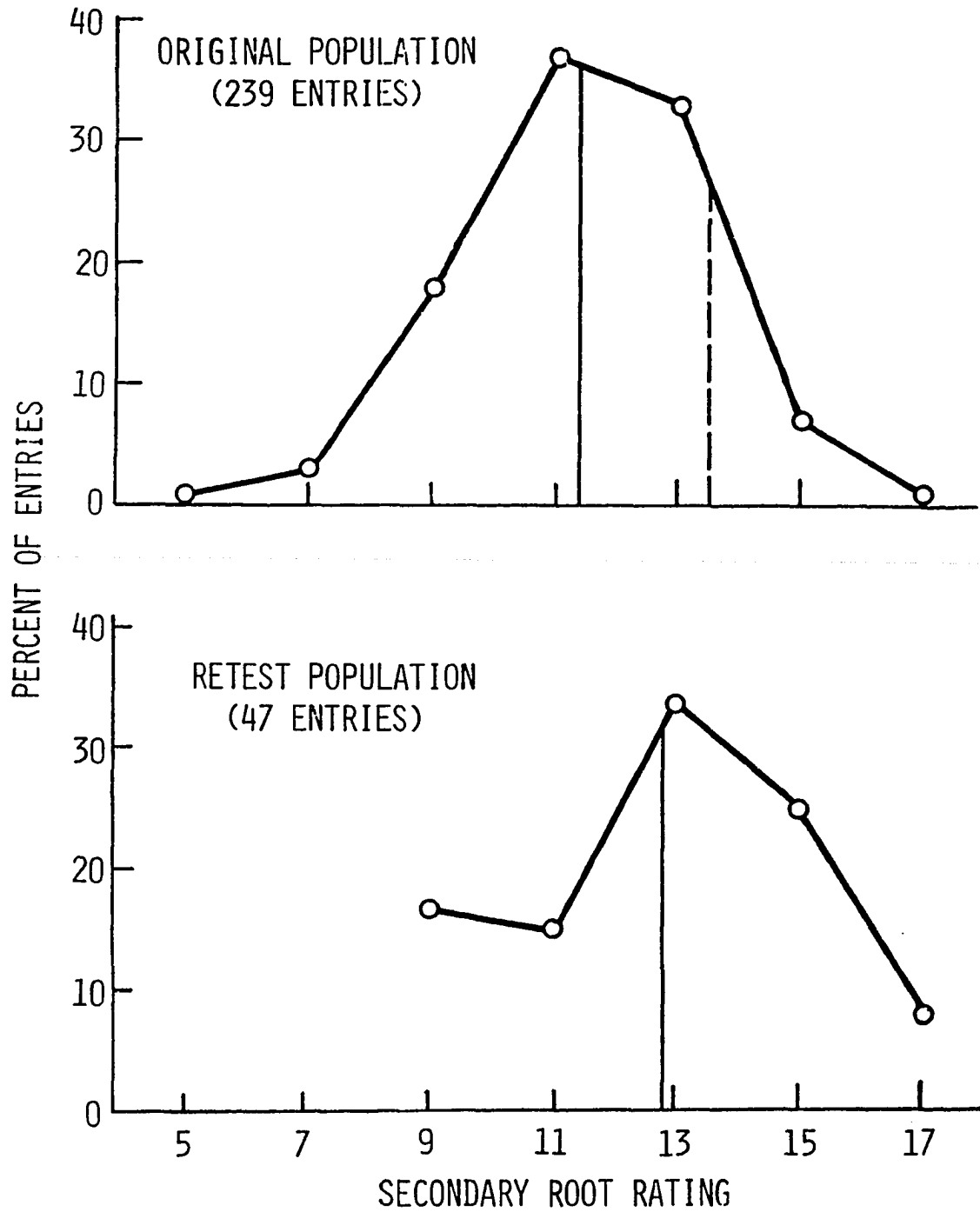
The average size rating for B67 was 12.8 and for WF9
was 10.5, both of which can be compared with the 11.1
mean observed in the sib lines. The largest sib averaged
14.3. Mean secondary rating for B67 was 16.3, for WF9
was 8.5, and for the sib lines was 12.8. The sib with the
best secondary development averaged 18.0 which is the
maximum under the rating system employed.

The histogram for percent lodging observed in the
original population at Newell in 1969 is displayed in
Figure 8. As was observed in the selfed lines (Figure 4),
lodging was clearly skewed toward zero in the full sib lines.
Data in Table 4 characterize this distribution; full sib
lines had a range of 67.8 and a median of only 8.3.
Unfortunately, 1970 weather conditions at the retest site
near Sanborn did not cause lodging in the experimental
plots.

S_1 lines

Differential response of S_1 lines to rootworm feeding
is portrayed in Figure 9 for both the original and retest
populations. As was the case in the full sib lines, dif-
ferences in rootworm infestations make direct comparison
of the two distributions difficult. The distributions do,
however, give some indication of response to selection for
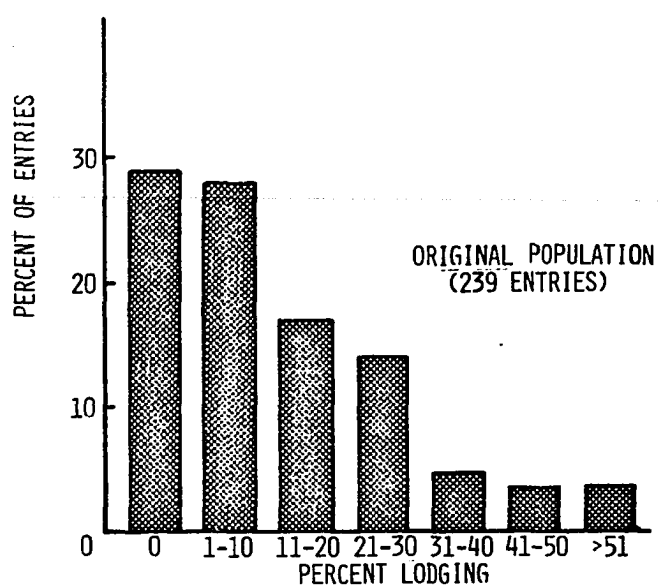rootworm tolerance. Three rootworm tolerant single crosses

Figure 8. Histogram for average percent lodging of full
sib lines. Original population, Newell,
Iowa, 1969

Figure 9.　Frequency distributions for average rootworm
feeding damage of S_1 lines.　Original popula-
tion, Newell, Iowa, 1969.　Retest population,
Sanborn, Iowa, 1970.　In each distribution the
mean is indicated by a solid vertical line,
and the mean of superior entries chosen for
retest by a broken vertical line in the original
population
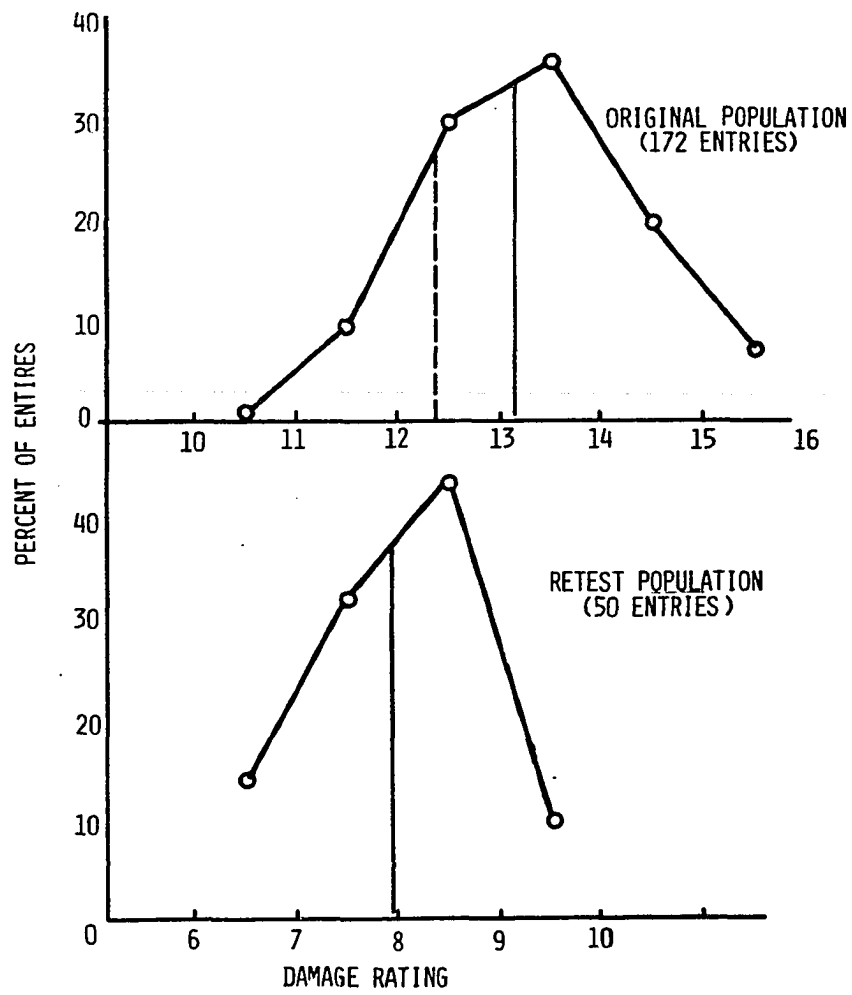
(B14A x SD10, F2J x H3839, and CI21E x H3839) and one root-
worm susceptible single cross (B37 x B65) were included
in the retest population at Sanborn. The mean plot damage
ratings were as follows: B14A x SD10, 7.0; F2J x H3839,
5.3; CI21E x H3839, 6.8; B37 x B65, 8.0; and the S_1 lines,
7.9. The least damaged S_1 had a mean of 6.3.

Frequency distributions for secondary root ratings of
both populations are presented in Figure 10. The modified
secondary rating used in the original population was converted
to the original scheme of the retest population to make
easier comparisons of the two distributions. When drouth
conditions are considered, it is probable that selection
for rootworm tolerance resulted in selection for superior
secondary development. The shift in the mean of the retest
population from its mean in the original population was
most likely due to environmental differences between loca-
tions. The average secondary root ratings for the single
crosses and S_1 lines were as follows: B14A x SD10, 9.5;
F2J x H3839, 12.0; CI21E x H3839, 12.3; B37 x B65, 7.8;
and S_1 lines 10.6. The S_1 line with the best secondary
root development averaged 15.3.

The frequency distribution for size rating of the
retest population is portrayed in Figure 11. No selection
for size was made in the original population and any gain
in size can be attributed to correlated selection with

Figure 10. Frequency distributions for average secondary
root rating of S_1 lines. Original population,
Newell, Iowa, 1969. Retest population, Sanborn,
Iowa, 1970. In each distribution the mean is
indicated by a solid vertical line, and the
mean of superior entries chosen for retest by
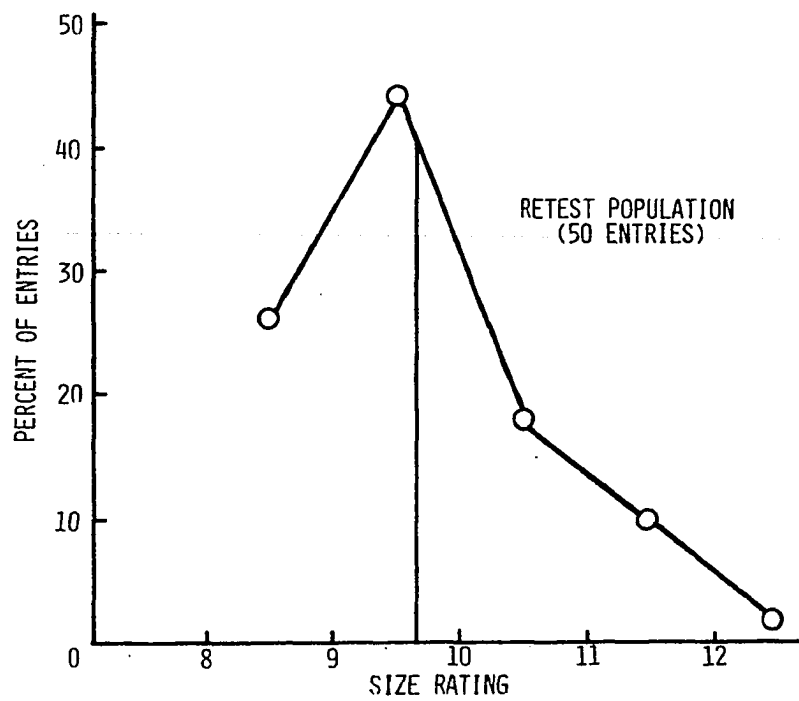a broken vertical line in the original popula-
tion
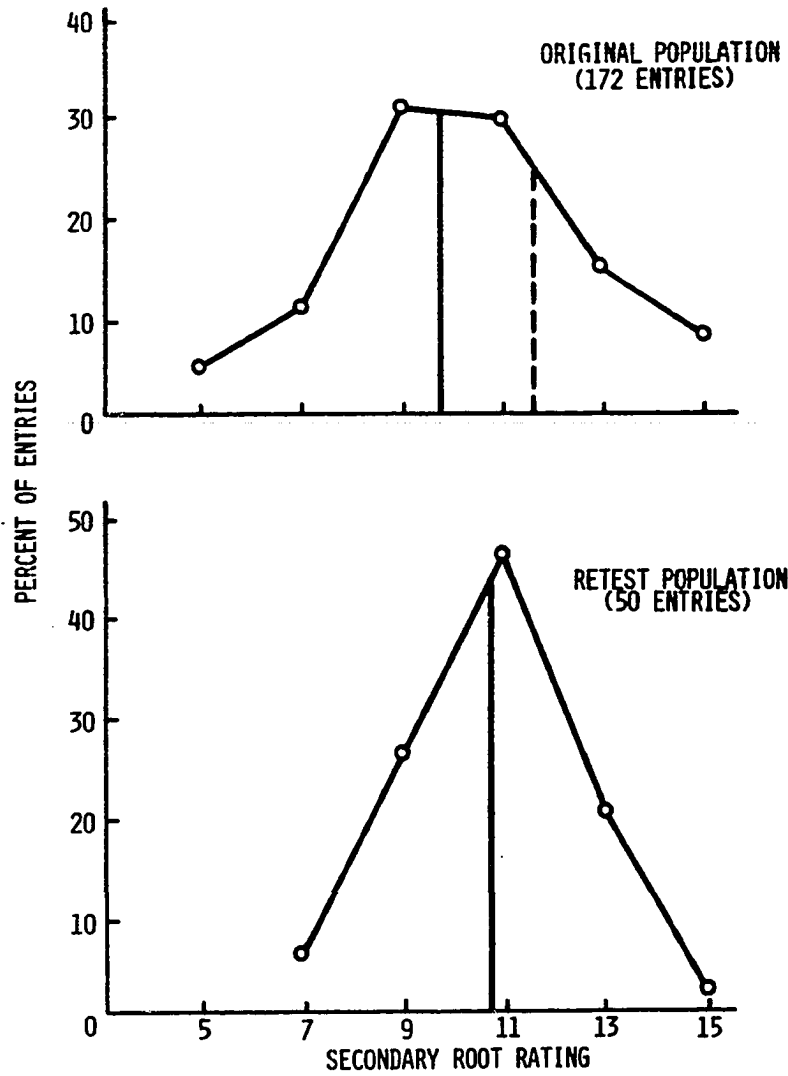
Figure 11. Frequency distribution for average size
rating of S_1 lines. Retest population,
Sanborn, Iowa, 1970. The mean is indicated
by the solid vertical line

secondary development as the selection criterion. Although extremely large plants were not present in the retest population, selection for secondary root development did result in the probable elimination of those entries with the smallest roots. It would seem, however, that even greater gains in root size might have been made if selection in the original population had included size. This indicates that selection for secondary development alone can also produce gains in size, but that the inclusion of size in the selection process would seem more appropriate in most circumstances. The average root size ratings per plot for the single crosses and S_1 lines were as follows: B14A x SD10, 11.5; F2J x H3839, 10.8; CI21E x H3839, 11.3; B37 x B65, 10.8; and S_1 lines, 9.6. The largest S_1 line had an average plot rating of 12.5.

The histogram for percent lodging observed in the original population at the Allee farm in 1969 is portrayed in Figure 12. Lodging was skewed toward zero lodging as was the case for the selfed and full sib lines. A direct comparison of the S_1 lines with the full sib lines (Figure 8) is possible since the two populations were grown in the same field and bordered each other. It is readily evident that more lodging occurred in the S_1 lines than in the full sib lines.
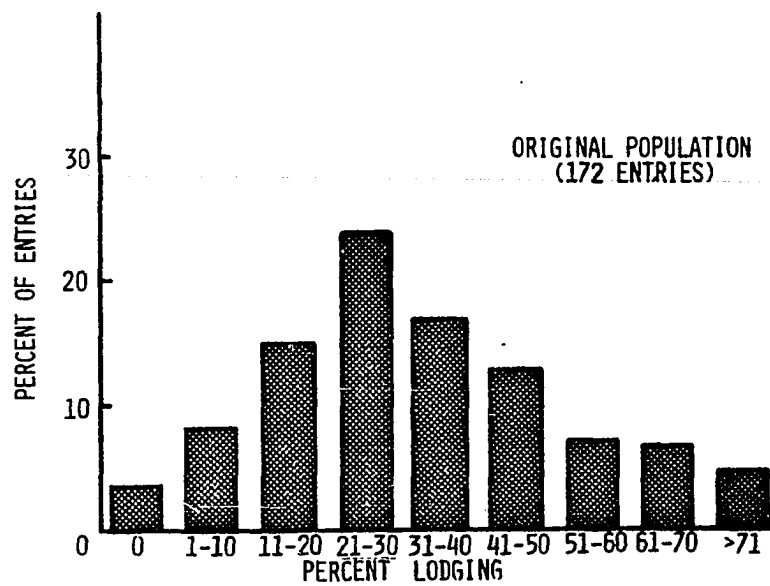
Figure 12. Histogram for average percent lodging of S_1 lines. Original population, Newell, Iowa, 1969

Selection Methods

A selection index was computed for the original population of full sib lines to provide a basis of comparison for the selection method which was actually employed in this study. The index for the full sib population became:

Root Tolerance Index = $0.44 X_1 + 1.33 X_2 - 1.58 X_3 - 0.47 X_4$

where, for the average plot rating of each entry, X_1 = secondary root rating, X_2 = root size rating, X_3 = rootworm damage rating, X_4 = percent lodging. The index was applied to each entry of the original population and the index values for all entries were arranged from most to least desirable. A similar arrangement was made for the entries chosen by the actual selection method used. Direct comparison of entries chosen as superior by the two methods revealed 100% agreement on the upper 16 entries. Agreement of the 50 superior selections for each method was found to be 74%. As might be expected, disagreement between the two methods became more obvious in the lower 40% of the chosen entries. The index did not utilize maturity information, and when this character is considered the two methods reach even closer agreement. Since final selection would likely be for only the upper 10% of the entries, it would appear that the two methods of selection are approximately equal in effectiveness.

Four primary characters and one secondary character
were utilized in the selection methods and the complexity
of selecting for rootworm tolerance is readily evident.
It appears that if interrelationships between characters
are known and considered, the actual selection method
employed is adequate. Index selection would be superior,
however, if the actual method of selection were based on a
peremptory combination of component characters.

SUMMARY AND CONCLUSIONS

Tolerance, or the ability of a plant to withstand insect infestation, is an important factor in resistance of maize to corn rootworms. Tolerant corn plants would be able to develop new roots above the feeding points of the larvae almost as fast as the insect destroys root tissue. Rootworm studies have detected differential responses of certain lines to larval feeding, but little information existed on the heritability and interrelationships of root characters used as indicators of tolerance.

Selfed, full sib, and S_1 lines of corn were grown under natural rootworm infestations and evaluated for rootworm tolerance. The study was conducted at three locations over three growing seasons (1968-1970). Entries of each line were screened initially for tolerance and approximately 50 superior entries were chosen from each population for retest at a different location the following year. Rootworm feeding damage, size of root systems, degree of secondary root development, and percent lodging were the primary character-istics considered as indicators of rootworm tolerance.

Results indicated that heritability for rootworm damage was relatively low which suggested that selection for resistance to damage alone would be relatively ineffective. Heritability for root size, secondary root development, and lodging were found to be relatively high and gains could be

expected from selection for any of these characters.
Genotypic, phenotypic, and error correlations between the
various characters were constructed for all lines. Gen-
erally, the correlation between characters appeared to be
consistent for the three populations, and the genotypic
correlations were slightly higher than the phenotypic.
Positive correlations were found for root size with secondary
roots and lodging with rootworm damage. Negative correla-
tions were found for size with lodging, secondary roots
with lodging, damage with secondary roots, and damage with
root size. Certain of these correlations were high enough
to merit consideration of correlated selection for one or
the other character.

Individual entries within each experiment were evaluated
on the basis of average performance and superior entries were
selected in accordance with the phenotypic values of the
four root characters. A selection index was computed for
the original population of full sib lines. Such an index
is said to maximize objectivity by giving proper weight to
each root character under consideration. A comparison of
the entries chosen as superior by the index was made with
those chosen as superior by the selection process actually
employed. The two methods were found to be in perfect
agreement in the upper percentiles of superior entries.
Such agreement supported the validity of the selection

method actually used. An important feature of index selection is that it is possible to select for resistance to more than one insect at the same time. This would be particularly useful when a single character of insect damage can be used as an indicator of resistance. Thus, presence or absence of European corn borer feeding lesions is an excellent indicator of leaf feeding resistance and this character could easily be incorporated into the index. It would appear that selection for disease resistance could be used in the same manner. Falconer (1960) points out that index selection presents no great problems when the component characters are uncorrelated, and this concept is compatible with selection for an additional insect or disease.

Results from selection for rootworm tolerance were portrayed for each character in all populations. Comparisons made between distributions of original and retest populations indicated that selection resulted in gains for each component character of tolerance.

Tolerance, as defined in this study, should not be limited to a single rootworm species. Damage is the only root character which might be specific for a given rootworm species. The remaining characters should be expressed in the same manner regardless of the predominant species infesting a particular field. On the basis of evaluations made in this study, superior entries from each

of the three experimental sources could be combined into

a single synthetic population which should possess a good

degree of tolerance to the corn rootworm complex.

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