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A genetic analysis of corn earworm (Heliothis zea Boddie) resistance in maize (Zea mays L.)

John R. Attewell

To the Graduate Council:

I am submitting herewith a dissertation written by John R. Attewell entitled "A genetic analysis of corn earworm (Heliothis zea Boddie) resistance in maize (Zea mays L.)." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Plant, Soil and Environmental Sciences.

Vernon H. Reich, Major Professor

We have read this dissertation and recommend its acceptance:

Dennis R. West, Fred L. Allen, Bob V. Conger, J.B. McLaren, Robert A. McLean

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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Accepted for the Council:

C. W. Minkel

The Graduate School

A GENETIC ANALYSIS OF CORN EARWORM (*HELIOTHIS ZEA* BODDIE) RESISTANCE IN MAIZE (*ZEA MAYS* L.)

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

John R. Attewell

March 1984

DEDICATION

To my wife, Deborah J. Attewell, whose love and sacrifice have made this work possible.

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ABSTRACT

Resistance to the corn earworm (*Heliothis zea* Boddie) in corn (*Zea mays* L.) was studied to determine the inheritance of several characters thought to contribute to this complex trait.

Genetic effects among the inbred lines: T115, T220, T222, T224, T232, Mo18W, Ga209, Ky226, and the Mexican flint corn 'Zapalote Chico' (PI217413) were obtained using combining ability and generation means analyses for depth of earworm penetration, husk extension, and depth of blank tip. Silk maysin content was included in the combining ability analysis. Laboratory reared corn earworm larvae were applied to ensure a uniform level of infestation for all genotypes. Problems with the supply of corn earworm larvae resulted in variation for the number of days between infestation and mid-silk. However, covariate analysis showed that, within the interval studied (zero to five days), this source of variation did not affect damage ratings.

Parent-offspring regression gave a heritability estimate of 0.01 for depth of earworm penetration and 0.59 for husk extension. A preponderance of the genetic effects for depth of earworm penetration, husk extension, and depth of blank tip were additive in nature, although significant dominance and epistatic effects were also found in several crosses. Since additive genetic effects provided the most consistent source of variation (significant in 67% of the crosses for depth of penetration) selection methods which utilize this type of variation should increase the frequency of alleles for resistance.

The genotypes which had the highest level of resistance and would be useful in a breeding program were T232, Ky226, and PI217413.

The analysis for maysin content gave results which are inconsistent with those found by others. In particular, PI217413 had a low maysin content among the genotypes studied.

The relationship between depth of penetration and husk extension appeared to be somewhat dependent on the level of resistance. In resistant crosses, such as T232 x PI217413, this correlation did not differ from zero, while in some susceptible crosses, such as T220 x T224 ($r = -0.37$) this relationship appeared to be stronger.

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CHAPTER I

INTRODUCTION

Since the mid-1900's, the corn earworm (Heliothis zea Boddie) has been a serious pest on corn (Zea mays L.) in the United States. The larval stage feeds on the ears of corn and not only causes direct damage itself but also permits other pests to enter the husk environment and further reduce the yield of grain.

Larval feeding is usually limited to an area of a few centimeters on the tip of the ear. Since the damage to an individual ear is not striking, this insect is not often considered a serious pest of corn. However, the accumulated loss over a large region can be significant. Annually 2 percent of the U.S. corn crop is lost to the earworm. This amounts to slightly more than two million acres, and a monetary loss of two to three hundred million dollars annually (McMillian and Wiseman 1972, Hardwick 1965). Attempts with cultural, mechanical, biological, and chemical control methods have been either inadequate or not economical.

The use of host-plant resistance has been an effective means of control for many pests. The development of plant resistance to insect pests such as the corn earworm, offers promise of reducing yield losses as well as a material reduction in the use of insecticides (Sprague and Dahms 1972). Insect-resistant varieties have contributed significantly to the control of insect populations.

A knowledge of the method of inheritance for resistance is of great practical importance in planning a breeding method to isolate and transfer earworm resistance.

The investigations reported herein were designed to elucidate the genetic effects for depth of penetration, husk extension, depth of blank tip, and maysin content in a population of corn inbreds and hybrids that are an important source of breeding material for Tennessee.

The information derived from these analyses will furnish knowledge that is essential to corn earworm resistance breeding programs. These studies also include a plant introduction that may provide a unique and transferable source of resistance.

CHAPTER II

REVIEW OF LITERATURE

I. EPIDEMIOLOGY

The corn earworm pupae overwinters in the soil primarily south of 40 degrees latitude. The adult is a small buff-colored moth which emerges from the soil during May in Tennessee. They are nocturnal and fly, mate, and deposit their eggs approximately between dusk and midnight. The average female moth can lay between 600 and 1000 eggs during her lifetime (Hardwick 1965, Fye and McAda 1972). In the spring these eggs are deposited on corn leaves in small clumps. The eggs hatch in about a week, depending on the temperature (Luckman 1963) and larvae begin feeding on the tender leaves of the plant. This feeding can also cause injury to the immature tassel. The small earworm larvae are subject to parasitation and predation during this time by other insects, especially members of the Coleoptera. They are also exposed to adverse weather conditions. These factors help keep earworm populations in check during the spring.

In the summer the female prefers to oviposit on fresh silks of the corn plant. The moth lays its eggs singly on the silks, unlike the egg masses on seedling leaves in the spring. When these eggs hatch, two to eight days after oviposition (Phillips and King 1923), the larvae eat their way down the silk channel and onto the developing

ear. This is where the earworm causes the major damage to the corn crop. These later generations are able to escape predation and the effects of insecticides as they feed inside the protective environment of the ear. Fortunately the earworm's most important predator at this stage is itself—they are highly cannibalistic (Barber 1936). This aggressive behavior generally results in only one larvae per ear.

As the larvae grow they molt five times. After 13 to 28 days they are fully grown and are three to four centimeters in length (Phillips and King 1923, Hardwick 1965). They appear in a variety of colors and are often confused with the fall armyworm (Spodoptera frugiperda Smith). They eat the immature kernels and foul the ear with their frass. The odor of this decaying matter attracts adult sap beetles (Carpophilus spp.) which deposit their eggs within this area. Thus, a secondary pest infestation occurs. The maize weevil (Stitophilus zeamaize Motschulsky) also gains entrance following earworm infestation. Secondary disease effects occur with the introduction of molds. This is a common occurrence and is currently under investigation (Fennel et al. 1978, Lillehoj et al. 1978, Widstrom 1979).

Upon maturity, the larva has penetrated deep inside the ear and is strong enough to chew its way through the husk, leaving a small exit hole. It drops to the ground and digs a burrow in which it pupates.

During this resting stage the larva becomes a moth. Depending on several developmental factors (inbreeding, temperature, moisture,

and nutrition the moth emerges from the soil 10 to 37 days later (Hardwick 1965). This short life cycle results in several generations of corn earworm each season.

II. RESISTANCE STUDIES

Many researchers have reported resistance to the corn earworm in corn (Collins and Kempton 1917, Burk et al. 1936, Poole 1936, Walker and Anderson 1938, Painter and Brunsen 1940, Richey 1944, Dicke and Jenkins 1945, Douglas and Eckhardt 1957, Guthrie and Walter 1961, Walter 1962, Tereshkovich and Brantley 1965, Del Valle and Harmon 1966, Bennet et al. 1967, Kaniuka 1973, Chalfant 1974, Webster and Walker 1976, McMillian et al. 1977, Wiseman et al. 1978, Wann 1980). In 1962 Walter reported on a Mexican flint corn, 'Zapalote Chico' (PI217413), that he had studied for four years. He noted that this genotype was the most resistant he had found in extensive screenings and suggested that it might prove to be a good source of breeding material. In 1966, Josephson et al. began a study of the factors influencing corn earworm resistance using 'Zapalote Chico' in combination with adapted Tennessee inbreds. They found two plant characteristics to be important in resistance: (1) a long tight tough husk, and (2) some form of silk resistance.[1] A resistance factor in the grain was also indicated but subsequent research has not been able to verify this (Starks et al. 1965, McMillian et al. 1966, Wiseman

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[1]A "silk lethal factor" was theorized by Blanchard et al. in 1941 and Walter in 1957.

et al. 1969, McMillian et al. 1970, Straub and Fairchild 1970, Wiseman et al. 1970). Since the early sixties, 'Zapalote Chico' has been widely used for corn earworm resistance in breeding programs—especially by research groups in Georgia, Missouri, and Tennessee.

III. DAMAGE CHARACTERIZATION AND MEASUREMENT

There are several ways in which Heliothis inflicts damage to the corn ear. The most obvious is direct kernel feeding. Generally, the smaller kernels are entirely eaten while the germ of the larger kernels is primarily consumed.

Indirect injury is often as great as the direct injury. Boring into the larger kernels loosens the remaining endosperm which may cause it to be lost at harvest or render it available to secondary pests. The young larvae also feed on the silks which restricts fertilization causing poorly filled tips (i.e., blank tip). In sweetcorn they reduce the marketability as a result of their excrement left among the kernels. Molds, which would not otherwise gain entrance to the ear, are introduced by earworm feeding. The earworm frass allows a moist environment for germination of spores (Painter and Brunson 1940). Fungi easily colonize earworm damaged kernels and often infect the remaining uninjured kernels. Ears that are infected with Aspergillis flavus (Link ex Fries) and other toxin producing fungi pose a health hazard when used in animal feeds.

Since earworm injury is manifest in several ways, quantification of the damage is somewhat subjective. Several methods of damage measurement have been used by researchers. Collins and Kempton (1917)

subjectively rated damage on a scale of one to ten. They also counted the number of larvae present inside the husks at harvest. An "injury index" method of scoring was proposed by Poole (1934). It dealt with categories of "percent marketability." Phillips and Barber (1931) defined earworm injury as the number of kernels injured or destroyed and conducted many experiments using this rating scheme. Blanchard et al. (1941) used three methods of rating the amount of damage:

1. Percentage of ears infested.
2. Average degree of damage to individual ears.
3. Percentage of infested ears with damage extending more than three-quarters of an inch from the ear tip.

Dicke and Jenkins (1945) refined this by grouping the number of kernels damaged into classes. Robertson and Walter (1963) developed classes based on the depth of penetration (i.e., class #1: "slight or no feeding"; class #2: "feeding to one-half inch"; ... etc.). Wadley (1949) used weighted classes on the basis of the number of kernels damaged. He reasoned that the kernels near the tip of the ear should not be given the same weight as the larger kernels farther away from the tip. Ditman and Ditman (1957) developed a complicated measuring apparatus which, when calibrated for each variety, measured the length of the ear in inches, the depth of penetration, and the percent of grain loss.

Several workers have estimated the degree of corn earworm injury by two basic methods:

1. The percentage of injured or uninjured ears.
2. An injury index showing the average degree of injury per ear.

To determine the injury index, numbered categories are arbitrarily based on the depth of injury from the tip of the ear. The number of ears in each category is multiplied by the category number and divided by the total number of ears examined. Harris (1958) compared the injury index method to the percent worm-free ears for detecting significant differences among varieties by examining F values, coefficients of variation, and multiple range tests. He found the injury index method to be superior to percentage estimates. Widstrom (1967) evaluated several methods for measuring injury. He compared the magnitude of the coefficients of variation obtained from each scoring system. He found that measuring the depth of penetration (in centimeters) as a linear function produced the lowest coefficient of variation for individual plots under artificial infestation. Since this method shows anormal distributions for individual plant data, he proposed a "revised centimeter scale." However, if plot means are taken the centimeter scale can be used.

IV. METHODS FOR TESTING RESISTANCE

The main objective of genotype evaluation is to differentiate between resistant and susceptible plants. In many host/pathogen situations it is relatively easy to distinguish between resistant and susceptible individuals since most forms of resistance are governed by one or a very few major genes. Variation in these cases is discontinuous. However, resistance in many host/insect systems (and especially in the corn/corn earworm system) does not provide a clear

distinction between resistant and susceptible plants. The difference in resistance is quantitative rather than qualitative, thus it is necessary to measure the level of resistance (Dahms 1972).

Several methods are available for estimating resistance:

1. Measuring the number of discrete infections or individuals preying on the plant.
2. Estimating the area of the plant affected.
3. Using a subjective scoring system.
4. Scoring or measuring the area, volume, or weight of attacked tissue through a correlated parameter. These correlated parameters can either be measured directly on the plant or indirectly from the pest organism (e.g., larval weights, behavioral and developmental parameters, percent food ingestion and retention).

The evaluation of resistance can be done in the field, laboratory, or greenhouse. In field evaluations, the results are subject to environmental interactions between the plant and the pest which may be difficult to control since the populations of the pest may not be evenly distributed over the experimental area. This unequal distribution may be due to factors other than those imparted by the plant's own resistance or susceptibility. In breeding for resistance to a pest, plant populations must be exposed to the organism in such a way that resistant and susceptible plants can readily be distinguished. All plants should be exposed to the same level of attack so that analyses are able to detect the differences

among cultivars. For some pests and diseases this exposure can be carried out under natural field conditions. However, natural epidemics do not occur in every year and location, thus an artificial epidemic must be created to insure the uniform exposure of the plant material (Dahms 1972, Duvick 1975, Gallun et al. 1975, Guthrie 1975, Russell 1975).

Attractant chemicals or susceptible plants ("bait crops") have been used to encourage epidemics (Painter 1951), however artificial inoculation provides more reliable, cost effective, rapid, and uniform infestation levels. Very often artificial infestation methods are used to supplement natural populations of pests. This supplementation reduces "escapes" which would otherwise be classified as resistant. It is important to synchronize infestation with the developmental stage of the insect and of the crop and to determine the number of insects to use.

Corn varieties differ in time of silking and, in a large experiment, all will not be ready for artificial infestation at the same time. Thus, a controlled infestation based on silking date is desirable. Many methods have been developed for artificially inoculating corn with the corn earworm. Blanchard et al. (1942) placed newly hatched larvae on the fresh corn silks by means of a small camel's-hair brush. This is often referred to as the "paint brush" method.

In 1962, Bennett and Josephson reported on an experiment comparing the use of paint-brush-applied larvae versus laboratory and

field collected eggs, and natural versus artificial infestation from the standpoint of inflicting earworm injury. They observed that increasing the number of larvae used in the infestation resulted in a greater mean damage score. They found a small difference in damage between artifically and naturally infested larvae. They also attempted to place paired pupae in cages surrounding the ears, allowing the moths to emerge, mate, and oviposit on the silks. This method was not effective because most of the pupae died.

Josephson et al. (1966) reported that infesting with three first instar larvae per ear were adequate to differentiate resistance and susceptibility. Applications of eggs or third or fourth instar larvae were inadequate. Many experiments up to this time were conducted using all ages of larvae, adults, eggs, and multiple application dates. Widstrom and Burton (1970) felt that applications of this type were time consuming and laborious, and that this limited the number of plants that could be screened. In 1966 they developed a method whereby earworm eggs were suspended in an agar solution and injected with a syringe directly into the silk mass. They found that inoculation required at least 30 eggs to produce damage comparable to three-larvae-per-silk applications.

The "bazooka" applicator was developed by Mihm in 1978. The "bazooka" is a manual larval dispensor that can be precalibrated to deliver a uniform number of larvae mixed in a carrier of corn cob grits. This mechanical infestation device is more desirable than the

"paint brush" application or the "egg suspension" inoculation. This larval dispensor requires a smaller supply of pest insects, is as easy and rapid as the hypodermic injector, gives infestations that are repeatable by different researchers, and has been shown to be effective in imparting a high level of damage (Roberson et al. 1978).

V. COMPONENTS OF RESISTANCE

The mechanisms of host plant resistance to insects has been classified into three categories and defined by Painter (1951):

1. Preference or nonpreference. "A group of plant characters and insect responses which lead to, or away from, the use of a particular plant or variety, for oviposition, for food, or for shelter, or any combination of the three."

2. Tolerance. "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."

3. Antibiosis. "The tendency to prevent injury or destroy insect life. The term was proposed for those adverse effects on the insect's life history which resulted when the insect used a resistant host plant variety for food. The effects on the insect take the form of reduced fecundity, decreased size, abnormal length of life, and increased mortality."

These three mechanisms often interact to produce resistant varieties. Each of these types of resistance have been shown to be associated with corn earworm resistance.

A form of preference was examined by Barber (1937). He found that corn earworm moths preferred sweet corn over field corn for oviposition. He suggested that sweet corn silks were somehow more attractive and consequently received a greater number of eggs.

Husk characteristics have been studied as a tolerance mechanism. Although husk extension and husk tightness seem to be significantly correlated with corn earworm resistance, many researchers have found confusing and often conflicting results. Data presented by Collins and Kempton (1917), Phillips and Barber (1931), Walter (1961), Starks and McMillian (1967), Widstrom and Davis (1967), Widstrom et al. (1970a), Wiseman et al. (1970), Straub (1972), Wiseman et al. (1972), and Kim and Brewbaker (1975) have shown an association between husk extension, husk tightness, number of husk leaves, or texture of husks and earworm resistance. Other researchers have presented data that seem to indicate that little protection is offered by the husks (McClelland 1929, Cartwright 1930, Poole 1941, Cameron and Anderson (1966). Walter (1961) and Straub (1972) have criticized McClelland's and Cartwright's rating system—that of percentage of ears within a plot that were attacked—as failing to differentiate between infestation and actual damage. The study by Widstrom et al. (1970a) seems to be the most reasonable in terms of methodology, rating, analysis, and biological foundation. They evaluated several chemical, physical, and climatic conditions and their interrelationships as

they apply to resistance. They concluded that husk protection and feeding stimulation from chemical factors were related to corn earworm damage.

Other factors that have been implicated in corn earworm tolerance are silk balling (Snyder 1958, and Luckman et al. 1964) and time of silking (Poole 1935).

A form of antibiotic resistance has recently gained considerable attention and has some important implications from a breeding standpoint. The search for this antibiotic factor began with studies involving the force-feeding of plant parts on laboratory reared larvae. Blanchard et al. (1941) and Walter (1957) first suggested an earworm lethal factor was present. They observed that many larvae died while still in the fresh silks and conjectured that the lethal factor was due to some substance found within the silk tissue. Eden et al. (1962) began a search for this lethal factor. They analyzed resistant and susceptible corn silks for glucose and starch levels but found no differences. Knapp et al. (1965) analyzed silks for amino acids and reducing sugars and found no difference among resistant and susceptible varieties. Larval growth, developmental periods, and food retention were examined in a bioassay between corn kernels and corn silks by McMillian et al. (1966). They found differences in all response variables between kernels and silks and concluded that corn kernels provided better nutrition. Studies in larval mortality and several developmental parameters by Knapp et al. (1967) indicated the presence of a growth inhibitor. Bennett et al. (1967) proved that

this growth inhibitor was present in the silks of 'Zapalote Chico' (PI217413) but not in the kernels. Straub and Fairchild (1970) and Chamblis and Wann (1971) confirmed these results. Wiseman et al. (1976) and Wiseman et al. (1977) extended the experiments with 'Zapalote Chico' and concluded that the long tight husks of this variety were not the sole contributing factor of resistance, but that physical and chemical factors of the silks were also important.

Attempts to extract this chemical factor were delayed, due to misinterpretation of experimental results. Water, alcohol, and ether extractions of resistant and susceptible varieties were fed to laboratory larvae (Starks et al. 1965, McMillian and Starks 1966, McMillian et al. 1967, McMillian et al. 1970, Jones et al. 1972). Growth and developmental factors differed widely between resistant and susceptible plants. The researchers erroneously interpreted these differences to be due to a feeding stimulant in the susceptible varieties rather than an inhibitor in the resistant varieties. Consequently, a great deal of effort was applied to the examination of susceptible, rather than resistant, varieties.

In 1977 Widstrom et al. examined methods whereby the growth inhibition found in field studies could be studied in a laboratory environment. Although their bioassays were unsuccessful, the preliminary results led Waiss et al. (1979) to search for, and isolate, a compound which severely retarded the growth of the corn earworm. They described the purification and initial characterization of this compound and named it "maysin." Elliger et al. (1979) completed the

identification of maysin's chemical structure and reported the existence of several analogs.

VI. GENETIC STUDIES

Observations by Blanchard et al. (1941) indicated that hybrids were generally more resistant to corn earworm attack than inbred lines. This hypothesis was tested and accepted by Widstrom and Davis in 1967. They speculated that resistance in the F1 plants might be explained by increased vigor of the hybrid or by dominant gene action in the overdominance range. They estimated the minimal number of genes involved in resistance to be in excess of three and suggested a complex inheritance pattern to be probable. From examination of V_r/W_r graphs from a diallel analysis they suspected epistatic gene action or correlated gene distributions to also contribute significantly to reduced earworm damage. General and specific combining ability were both found to be significant.

Other diallel studies (Widstrom and Hamm 1969 and Widstrom 1972) found general combining ability effects to be important but offered conflicting evidence for the importance of specific combining ability. Constant parent regressions in these two studies also gave inconsistent estimates as to the level of dominance.

Reciprocal effects were found to be nonsignificant and genotype by environment interactions were found to be significant by Widstrom and Starks (1967), Widstrom and Hamm (1969), and Widstrom (1972). Widstrom and Davis (1967) also reported nonsignificant reciprocal effects.

In 1973 Widstrom and McMillian evaluated a population of selected sweet corn inbreds and a population of selected dent corn inbreds using the generation means analysis. They found additive, dominance, and digenic epistatic effects to be highly significant in both populations. The proportion of epistatic effects, however, was very low. Oddly enough, dominance was the major genetic effect among the dent crosses while additive genetic effects were more important among the sweet inbreds. They also found a substantial inbreeding depression and indications that environment contributes a significant proportion to the total variance. Heritability of resistance was estimated at 29 percent for both populations. Widstrom and Hamm (1969) calculated a similar estimate for heritability at about 37 percent.

Widstrom et al. (1970b) were able to use recurrent selection to reduce earworm injury while Zuber et al. (1971) were successful with a mass selection technique.

Widstrom et al. (1983) examined the repeatability and inheritance pattern of maysin among several susceptible and resistant lines, again, using the generation means analysis. They found highly significant differences among lines and nearly equal portions of additive and nonadditive genetic effects. They could not detect any reciprocal or cross by year interaction effects.

CHAPTER III

MATERIALS AND METHODS

I. POPULATIONS

Eight inbred lines of dent corn (T232, T220, T222, T224, T115, Mo18W, Ga209, and Ky226) and the Mexican flint corn 'Zapalote Chico' (PI217413) were used as parents to make all possible F_1's without reciprocals in a combining ability analysis. In addition to the F_1's, the F_2 and backcross generations to both parents (BC_1 and BC_2) were made for use in a generation means analysis.

Zapalote Chico was also crossed with each adapted inbred and the progeny of these eight lines were sibbed for twelve generations. This population was used as the parental generation in a parent-offspring regression analysis. The offspring generation was made by selfing each of the parents.

II. FIELD PLOT PROCEDURE

The parent and offspring generations of the sibbed lines were grown in 1980 and 1981, respectively, in a completely randomized experimental design. The parents, F_1's, F_2's and backcross generations were grown in 1982 in a modified randomized complete block design. The F_1's in the combining ability analysis for maysin content were taken from a single block within the generation means analysis and analyzed as a completely randomized design.

All experiments were conducted at the Tennessee Agricultural Experiment Station Plant Science Field Laboratory, Knoxville, Tennessee. All the experimental material was planted in two-row plots. Each row was 274 cm in length with 91 cm between rows with the exception of the parents of the sibbed lines which were in rows 183 cm long. Thirty-eight seeds per plot were planted and thinned to 30 seedlings per plot five weeks later. P_2O_5 and K_2O were broadcast at rates of 134.4 kg/ha along with 67.2 kg/ha nitrogen prior to seeding. A side dressing of 100.8 kg/ha nitrogen was applied approximately 30 days after planting. Atrazine was applied at planting for broad-leaf weed control and alachlor was applied six weeks later for grass weed control.

The first ear of each parent of the sibbed lines was infested with three first-instar corn earworm larvae by means of a camel's-hair brush when the silks were three to five days old after silk emergence. These earworm larvae were reared at the Knoxville Experiment Station. Ten ears from each parent were selected on the basis of depth of penetration. Five ears with the lowest and five ears with the highest penetration were selected.

Each offspring of the sibbed lines and all generations of the combining ability and generation means analyses were infested within five days from silk emergence using a "bazooka" applicator and larvae reared at the United States Department of Agriculture Southern Grain Insects Laboratory in Tifton, Georgia.

The earworm damage in all generations was measured as depth of penetration in centimeters from the lowest feeding point on the ear to the ear tip. Husk extension was measured in centimeters from the tip of the ear to the tip of the husk sheath.

Several other variables were measured for the generation means analysis. Blank tip was measured in centimeters from the lowest point of nonfilled kernels on the ear to the ear tip. Two classes of infestation were recorded: those ears that were artificially infested and those ears which were not. The number of days from planting to mid-silk of each plot was recorded and subtracted from the number of days from planting to artificial infestation of each plot.

Because of differences in vigor for the combining ability and generation means analyses, the parents were not intermixed but were grown separately within each block. This was done to avoid hybrid/inbred competition.

Earworm eggs were supplied twice per week by the United States Department of Agriculture Southern Grain Insects Laboratory, Tifton, Georgia. First instar larvae were applied at a rate of three larvae per ear using a "bazooka" applicator. As problems with mail shipments and poor hatching percentage limited the larval supply, the number of plants infested per plot was determined by the daily availability of earworm larvae and the number of three- to five-day-old silks present in the experiment. Plants that

were infested were marked with red paint on the husk near the base of the ear. The plants were rated approximately four weeks later.

All data for each of the experiments were checked for univariate normality.

III. MAYSIN EXTRACTION PROCEDURE

Three- to five-day-old silks were collected, placed in plastic bags, frozen in the field with dry ice, and stored at 3°C until analyzed. Samples were prepared for analysis by trimming the exposed portion of the silks. Any husk material around the silk was also removed.

Seven samples from each genotype were placed on pre-weighed pieces of aluminum foil and weighed to obtain wet weights. One of the samples was dried in a convection oven overnight to obtain dry weight and percent moisture. The remaining six samples were ground separately with a mortar and pestle in approximately ten ml of methanol. Each sample was then vacuum filtered with a buchner funnel and coarse filter paper (Fisher ® #09-795BB). The mortar, pestle, and residue were washed with approximately ten ml of methanol. This eluate was also filtered. The combined filtrate was transferred to a test tube and the volume recorded. The test tubes were sealed with Parafilm ® and stored in a cold room overnight to allow any flocculate to settle out.

Percent transmission of light at 352 nm was recorded using a Spectronic 20 ® spectrophotometer. Micrograms of maysin per gram of

dry silk tissue was calculated using Beer's Law and the percent dry weight of the moisture sample.

IV. ESTIMATE OF HERITABILITY USING PARENT-OFFSPRING REGRESSION

Heritability estimates on an individual plant basis were calculated for depth of penetration and husk extension using the relationship of $h^2 = b_{xy}$ as described by Hansen (1963).

V. COMBINING ABILITY ANALYSIS

F_1 cross means, general and specific combining ability mean squares, and general and specific combining ability effects for maysin content were estimated using Griffing's method four model I diallel analysis (Griffing 1956). In addition to maysin content, the combining ability analysis for depth of penetration, husk extension, and depth of blank tip was performed. The model for this analysis is as follows:

$$y_{ijk\ell m} = \mu + B_i + \delta_{(i)j} + C_{k\ell} + \varepsilon_{(ijk\ell)m}$$

$$i = 1, \ldots, b, \quad j = 1, \quad k = 1, \ldots, p, \quad \ell = 1, \ldots, p,$$

$$\text{and } m = 1, \ldots, n$$

where

$y_{ijk\ell m}$ = micrograms of maysin per gram of dry silk of the m^{th} plant of the $k\ell^{th}$ cross in the j^{th} randomization in the i^{th} block,

μ = the overall mean,

B_i = the fixed effect of the i^{th} block,

$\delta_{(i)j}$ = the j^{th} restriction error within the i^{th} block, NID $(0,\sigma^2_\delta)$. This term illustrates the restriction on the randomization of the treatments into the i^{th} block's experimental units. It is completely confounded with B_i (Anderson and McLean 1974),

$C_{k\ell}$ = the fixed effect of the $k\ell^{th}$ cross, and

$\varepsilon_{(ijk\ell)m}$ = the random error associated with the m^{th} plant in the $k\ell^{th}$ cross subjected to the j^{th} restriction on the i^{th} block, NID $(0,\sigma^2)$.

Table 1 shows the general form of the analysis of variance where

$\phi(B)$ = the variance of blocks,

σ^2_δ = the variance of the restriction error,

$\phi(C)$ = the variance of crosses,

g_k = the general combining ability effects,

$s_{k\ell}$ = the specific combining ability effects,

$\sigma^2_{e'}$ = the error variance of the general and specific combining ability effects, and

σ^2 = the experimental error variance.

The effects g_k and $s_{k\ell}$ are estimated as follows:

$$\hat{g}_k = \frac{(pX_{i.} - 2X_{..})}{p(p-2)},$$

$$\hat{s}_{k\ell} = X_{k\ell} - \frac{(X_{k.} - X_{.\ell})}{p-2} + \frac{2X_{..}}{(p-1)(p-2)},$$

Table 1. The general form of the combining ability analysis of variance.

Source of variation	d.f.		M.S.	E.M.S.
Blocks (B_i)	b-1		MSB	$\sigma^2 + cn\sigma^2 + cn\phi(B)$
Restriction error ($\delta_{(i)j}$)	0		None	$\sigma^2 + cn\sigma^2_\delta$
Crosses ($C_{k\ell}$)	c-1		MSC	$\sigma^2 + b\phi(C)$
general combining ability (gca)		p-1	MSg	$\sigma^2_{e'} + (p-2)[\frac{1}{p-1}] \sum_k g^2_k$
specific combining ability (sca)		$\frac{p(p-3)}{2}$	MSs	$\sigma^2_{e'} + [\frac{2}{p(p-3)}] \sum_{k<\ell} \sum s^2_{k\ell}$
partition error†		n(b-1)(p-1)	MSe'	$\sigma^2_{e'}$
Error ($\varepsilon_{(ijk\ell)m}$)	n(b-1)(p-1)		MSE	σ^2
Total	N-1			

†Partition error = $\frac{MSE}{bc}$.

where

$X_{k.}$ = the marginal sum of the k^{th} inbred,

$X_{.\ell}$ = the marginal sum of the ℓ^{th} inbred, and

$X_{..}$ = the sum of all the $k\ell^{th}$ cell means.

The following restrictions are imposed on the combining ability effects:

$$\sum_{k} g_k = 0$$

and

$$\sum_{k \neq \ell} s_{k\ell} = 0 \quad \text{(for each } \ell\text{)}.$$

The standard error of the g_k^{th} estimate is:

$$\left(\frac{(p-1)M_{e'}}{p(p-2)}\right)^{1/2}.$$

The standard error of the $s_{k\ell}^{th}$ estimate is:

$$\left(\frac{(p-3)M_{e'}}{p-1}\right)^{1/2}.$$

The standard error of the $(g_k - g_\ell)^{th}$ difference is:

$$\left(\frac{2M_{e'}}{p-2}\right)^{1/2} \qquad (k \neq \ell).$$

The standard error of the $(s_{k\ell} - s_{k\ell})^{th}$ difference is:

$$\left(\frac{2(p-3)M_{e'}}{p-2}\right)^{1/2} \qquad (k \neq \ell).$$

VI. GENETIC ANALYSIS OF THREE EAR CHARACTERISTICS MEASURED IN THE FIELD

A generation means analysis was conducted for depth of penetration, husk extension, and depth of blank tip.

Model Construction

A modified stepwise procedure was used to determine a useful model for the final analysis. Three variables in addition to the variables for block and generation were available to control the total variation. The variable, method of infestation, was examined on an individual plant basis. An appropriate model was determined from this step. In the next step, the variables days between infestation and silking and block by generation interaction were added and the model tested on a plot basis.

a. The effect of artificial infestation. The following linear model was tested to examine the effect of artificial infestation:

$$y_{ijk\ell m} = \mu + B_i + \delta_{(i)j} + G_k + M_\ell + \varepsilon_{(ijk\ell)m}$$

$i = 1, \ldots, b$, $j = 1$, $k = 1, \ldots, g$, $\ell = 1, \ldots, h$, and

$m = 1, \ldots, n$

where

$y_{ijk\ell m}$ = the response of the m^{th} individual plant in block i of the j^{th} randomization, given the ℓ^{th} method of infestation and the k^{th} generation,

μ = the overall mean,

B_i = the fixed effect of the i^{th} block,

$\delta_{(i)j}$ = the j^{th} restriction error within the i^{th} block, NID $(0,\sigma^2_\delta)$. This term illustrates the restriction on the randomization of the treatments into the i^{th} block's experimental units. It is completely confounded with B_i (Anderson and McLean 1974),

G_k = the fixed effect of the k^{th} generation,

M_ℓ = the fixed effect of the ℓ^{th} method of infestation, and

$\varepsilon_{(ijk\ell)m}$ = the random error associated with the m^{th} plant in the ℓ^{th} method of infestation of the k^{th} generation subjected to the j^{th} restriction on the i^{th} block, NID $(0,\sigma^2)$.

The general form of the analysis of variance is shown in Table 2 where

$\phi(B)$ = the variance of blocks,

σ^2_δ = the variance of the restriction error,

$\phi(G)$ = the variance of generations,

$\phi(M)$ = the variance of methods of infestation, and

σ^2 = the error variance.

b. <u>The effect of block by generation interaction and days between infestation and silking</u>. This model was constructed to determine if the block by generation and days between infestation and silking may have contributed significant sources of variation. The following linear covariance model was used to test these effects:

Table 2. The general form of the artificial infestation analysis of variance.

Source of variation	d.f.	M.S.	E.M.S.
Blocks (B_i)	b-1	MSB	$\sigma^2 + ghn\sigma^2_\delta + ghn\phi(B)$
Restriction error ($\delta_{(i)j}$)	0	None	$\sigma^2 + ghn\sigma^2_\delta$
Generations (G_k)	g-1	MSG	$\sigma^2 + bhn\phi(G)$
Method (M_e)	h-1	MSM	$\sigma^2 + bgn\phi(M)$
Error ($\varepsilon_{ijk\ell)m}$)	n(h-1)(g-1)(b-1)	MSE	σ^2
Total	N-1		

$$y_{ijk\ell} = \mu + B_i + \delta_{(i)j} + G_k + BG_{ik} + \beta_1 Z_{(ijk)\ell} + \varepsilon_{(ijk)\ell}$$

$i = 1, \ldots, b$, $j = 1$, $k = 1, \ldots, g$, and $\ell = 1, \ldots, n$

where

$y_{ijk\ell}$ = the response of the ℓ^{th} plant in block i of the j^{th} randomization, given the k^{th} generation and the covariance of days between infestation and silking on the ℓ^{th} plant,

μ = the overall mean,

B_i = the fixed effect of the i^{th} block,

$\delta_{(i)j}$ = the j^{th} restriction error within the i^{th} block, NID $(0,\sigma^2_\theta)$. This term illustrates the restriction on the randomization of the treatments into the i^{th} block's experimental units. It is completely confounded with B_i (Anderson and McLean 1974),

G_k = the fixed effect of the k^{th} generation,

BG_{ik} = the fixed effect of the interaction between the i^{th} block and the k^{th} generation,

$\beta_1 Z_{(ijk)\ell}$ = the covariate effect of days between infestation and silking on the ℓ^{th} plant in block i of the j^{th} randomization, given the k^{th} generation, and

$\varepsilon_{(ijk)\ell}$ = the random error associated with the ℓ^{th} plant in block i of the j^{th} randomization, given the k^{th} generation, NID $(0,\sigma^2)$.

The general form of the analysis of covariance is shown in Table 3 where

Table 3. The general form of the block by generation interaction and days between silking analysis of covariance.

Source of variation	d.f.	M.S.	E.M.S.
Blocks (B_i)	b-1	MSB	$\sigma^2 + gn\sigma^2_\delta + gn\phi(B)$
Restriction error ($\delta_{(i)j}$)	0	None	$\sigma^2 + gn\sigma^2$
Generations (G_k)	g-1	MSG	$\sigma^2 + bn\phi(G)$
BG_{ik}	(b-1)(g-1)	MSBG	$\sigma^2 + n\phi(BG)$
Days between infestation and silking ($Z_{(ijk)\ell}$)	1	MSZ	$\sigma^2 + n\sigma^2_Z$
Error	n(b-1)(g-1)	MSE	σ^2
Total	N-1		

$\phi(B)$ = the variance of blocks,

σ^2_δ = the variance of the restriction error,

$\phi(G)$ = the variance of generations,

$\phi(BG)$ = the variance of the block by generation interaction,

σ^2_z = the covariance of days between infestation and silking, and

σ^2 = the error variance.

Generation Means Analysis

The procedure for calculating the parameters is given by Mather and Jinks (1971). The notation used, however, is that of Gamble (1962).[1] The relative importance of the additive, dominance, and digenic epistatic effects for the variation of the three ear characteristics described earlier was considered. A weighted least least squares technique was used (Searle 1971). The weighting constant was the number of observations composing each experimental unit mean.

The expectations of the generation means of two inbred lines with an arbitrary number of unlinked genes and their descendants resulting from selfing and crossing can be written as follows:

---

[1]Gamble used Hayman's (1958) model).

Generation	Cumulative Gene Effects					
	m	a	d	aa	ad	dd
P_1	1	1	0	1	0	0
P_2	1	-1	0	1	0	0
F_1	1	0	1	0	0	1
F_2	1	0	1/2	0	0	1/4
BC_1	1	1/2	1/2	1/4	1/4	1/4
BC_2	1	-1/2	1/2	1/4	-1/4	1/4

where

m = the mean of the two parents,

a = the pooled additive genetic effects,

d = the pooled dominance genetic effects,

aa = the pooled additive by additive genetic effects,

ad = the pooled additive by dominance genetic effects, and

dd = the pooled dominance by dominance genetic effects.

To get the estimates of these six parameters, the six equations are solved simultaneously to give:

$$\hat{m} = 1/2\ P_1 + 1/2\ P_2 + 4F_2 - 2BC_1 - 2BC_2 ,$$

$$\hat{a} = 1/2\ P_1 - 1/2\ P_2 ,$$

$$\hat{d} = -1\ 1/2\ P_1 - 1\ 1/2\ P_2 - F_1 - 8F_2 + 6BC_1 + 6BC_2 ,$$

$$\hat{aa} = -4F_2 + 2BC_1 + 2BC_2 ,$$

$$\hat{ad} = -P_1 + P_2 + 2BC_1 - 2BC_2 , \text{ and}$$

$$\hat{dd} = P_1 + P_2 + 2F_1 + 4F_2 - 4BC_1 - 4BC_2 .$$

The variance of these estimates are calculated as follows:

$$V(\hat{m}) = 1/4\ V(P_1) + 1/4\ V(P_2) + 16\ V(F_2) + 4\ V(BC_1) + 4\ V(BC_2)\ ,$$

$$V(\hat{a}) = 1/4\ V(P_1) + 1/4\ V(P_2)\ ,$$

$$V(\hat{d}) = 2.25\ V(P_1) + 2.25\ V(P_2) + 64\ V(F_1) + 36\ V(BC_1) + 36\ V(BC_2)\ ,$$

$$V(\hat{aa}) = 16\ V(F_2) + 4\ V(BC_1) + 4\ V(BC_2)\ ,$$

$$V(\hat{ad}) = V(P_1) + V(P_2) + 4\ V(BC_1) + 4\ V(BC_2)\ ,\ \text{and}$$

$$V(\hat{dd}) = V(P_1) + V(P_2) + 4\ V(F_1) + 16\ V(P_2) + 16\ V(BC_1) + 16\ V(BC_2)\ .$$

The linear additive model for this analysis is as follows:

$$\bar{y}_{ijk} = \mu + B_i + \delta_{(i)j} + G_k + \varepsilon_{ijk}$$

$i = 1, \ldots, b$, $j = 1$, and $k = 1, \ldots, g$,

where

$\bar{y}_{ijk}$ = the response of the k^{th} generation mean in block i of the j^{th} randomization,

μ = the overall mean,

B_i = the fixed effect of the i^{th} block,

$\delta_{(i)j}$ = the j^{th} restriction error within the i^{th} block, NID $(0,\sigma^2_\delta)$. This term illustrates the restriction on the randomization of the treatments into the i^{th} block's

experimental units. It is completely confounded with B_i (Anderson and McLean 1974),

G_k = the fixed effect of the k^{th} generation, and

ε_{ijk} = the random error associated with the k^{th} generation mean subjected to the j^{th} restriction on the i^{th} block, NID $(0,\sigma^2)$.

Table 4 shows the general form of the analysis of variance where

$\phi(B)$ = the variance of blocks,

σ^2_δ = the variance of the restriction error,

$\phi(G)$ = the variance of generations,

$\phi(a)$ = the variance of the additive gene effects,

$\phi(d)$ = the variance of the dominance gene effects,

$\phi(aa)$ = the variance of the additive by additive gene effects,

$\phi(ad)$ = the variance of the additive by dominance gene effects,

$\phi(dd)$ = the variance of the dominance by dominance gene effects, and

σ^2 = the error variance.

The percentage of the total genetic variance for each individual genetic effect was computed as follows:

$$\text{percent of genetic variance} = \frac{\text{effect sum of squares}}{\text{generation sum of squares}} \times 100 .$$

The test for additive, dominance, and digenic epistatic effects was conducted using a priori contrasts. The significance of the

Table 4. The general form of the generation means analysis of variance.

Source of variation	d.f.	M.S.	E.M.S.
Blocks (B_i)	b-1	MSB	$\sigma^2 + gn\sigma^2 + gn\phi(B)$
Restriction error ($\delta_{(i)j}$)	0	None	$\sigma^2 + gn\sigma^2_\delta$
Generation (G_k)	g-1	MSG	$\sigma^2 + bn\phi(G)$
additive effects (a)	1	MSa	$\sigma^2 + n\phi(a)$
dominance effects (d)	1	MSd	$\sigma^2 + n\phi(d)$
additive x additive effects (aa)	1	MSaa	$\sigma^2 + n\phi(aa)$
additive x dominance effects (ad)	1	MSad	$\sigma^2 + n\phi(ad)$
dominance x dominance effects (dd)	1	MSdd	$\sigma^2 + n\phi(dd)$
Error	(b-1)(g-1)	MSE	σ^2
Total	N-1		

estimates were tested using an F-test. Experimentwise adjustment of the α significance level was computed as follows:

$$E = 1 - (1 - \alpha)^t ,$$

where

E = the experimentwise error rate and

t = the number of dependent variables tested.

Heterosis, percent heterosis, inbreeding depression, and percent inbreeding depression were calculated for the overall population by the following methods:

$$\text{Heterosis} = \bar{F}_1 - \frac{\bar{P}_1 + \bar{P}_2}{2} ,$$

$$\text{Percent heterosis} = \frac{\bar{F}_1 - (\bar{P}_1 + \bar{P}_2)/2}{(\bar{P}_1 + \bar{P}_2)/2} (100) ,$$

$$\text{Inbreeding depression} = \bar{F}_1 - \bar{F}_2 , \text{ and}$$

$$\text{Percent inbreeding depression} = ((\bar{F}_1 - \bar{F}_2)/\bar{F}_1)(100) .$$

The standard errors of the heterosis and inbreeding depression were calculated for the above functions.

Character correlations were computed using the Pearson product-moment correlation coefficient.

CHAPTER IV

RESULTS

I. ESTIMATE OF HERITABILITY USING OFFSPRING ON PARENT REGRESSION

The heritability for the sibbed population of inbreds crossed with PI217413 is estimated to be -0.01 for depth of penetration and 0.59 for husk extension.

II. COMBINING ABILITY ANALYSIS

Table 5 shows that general and specific combining ability are highly significant for depth of penetration, husk extension, depth of blank tip, and maysin content.

The diallel means, given in Table 6, indicate dichotomous groupings for inbreds and hybrids. The groups for the inbreds are based on gca significance. The groups for F_1 hybrids are subjective, based on the mean values alone. PI217413 shows a very low mean depth of penetration followed by T222 and Ky226. These inbreds will be referred to as resistant. Conversely, T220 exhibits a very deep penetration mean. Ga209 and Mo18W are likewise high in depth of penetration. These inbreds will be referred to as susceptible. Husk extension presents a similar relationship. T222, Ky226, and PI217413 all possess husk extensions greater than 5.0 cm while Mo18W, T232, Ga209, T224, T115, and T220 have husk extensions

Table 5. Analysis of variance of 36 single crosses for depth of penetration, husk extension, blank tip, and maysin content.

Source of variation	Depth of penetration		Husk extension		Depth of blank tip		Maysin content	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Block	3	1.90	3	1.18	3	4.03	†	†
Cross	35	3.93**	35	17.42**	35	6.16**	35	6.20**
gca	8	12.41**	8	65.36**	8	31.76**	8	13.52**
sca	27	1.41**	27	3.21**	27	2.36**	27	4.08**
error (MSe')	106	0.22	106	0.20	86	0.28	179	0.38
Error (MSE)	106	0.88	106	0.78	86	1.14	179	0.38
Total	171		171		134		214	

**Indicates significance at the 0.01 level of probability.

†Analysis for maysin content was not partitioned by block effects.

Table 6. Means of nine parents (over crosses) and 36 F_1 crosses for depth of penetration, husk extension, depth of blank tip, and maysin content from a combining ability analysis conducted at the Knoxville Experiment Station in 1982.

Parent or F_1 cross	Depth of penetration (cm)	Husk extension (cm)	Depth of blank tip (cm)	Maysin content (µg/g)
T232	2.69	3.51	2.52	2.89
T220	3.85	2.00	3.20	3.64
T222	2.33	5.99	3.69	2.73
T224	3.02	3.16	2.09	2.00
T115	2.78	2.98	1.95	2.88
Mo18W	3.39	3.86	4.31	2.95
Ga209	3.68	3.35	2.76	2.02
Ky226	2.45	5.68	3.08	2.80
PI217413	2.28	5.06	1.27	2.85
T232 x T220	3.95	0.64	2.12	2.12
T232 x T222	2.15	6.15	4.14	4.14
T232 x T224	3.09	2.32	2.12	2.17
T232 x T115	2.48	2.70	2.00	2.90
T232 x Mo18W	3.31	3.35	3.75	4.18
T232 x Ga209	3.84	2.39	2.33	1.52
T232 x Ky226	1.81	5.80	3.12	2.84
T232 x PI217413	0.88	4.74	0.59	2.67
T220 x T222	2.88	4.02	5.66	3.98
T220 x T224	5.30	0.54	2.58	3.91
T220 x T115	3.67	0.57	2.09	4.48
T220 x Mo18W	4.05	1.70	5.27	4.21
T220 x Ga209	4.72	1.01	2.80	4.07
T220 x Ky226	3.86	4.16	4.45	3.05
T220 x PI217413	2.36	3.36	0.60	3.30
T222 x T224	1.94	4.77	1.64	1.67
T222 x T115	1.61	4.56	1.93	2.80
T222 x Mo18W	2.45	6.31	5.03	2.85
T222 x Ga209	2.73	6.97	4.26	1.04
T222 x Ky226	2.39	8.55	5.37	2.69
T222 x PI217413	2.52	6.57	1.50	2.65
T224 x T115	2.92	4.60	2.11	1.89
T224 x Mo18W	2.82	2.80	3.36	0.76
T224 x Ga209	4.17	1.60	1.74	0.99
T224 x Ky226	1.79	4.99	1.97	1.59
T224 x PI217413	2.13	3.67	1.18	2.51
T115 x Mo18W	3.19	1.15	3.34	1.60
T115 x Ga209	3.95	1.36	2.25	2.44
T115 x Ky226	2.54	4.92	1.51	3.77
T115 x PI217413	1.88	4.01	0.37	3.12
Mo18W x Ga209	4.56	4.55	5.07	2.87
Mo18W x Ky226	3.04	4.68	4.72	3.33
Mo18W x PI217413	3.70	6.34	3.94	3.76
Ga209 x Ky226	2.45	4.70	2.59	1.75
Ga209 x PI217413	3.02	4.21	1.06	1.44
Ky226 x PI217413	1.75	7.61	0.90	3.34
L.S.D.	0.47	0.41	0.51	0.24

shorter than 4.0 cm. A different pattern is exhibited for depth of blank tip. PI217413, T115, and T224 all had blank tip means less than 2.5 cm. T222, T232, and Mo18W had blank tips exceeding 3.0 cm in depth with Mo18W being the largest at 4.31 cm. Only T220 was found to have a high maysin content—above 3.0 µg/g—while Ga209 and T224 were lowest with means near 2.0 µg/g.

Expectations for the performance of these groups compared well with the results found in specific crosses. The inbreds from the resistant and susceptible classes produced F_1 progeny with less than 2.9 cm damage and greater than 4.0 cm damage, respectively. The inbreds with long husk extensions produced hybrids with protracted husks, while those with short husk extensions produced short-husked crosses. The inbreds of the two classes under the blank tip comparison also gave hybrids that resembled the parents with the exception of T220. One cross with T220 was in the opposite (negative) class (T220 x PI217413). Ga209 also displayed this type of variation in hybrid efficacy for maysin content in the cross T220 x Ga209. T220 (>3.0 µg/g class) and T224 (<2.5 µg.g class) performed as anticipated in hybrid combination.

Table 7 shows the summary results from the combining ability analysis. It is notable that two crosses did not perform as expected based on parental means. T220 x PI217413 (Tables 6 and 7) had a small blank tip and fell in the class of "less than 1.0 cm." A more average value, between 1.0 and 4.5, would have been expected based on gca effects of the parents. T220 x Ga209 also exhibited this

Table 7. General combining ability of nine parents and specific combining ability of 36 F_2 crosses for depth of penetration, husk extension, depth of blank tip, and maysin content from a combining ability analysis conducted at the Knoxville Experiment Station in 1982.

Parent gca or F_1 cross sca	Depth of penetration (cm)	Husk extension (cm)	Depth of blank tip (cm)	Maysin content (µg/g)
T232	-0.29	-0.51**	-0.23	0.16
T220	1.04**	-2.23**	0.50*	1.02**
T222	-0.70**	2.32**	1.06**	-0.02
T224	0.09	-0.91**	-0.77**	-0.85**
T115	-0.19	-1.11**	-0.93**	0.15
Mo18W	0.51**	-0.11	1.77**	0.22
Ga209	0.85**	-0.69**	0.00	-0.84**
Ky226	-0.56**	1.97**	0.36	0.05
PI217413	-0.76**	1.27**	-1.71**	0.11
T232 x T220	0.27	-0.58	-0.86	-1.81**
T232 x T222	0.19	0.38	0.59	1.26*
T232 x T224	0.35	-0.23	0.41	0.65
T232 x T115	0.01	0.36	0.44	-0.15*
T232 x Mo18W	0.14	0.01	-0.51	1.05
T232 x Ga209	0.34	-0.37	-0.16	-0.55
T232 x Ky226	0.29	0.39	0.27	-0.11
T232 x PI217413	-1.02	0.03	-0.18	-0.35
T220 x T222	-0.40	-0.03	1.34*	0.23
T220 x T224	1.23**	-0.28	0.09	1.00
T220 x T115	-0.12	-0.04	-0.24	0.57
T220 x Mo18W	-0.44	0.08	0.25	0.22
T220 x Ga209	-0.11	-0.02	-0.46	1.14*
T220 x Ky226	0.44	0.47	0.83	-0.77
T220 x PI217413	-0.87*	0.38	-0.95*	-0.58
T222 x T224	-0.39	-0.60	-1.41**	-0.20
T222 x T115	-0.46	-0.61	-0.96*	-0.07
T222 x Mo18W	-0.31	0.14	-0.56	-0.10
T222 x Ga209	-0.36	1.39**	0.44	-0.85
T222 x Ky226	0.70	0.30	1.18*	-0.09
T222 x PI217413	1.03*	-0.98*	-0.62	-0.19
T224 x T115	0.73	2.66**	0.12	-0.15
T224 x Mo18W	-0.73	-0.14	-0.40	-1.36*
T224 x Ga209	0.29	-0.75	-0.26	-0.07
T224 x Ky226	-0.69	-0.03	-0.38	-0.36
T224 x PI217413	2.80**	-0.64	0.89	0.50
T115 x Mo18W	-0.08	-1.59**	-0.27	-1.52*
T115 x Ga209	0.35	-0.80	0.42	0.39
T115 x Ky226	0.34	0.11	-0.68	0.82
T115 x PI217413	-0.12	-0.10	0.25	0.11
Mo18W x Ga209	0.27	1.40**	0.54	0.73
Mo18W x Ky226	1.44**	-1.13*	-0.17	0.30
Mo18W x PI217413	1.01**	1.22**	1.12*	0.67
Ga209 x Ky226	-0.78	-0.53	-0.53	-0.21
Ga209 x Pi217413	-0.01	-0.33	0.01	-0.61
Ky226 x PI217413	0.12	0.42	-0.52	0.42

* and ** indicate the estimate exceeds its standard error by two and three times, respectively.

unexpected performance (Tables 6 and 7) for maysin content. This cross had a maysin content greater than 4.0 µg/g. The predicted value would have been between 4.0 µg/g and 1.6 µg/g.

Many crosses produced divergent means and/or significant specific combining ability. Those that gave a highly desirable mean and exhibited a specific combining ability effect are T232 x PI217413 for depth of penetration, T222 x Ga209 and Mo18W x PI217413 for husk extension, T220 x PI217413 for depth of blank tip, and T232 x T222 along with T220 x Ga209 for maysin content. Those crosses that gave an undesirable mean and produced a significant combining ability effect were T115 x Mo18W and T115 x Ga209 for husk extension and T222 x Ky226 along with T220 x T222 for depth of blank tip.

III. ADDITIVE, DOMINANCE, AND EPISTATIC EFFECTS OF THREE EAR CHARACTERISTICS

Model Construction

Tables 8 and 9 show the results of the effect of artificial infestation on the three ear characteristics. Multivariate analysis showed "method of infestation" to be important and subsequent analyses were performed using only the artifically infested plants.

The variable, "days between infestation and silking" and "block by generation," were found to be nonsignificant (Table 10). These two variables were dropped for the final analysis to increase the error degrees of freedom.

Table 8. Analysis of variance for the effect of artificial infestation on three ear characteristics.

Source of variation	d.f.	Depth of penetration M.S.	Husk extension M.S.	Depth of blank tip M.S.
Block	3	72.3	12.8	91.1
Generation	4	94.2**	2229.7**	345.6**
Artificial infestation	1	1095.5**	21.4	2688.9**
Error	13053	7.4	10.3	11.3

**Indicates significance at 0.01 level of probability.

Table 9. Least squares means and corresponding standard errors and probabilities for three ear characteristics.

Ear characteristic	Method of infestation	Least squares mean (cm)	Standard error	Prob. >|T| H_0: L.S. mean=0	Prob. >|T| H_0: L.S. mean 1=L.S. mean 2
Depth of penetration	Natural	2.2	0.04	0.002	0.002
	Artificial	3.3	0.04	0.002	
Husk extension	Natural	5.5	0.05	0.002	0.002
	Artificial	5.6	0.04	0.002	
Depth of blank tip	Natural	2.6	0.05	0.002	0.002
	Artificial	3.5	0.05	0.002	

Table 10. Analysis of variance for the effects of days between infestation and silking and the block by generation interaction.

Source of variation	d.f.	Depth of penetration M.S.	Husk extension M.S.	Depth of blank tip M.S.
Block	3	94.0	219.8	241.4
Days between infestation and silking	1	9.8	1016.0**	111.4
Generation	5	176.4**	2447.6**	281.9
Block by generation	15	44.1	72.6	157.1
Error	749	46.7	88.8	118.1

**Indicates significance at the 0.001 level of probability.

Generation Means Analysis

The results of the generation means analyses for each cross appear in the Appendix. A summary table of the significant mean squares for each effect and the generation mean squares associated with the significant effect(s) are presented in Table 11 for depth of penetration, Table 12 for husk extension, and Table 13 for depth of blank tip.

The preponderance of the effects for all three ear characters are additive in nature. Dominance and digenic epistatic effects are significant in several crosses for the three ear characteristics. Sixty-seven percent of the crosses under depth of penetration had significant additive effects followed by 8, 11, 11, and 2 percent exhibiting dominance interaction, respectively. Percentage of additive, dominance, additive by additive, additive by dominance, and dominance by dominance genetic effects for husk extension were 83, 16, 3, 36, and 8 percent with 69, 3, 25, and 8 percent for depth of blank tip, respectively, among crosses.

Heterosis, percent heterosis, inbreeding depression, and percent inbreeding depression are presented for each trait in Table 14, along with the standard errors for heterosis and inbreeding depression. Depth of penetration shows a moderate level of heterosis with only a small degree of inbreeding depression. A moderate level of heterosis and inbreeding depression is shown for depth of blank tip. Husk extension, on the other hand, shows an unusual pattern,

Table 11. Summary of significant ($p \leq 0.05$) additive (a), dominance (d), and epistatic (aa, ad, and dd) effect mean squares and generation mean squares for depth of penetration of each cross.†

Cross	Mean squares					
	a	d	aa	ad	dd	Generation
T232 x T220						
T232 x T222	104			70		43
T232 x T224						
T232 x T115	125					47
T232 x Mo18W	620					201
T232 x Ga209						
T232 x Ky226						
T232 x PI217413	539			54		135
T220 x T222	70					23
T220 x T224						
T220 x T115						
T220 x Mo18W	581					205
T220 x Ga209						
T220 x Ky226						
T220 x PI217413	403					96
T222 x T224						
T222 x T115		9	23			17
T222 x Mo18W	1104	205	195		279	454
T222 x Ga209	198					55
T222 x Ky226	127			56		38
T222 x PI217413	148		65			70
T224 x T115						
T224 x Mo18W	801					260
T224 x Ga209	99					22
T224 x Ky226	65					35
T224 x PI217413	245					64
T115 x Mo18W	1232					286
T115 x Ga209	226					58
T115 x Ky226	154					50
T115 x PI217413	155					40
Mo18W x Ga209	397					139
Mo18W x Ky226	347					278
Mo18W x PI217413	2074					528
Ga209 x Ky226						
Ga209 x PI217413	682					147
Ky226 x PI217413	515	21	21	32		109

†Nonsignificant mean squares are omitted.

Table 12. Summary of significant ($p \leq 0.05$) additive (a), dominance (d), and epistatic (aa, ad, and dd) effect mean squares and generation mean squares for husk extension of each cross.†

Cross	Mean squares					
	a	d	aa	ad	dd	Generation
T232 x T220	70	534	147	204	125	3309
T232 x T222	351					167
T232 x T224	285					141
T232 x T115	105					57
T232 x Mo18W	1004					272
T232 x Ga209						
T232 x Ky226	1312					298
T232 x PI217413	432					120
T220 x T222	800			806		607
T220 x T224	788			318		911
T220 x T115	1466	64		64		931
T220 x Mo18W	337	182		254	146	1117
T220 x Ga209	2631	94		259		877
T220 x Ky226		217				744
T220 x PI217413	691	249		210	218	609
T222 x T224				130		90
T222 x T115	77			77		93
T222 x Mo18W	132			261		98
T222 x Ga209	528			141		258
T222 x Ky226	310			113		72
T222 x PI217413						25
T224 x T115	62					
T224 x Mo18W	138					373
T224 x Ga209	479					201
T224 x Ky226	332					206
T224 x PI217413						
T115 x Mo18W	432					427
T115 x Ga209	237					131
T115 x Ky226	685			113		195
T115 x PI217413	118					100
Mo18W x Ga209	1290					362
Mo18W x Ky226						
Mo18W x PI217413	86					92
Ga209 x Ky226	1557					333
Ga209 x PI217413	620					220
Ky226 x PI217413	246					90

†Nonsignificant mean squares are omitted.

Table 13. Summary of significant ($p \leq 0.05$) additive (a), dominance (d), and epistatic (aa, ad, and dd) effect mean squares and generation mean squares for depth of blank tip of each cross.[†]

Cross	Mean squares					
	a	d	aa	ad	dd	Generation
T232 x T220	623			88		170
T232 x T222						
T232 x T224	221					76
T232 x T115						
T232 x Mo18W	2828					673
T232 x Ga209						
T232 x Ky226	323					91
T232 x PI217413	109					43
T220 x T222	899			338		220
T220 x T224	89					147
T220 x T115	835					206
T220 x Mo18W	578					479
T220 x Ga209	894					199
T220 x Ky226						
T220 x PI217413	1094					307
T222 x T224	396			341		125
T222 x T115		59		142	82	84
T222 x Mo18W	3107	773	469		1005	946
T222 x Ga209		62		81	52	93
T222 x Ky226	535					151
T222 x PI217413				84		34
T224 x T115	367					100
T224 x Mo18W	1117					533
T224 x Ga209	74			44		110
T224 x Ky226						
T224 x PI217413	558			80		152
T115 x Mo18W	3241					812
T115 x Ga209						
T115 x Ky226	464					123
T115 x PI217413	35					18
Mo18W x Ga209	3152					760
Mo18W x Ky226						
Mo18W x PI217413	3441			275		960
Ga209 x Ky226	514					109
Ga209 x PI217413						
Ky226 x PI217413	656					225

[†]Nonsignificant mean squares are omitted.

Table 14. Heterosis, percent heterosis, inbreeding depression, and percent inbreeding depression for three ear characteristics measured in the overall population.

Character measured	Heterosis (cm)	Heterosis (%)	Inbreeding depression (cm)	Inbreeding depression (%)
Depth of penetration	-0.872 ± 0.035	-23.2	-0.403 ± 0.234	-14.02
Husk extension	-3.257 ± 0.066	-45.4	-1.862 ± 0.323	-47.44
Depth of blank tip	-1.256 ± 0.090	-31.5	-0.752 ± 0.375	-27.55

high negative heterosis and high negative inbreeding depression were found for this characteristic.

Least squares means for each generation within depth of penetration, husk extension, and depth of blank tip are shown in Table 15. Correlations for the overall population are presented in Table 16 and for each cross in Table 17. The overall generation means analysis of variance is given in Table 18.

Table 15. Least squares means and their corresponding standard errors of three ear characteristics for each generation studied.

Character measured	Generation					
	P1	P2	F1	F2	BC1	BC2
Depth of penetration, cm	3.8 ± 0.1	3.7 ± 0.1	2.9 ± 0.2	3.3 ± 0.2	3.3 ± 0.2	3.4 ± 0.2
Husk extension, cm	7.1 ± 0.2	7.3 ± 0.2	3.9 ± 0.2	5.8 ± 0.2	5.6 ± 0.2	5.2 ± 0.2
Depth of blank tip, cm	4.0 ± 0.2	3.9 ± 0.2	2.7 ± 0.3	3.5 ± 0.3	3.7 ± 0.3	3.7 ± 0.3

Table 16. Correlation coefficients among depth of penetration, husk extension, and depth of blank tip for the overall population.

Variable	Depth of penetration	Husk extension	Depth of blank tip
Depth of penetration		-0.136**	0.341**
Husk extension			0.184**

**Indicates significance at the 0.01 level of probability.

Table 17. Summary of significant correlation coefficients among depth of penetration, husk extension, and depth of blank tip for each cross.[†]

Cross	Depth of penetration with husk extension	Depth of penetration with depth of blank tip	Husk extension with depth of blank tip
T232 x T220			0.30
T232 x T222			
T232 x T224	-0.53		
T232 x T115	-0.35		0.35
T232 x Mo18W		0.40	
T232 x Ga209	-0.41	-0.30	
T232 x Ky226			
T232 x PI217413			
T220 x T222			
T220 x T224	-0.37		
T220 x T115	-0.26		
T220 x Mo18W		0.53	
T220 x Ga209			0.31
T220 x Ky226			
T220 x PI217413	-0.33	0.30	
T222 x T224	-0.23		0.34
T222 x T115			0.30
T222 x Mo18W		0.44	
T222 x Ga209	-0.20		0.24
T222 x Ky226			
T222 x PI217413		0.35	0.21
T224 x T115	-0.25	0.22	
T224 x Mo18W		0.32	0.20
T224 x Ga209	-0.47		
T224 x Ky226			0.40
T224 x PI217413	-0.24	0.28	
T115 x Mo18W		0.47	
T115 x Ga209	-0.36		
T115 x Ky226		0.27	0.24
T115 x PI217413	-0.18	0.45	
Mo18W x Ga209		0.46	
Mo18W x Ky226		0.45	
Mo18W x PI217413		0.60	
Ga209 x Ky226	-0.37		
Ga209 x PI217413			
Ky226 x PI217413			0.34

[†]Nonsignificant ($p > 0.05$) correlation coefficients are omitted.

Table 18. Analysis of variance of three ear characteristics and percent of generation variance attributable to different genetic effects in the overall population studied.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	154.8		326.7		293.8	
Generation	5	245.8**		3309.2**		450.8*	
a	1	39.2	3.2	70.2	0.4	11.6	0.5
d	1	2.2	0.2	534.9*	3.2	31.4	1.4
aa	1	2.6	0.2	146.9	0.9	43.6	1.9
ad	1	18.6	1.5	204.1	1.2	0.0	0.0
dd	1	2.0	0.2	124.8	0.8	137.7	6.1
Error	771	46.5		89.2		119.8	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

CHAPTER V

DISCUSSION

The experiments reported here were conducted to deduce the relative importance of the genetic effects for corn earworm resistance among a set of adapted inbreds and the plant introduction 'Zapalote Chico' and to determine if this germplasm might be suitable for selection to develop populations with increased earworm resistance.

The heritability for a sibbed population crossed by PI217413 was essentially zero for depth of penetration and moderate for husk extension. Artificial infestation was useful in reducing environmental variation. Days between infestation and silking and block by generation effects were not significant sources of variation. Both general and specific combining ability were found to be significant within the population chosen. The generation means analysis, for the most part, agreed with the combining ability analysis indicating that additive genetic effects were predominantly responsible for the variation found in the characters depth of penetration, husk extension, and depth of blank tip. However, dominance and epistatic effects were important in certain crosses.

The study of the sibbed population crossed by PI217413 showed that heritability was approximately zero for depth of penetration (-0.01) and 0.59 for husk extension. Vegetative characters generally

exhibit higher heritabilities than those characters which are more complex in nature. Depth of penetration was a fitness-related trait and might have been expected to have a low heritability. The estimate of zero heritability, however, showed that the mass selection technique practiced on this population was ineffective. The environmental variance was much greater than the genetic variance making detection of superior genotypes impossible. In addition, the additive genetic variance may have been low. That is, most loci had become fixed. The selection technique used on this population should be discontinued and a program utilizing a recurrent selection procedure should be implemented. Recurrent selection procedures were designed to further take advantage of any nonadditive variation, provided that this source of variation is present in the population.

Several effects and one covariable were suspected to be important in these experiments. They were examined to determine if they could remove significant confounding effects for the purpose of improving the overall precision of the genetic analysis.

Artificial infestation greatly improved the genetic model by reducing environmental bias. The factors that cause variation in naturally infested populations may have included effects other than those determined by plant genotype. Artificial infestation appears to have given uniform exposure and reduced the number of escapes. Examination of Table 8 (p. 42) shows that artificial infestation greatly affected depth of penetration and depth of blank tip while not

affecting husk extension. This relationship with husk extension was expected since artificial infestation was carried out after the plants had physically generated the husks. Artificial infestation increased the mean depth of penetration and blank tip by about 1.0 cm (Table 9, p. 43). These attributes of artificial infestation were also found by Blanchard et al. (1942), Bennett and Josephson (1962), and Josephson et al. (1966).

The characters, days between infestation and silking and the block by generation interaction, were found to be nonsignificant environmental effects. Due to problems with the supply of earworm larvae it was conjectured that delayed infestation may have had an effect on earworm mortality and development causing confounding in the measurements. However, this was not found for depth of penetration and depth of blank tip. Days between infestation and silking was found to be significant for husk extension (Table 10, p. 45). Since there was no logical explanation for this finding a type II error was assumed for this variable. It was concluded that delayed infestations did not bias the results. Block by generation interaction was found to be nonsignificant for all three characters and, along with days between infestation and silking, was dropped from the analysis.

Variation due to silking date was not considered in the analysis because infestations were controlled—eliminating the effects of ovipositional preference and corn earworm population

dynamics on the measurements.[1] Widstrom (1967) also notes that, "correction for maturity may remove genetic effects and reduce the value of the estimate from the standpoint of genetic resistance."

Several efforts to examine general and specific combining ability effects of corn earworm resistance have resulted in inconsistent conclusions (Widstrom and Davis 1967, Widstrom and Hamm 1969, and Widstrom 1972). The combining ability analysis in this study was supplemented by a generation means analysis to provide additional evidence so that cogent inferences could be built.

Significant general and specific combining ability effects were found for all traits studied (Table 5, p. 38). The overall generation means analysis (Table 18) showed no significance for genetic effects other than dominance for husk extension. The combining ability analysis, however, suggested that additive and nonadditive genetic effects were important for the traits studied. The generation means analysis for each cross (Tables 11-13, pp. 47-49) gave a further breakdown of genetic effects, revealing that additive effects were predominant, but that dominance and digenic epistatic components were important in several cases. The results for depth of penetration in this study did not agree with those of Widstrom and McMillian (1973). They found a preponderance of dominance effects among dent corn crosses. Genotype by environment interaction were confounded in the

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[1] Ovipositional preference (Nuttycombe 1930 and Barber 1937) and corn earworm population dynamics (Stinner 1977) have been shown to be important under natural conditions.

experiments reported herein and might have been a possible source of bias. However it did not seem likely that this source of variation would have accounted for such a wide discrepancy. A more likely explanation would have been to attribute these differences to the genetic composition of the two populations studied. Results from these two analyses were dependent on the specific alleles present in the homozygous parental lines, thus limiting the inferences. In this context it was not surprising that different sets of parental lines could have produced differing results.

Two primary objectives of genetic studies by plant breeders are to determine the germplasm and the method of selection that would be most productive for improvement of the characteristic(s) of interest. The following discussion focuses on the parental genotypes in this study that appeared most promising for the improvement of resistance to the corn earworm.

PI217413, as expected, had the highest inbred resistance, a long husk extension, and possessed the shortest depth of blank tip. It did not appear to have a high maysin content, which was unexpected, based on the work of Waiss et al. (1979) and Widstrom et al. (1983).

Among the resistant crosses, T232 x PI217413 was expected to perform well—as the parents had high negative general combining ability for depth of penetration. However, the actual performance was better than expected. This was illustrated by its high negative specific combining ability effect. It was the only cross, out of seven in the resistant category, that had both a high negative mean

and a high negative specific combining ability effect. This suggested that the genetic effects were not only desirable and additive but that there was also a large dominance and/or epistatic component. The generation means analysis confirmed this and further revealed that the additive by dominance effects contributed significantly to the specific combining ability.

This same type of inheritance pattern was shown for husk extension in the cross between T222 and Ga209 (Table 12, p. 48). Both T222 x Ga209 and Mo18W x PI217413 had desirable means (Table 6, p. 39) and high sca values (Table 7, p. 41). The generation means analysis, however, showed that only T222 x Ga209 had any significant nonadditive effects, again, those of the additive by dominance type.

The results from combining ability analysis and generation means analysis seemed contradictory for the second cross of the group (Mo18W x PI217413). A high specific combining ability effect was found but no dominance or digenic epistatic effects were indicated (Table 12, p. 48). This same pattern was observed in the cross T220 x PI217413 for depth of blank tip (Table 13, p. 49). These relationships could have been explained by the fact that the generation means analysis did not consider multigenic effects involving more than two loci (e.g., additive by additive by additive effects). These higher order effects may have contributed significantly to the specific combining ability but were undetected by the generation means analysis.

A second type of inheritance pattern was noted among those crosses with the following attributes: highly desirable F_1 means, no significant specific combining ability effects, and no detectable additive genetic variance in the generation means analysis. The crosses T232 x Ky226 and T222 x T224 for depth of penetration (Table 11, p. 47), and T222 x PI217413 for husk extension (Table 12, p. 48) showed this type of pattern. Here again the discrepancy could have been explained by multigenic effects involving more than two loci.

There was good agreement between the combining ability and the generation means analysis for the crosses T224 x Ky226 and T115 x PI217413 for depth of penetration (Table 12); T222 x Ky226 and Ky226 x PI217413 for husk extension (Table 13, p. 49); and T232 x PI217413, T115 x PI217413, and Ky226 x PI217413 for depth of blank tip. Combining ability analysis showed no dominance or epistatic effects present. This was corroborated by the detection of only additive genetic effects in the generation means analysis. Thus, these crosses performed in a highly desirable manner through additive genes.

Combining ability analysis means showed that T220 x Mo18W, T232 x Mo18W, T232 x T222, and T220 x Ga209 had appeared to be excellent sources of additive genetic variance for maysin (Table 6, p. 39). The latter two crosses also had significant dominance and epistatic genetic effects (Table 7, p. 41). PI217413 did not exhibit the high level of maysin content that Widstrom et al. (1983) and

Waiss et al. (1979) had observed. In fact, if maysin content (Table 6, p. 39) is compared to depth of penetration (Table 6), the cross T224 x Ky226 was considered resistant but displayed an unexpectedly low level of maysin. Likewise, two crosses (T220 x Mo18W and T220 x Ga209) and the inbred T220, averaged over crosses, were considered susceptible but presented a high maysin content. Only the susceptible inbred Ga209 displayed an expected low maysin content. It appears from these data that maysin is not a component of resistance. This conclusion is not consistent with the results of others (Waiss et al. 1979 and Widstrom et al. 1983).

In the study by Widstrom et al. (1983) a genotype by year interaction was not significant. However, Waiss et al. (1979) found a significant genotype by location interaction.[1] Confounding with a genotype by location interaction may have biased the maysin content measured herein. Also modification of the assay technique and/or oxidation during storage[2] may have biased these results. Furthermore, Waiss et al. (1979) caution that flavenoids are only one of several inhibitory factors. The presence of these other factors may have been the mechanism that was most important for resistance in the population studied here.

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[1]They suggested that this estimate may have been biased by different populations of PI217413 at the two locations in the test. The PI217413 populations grown in Missouri and Georgia (as well as Tennessee) have been subject to differential selection and drift for over a decade and may have become quite different in composition.

[2]Waiss et al. (1979) reported, however, that maysin appeared to have been relatively stable to oxidation.

Heterosis for depth of penetration and depth of blank tip were expectedly low. These two characters were reproductive in nature. Reproductive-type traits have generally exhibited such a response (Hallauer 1981). Inbreeding depression for these two traits was also low. Again, this was expected. A high negative heterosis and a high negative inbreeding depression were, however, estimated for husk extension (Table 14, p. 50). The following considerations were offered to explain such negative values.

Total husk length may have been a vegetative as opposed to a reproductive character (as were penetration and blank tip) and is predominantly additive in nature. Ear length, another reproductive character, has been shown to have a substantial percentage of dominance effects and thus exhibits a low heritability (Hallauer 1981). Husk extension, on the other hand, was dependent on total husk length and ear length.[1] If there was positive heterosis for total length of husk and if that amount of heterosis was less than that for ear length, then the heterosis for husk extension would have been a negative value. Since the value observed was large, the difference between the heterosis for total husk length and the heterosis for ear size must have been quite large. This would be expected based on the results of others (Hallauer 1981). In future studies ear length and total husk length should be measured.

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[1] Husk extension = total husk length - ear length.

An examination of the correlations from the overall experiment (Table 16, p. 53) showed that there was very little correlation between husk extension and depth of penetration and between husk extension and depth of blank tip. Snyder (1958) also found that husk extension had no correlation with blank tip. He observed that blank tip was influenced more by environment than by genetic causes. Thus, the results reported here for blank tip were likely to be confounded with environmental effects. The correlation between depth of penetration and blank tip was moderately low.

These observed correlations on the overall population have done little to settle the debate over whether husk extension influences resistance or not. However, examination of the correlations within each cross (Table 17, p. 54) offers the following empirical observation. Husk extension, while not an important factor to resistant crosses, appeared to have been slightly beneficial to several susceptible crosses. This may have accounted for the fact that some researches found significant correlations but others did not. Differences in susceptibility may have influenced the results.

Based on the results from these studies several conclusions with bearing on the genetic improvement of host plant resistance to the corn earworm seem justified.

Heritability was apparently low and in the same range as heritability for grain yield, indicating that mass selection would be ineffective.

Since these experiments were conducted in only one environment the results may be biased by genotype by environment interaction and inferences should be made in this context.

Combining ability analysis indicated those parents which show promise for future breeding programs. The parents are: T232 and PI217413 for depth of penetration; T222, PI217413, GA209, and Mo18W for husk extension; and T220 and PI217413 for depth of blank tip. Since the comparison between maysin content and depth of penetration was not consistent with the results of others no recommendation has been made.

Generation means analysis revealed that the preponderance of the genetic effects for resistance, husk extension, and depth of blank tip were additive in nature, yet, certain desirable crosses (notably T232 x PI217413 for depth of penetration) had significant dominance and/or epistatic effects. Thus, recurrent selection practices, such as those offered by Widstrom (1972) would be of the most benefit for advancing this material.

Artificial infestation should be considered a necessity for detecting differences in resistance among lines. Days between infestation and silking and block by generation interaction need not be considered within the limits found here.

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APPENDIX

RESULTS FROM THE GENERATION MEANS ANALYSIS

Table A-1. Analysis of variance of three ear characteristics and percent of generation variance attributable to different genetic effects in the T232 x T220 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	36.5		7.9		10.3	
Generation	5	31.4		894.5**		169.7**	
a	1	0.4	0.3	2355.3**	52.7	623.6**	73.5
d	1	33.1	21.1	143.8**	3.2	50.5	6.0
aa	1	8.6	5.4	51.3*	1.1	25.5	3.0
ad	1	0.0	0.0	609.7**	13.6	88.0*	10.0
dd	1	61.2	39.0	69.2*	1.5	37.1	4.3
Error	12	10.6		6.4		7.9	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-2. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T232 x T222 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	5.8		3.1		3.1	
Generation	5	43.2**		166.8**		55.0	
a	1	103.7**	47.7	351.9**	42.2	50.9	18.5
d	1	16.0	7.4	0.9	0.1	3.0	1.1
aa	1	20.3	9.4	11.9	1.4	0.1	0.0
ad	1	69.7*	32.3	13.2	1.6	72.8	26.5
dd	1	19.3	8.9	13.6	1.6	2.0	0.7
Error	21	6.3		11.8		12.3	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-3. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T232 x T224 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	9.7		17.4		8.4	
Generation	5	24.6		140.7**		75.5**	
a	1	37.4	30.3	284.9**	40.5	221.3**	58.6
d	1	4.8	3.9	11.8	1.7	30.4	8.1
aa	1	0.4	0.3	2.8	0.4	18.5	4.9
ad	1	0.1	0.1	1.2	0.1	33.7	8.9
dd	1	7.3	5.9	5.1	0.7	23.4	6.2
Error	12	15.4		14.2		8.2	

**Indicates significance at the 0.01 level of probability.

Table A-4. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T232 x T115 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	5.0		16.5		4.4	
Generation	5	44.6**		57.4**		11.3	
a	1	125.4**	53.8	105.9**	36.9	25.1	44.3
d	1	12.7	5.4	3.3	1.1	0.7	1.2
aa	1	12.7	5.4	1.0	0.3	0.9	1.5
ad	1	0.2	0.1	30.1	10.4	5.9	10.4
dd	1	19.2	8.2	0.6	0.2	0.1	0.2
Error	12	4.8		7.8		6.9	

**Indicates significance at the 0.01 level of probability.

Table A-5. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T232 x Mo18W cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	6.0		23.2		11.62	
Generation	5	200.8**		271.8**		672.8**	
a	1	619.9**	61.7	1003.9**	73.9	2828.4**	84.1
d	1	30.0	3.0	0.3	0.0	86.3	2.6
aa	1	5.6	0.6	4.4	0.3	105.4	3.1
ad	1	18.7	1.9	58.0	4.2	16.8	0.5
dd	1	24.9	2.4	4.7	0.3	32.9	1.0
Error	12	17.8		9.3		32.8	

**Indicates significance at the 0.01 level of probability.

Table A-6. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T232 x Ga209 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	17.4		2.7		0.9	
Generation	5	28.8		45.5		8.2	
a	1	15.8	11.0	31.5	13.8	34.7	84.4
d	1	0.7	0.4	3.1	1.4	0.2	0.0
aa	1	2.7	1.9	8.2	3.6	0.9	2.2
ad	1	27.2	18.9	16.1	7.1	0.2	0.0
dd	1	5.1	3.5	0.2	0.0	0.0	0.0
Error	13	8.7		14.3		4.8	

Table A-7. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T232 x Ky226 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	4.0		14.8		20.8	
Generation	5	55.4**		298.4**		91.1	
a	1	7.2	2.5	1311.9**	87.9	323.5*	71.0
d	1	6.9	2.5	6.1	0.4	32.8	7.2
aa	1	0.0	0.0	7.8	0.5	38.3	8.4
ad	1	1.4	0.5	17.6	1.1	30.7	6.7
dd	1	7.1	2.5	0.5	0.0	14.3	3.1
Error	14	7.2		5.2		32.5	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-8. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T232 x PI217413 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	0.7		14.0		6.1	
Generation	5	134.8**		119.6**		43.2**	
a	1	583.8**	80.0	432.2**	72.2	109.4**	50.6
d	1	32.2	4.8	64.5	10.8	2.3	1.1
aa	1	30.4	4.5	73.7	12.3	0.7	0.3
ad	1	53.6*	8.0	68.7	11.5	0.3	0.1
dd	1	18.5	2.7	32.5	5.4	0.7	0.3
Error	13	6.3		13.3		4.7	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-9. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T220 x T222 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	7.7		12.6		36.9	
Generation	5	23.0		606.8**		219.8**	
a	1	69.9*	60.8	800.1**	26.4	899.3**	81.8
d	1	1.6	1.4	2.7	0.1	49.0	4.5
aa	1	1.0	0.9	54.8	1.8	37.4	3.4
ad	1	4.3	3.7	805.7**	26.6	338.7**	30.8
dd	1	2.5	2.2	14.7	0.5	34.3	3.1
Error	14	7.2		24.0		11.7	

* and ** indicate significance at 0.05 and 0.01 levels of probability, respectively.

Table A-10. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T220 x T224 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	10.5		3.2		9.8	
Generation	5	22.5		911.4**		147.18**	
a	1	23.1	20.5	788.4**	17.3	89.4*	12.1
d	1	47.4	42.1	5.0	0.1	0.0	0.0
aa	1	54.9	48.7	53.2	1.1	24.7	3.3
ad	1	0.4	0.3	318.5**	7.0	15.1	2.1
dd	1	51.2	45.4	3.2	0.1	0.6	0.1
Error	11	19.7		11.7		11.3	

**Indicates significance at 0.01 level of probability.

Table A-11. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T220 x T115 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	7.2		0.9		15.7	
Generation	5	20.4		931.2**		205.8**	
a	1	82.8	81.0	1466.7**	31.5	853.9**	83.0
d	1	2.4	2.3	63.8*	1.3	5.9	0.6
aa	1	1.3	1.3	0.0	0.0	0.0	0.0
ad	1	9.9	9.7	64.8*	1.4	39.6	3.8
dd	1	4.6	4.5	45.0	1.0	4.2	0.4
Error	11	10.5		6.4		20.3	

* and ** indicate significance at 0.05 and 0.01 levels of probability, respectively.

Table A-12. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T220 x Mo18W cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	9.1		6.4		15.6	
Generation	5	205.4*		1116.8**		478.8**	
a	1	581.3*	56.6	336.8**	6.0	578.3*	24.2
d	1	2.5	0.2	181.7**	3.3	0.0	0.0
aa	1	18.9	1.8	0.1	0.0	29.8	1.2
ad	1	7.9	0.8	254.5**	4.5	117.9	4.9
dd	1	4.4	0.4	146.2**	2.6	1.4	0.1
Error	13	46.1		8.4		69.5	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-13. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T220 x Ga209 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	21.4		12.2		7.4	
Generation	5	14.9		877.4**		199.4**	
a	1	28.5	38.3	2631.7**	60.0	894.3**	89.7
d	1	2.1	2.8	94.6*	2.2	19.6	2.0
aa	1	1.9	2.6	6.6	0.2	11.4	1.1
ad	1	10.5	14.1	260.0**	5.9	34.1	3.4
dd	1	3.4	4.6	62.0	1.4	11.7	1.2
Error	11	13.6		9.9		12.4	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-14. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T220 x Ky226 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	28.3		26.7		51.6	
Generation	5	9.4	744.3**		96.2		
a	1	14.0	29.7	81.4	2.2	31.2	6.4
d	1	0.2	0.4	217.0*	5.8	2.9	0.6
aa	1	0.1	0.2	24.2	0.7	2.2	0.5
ad	1	5.9	1.3	162.3	4.4	13.1	2.7
dd	1	0.0	0.0	192.3	5.2	3.2	0.7
Error	14	7.9		29.1		27.1	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-15. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T220 x PI218413 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	3.3		22.1		11.4	
Generation	5	95.8**		608.9**		306.8**	
a	1	403.3**	84.2	691.0**	22.7	1093.7**	71.3
d	1	3.1	0.6	249.5**	8.2	3.7	0.2
aa	1	1.0	0.2	69.7	2.3	0.5	0.0
ad	1	0.0	0.0	210.0**	6.9	23.4	1.5
dd	1	5.2	1.1	218.0**	7.2	0.8	0.0
Error	13	8.2		12.3		10.3	

**Indicates significance at the 0.001 level of probability.

Table A-16. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T222 x T224 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	7.1		7.9		14.6	
Generation	5	12.3	19.9	90.5**		124.5**	
a	1	15.0	24.3	1.8	0.4	396.6**	63.7
d	1	21.9	35.4	1.0	0.2	0.0	0.0
aa	1	27.1	43.9	4.6	10.2	0.1	0.0
ad	1	6.7	10.9	130.9*	28.9	341.1**	54.7
dd	1	11.6	18.8	8.1	1.8	2.4	0.4
Error	14	11.9		13.1		4.9	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-17. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T222 x T115 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	3.0		48.0		22.1	
Generation	5	16.6**		93.3**		83.9**	
a	1	0.1	0.1	76.6**	16.4	5.1	1.2
d	1	9.1*	10.9	3.9	0.8	58.8*	14.0
aa	1	22.6**	27.1	0.0	0.0	21.1	5.0
ad	1	0.5	0.6	77.6**	16.6	141.7**	33.8
dd	1	1.2	1.4	21.7	4.7	82.1**	19.6
Error	12	1.2		4.4		5.1	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-18. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T222 x Mo18W cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	56.3		21.3		32.0	
Generation	5	454.4**		97.6**		946.0**	
a	1	1104.5**	48.6	131.6*	27.0	3106.8**	65.7
d	1	204.7*	9.0	4.3	0.9	773.3**	16.3
aa	1	194.6*	8.6	10.4	2.1	469.4**	10.5
ad	1	55.8	2.4	261.5**	53.6	12.7	0.3
dd	1	279.5**	12.3	12.5	2.6	1005.1**	21.3
Error	12	15.7		11.9		28.1	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-19. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T222 x Ga209 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	2.9		7.8		24.7	
Generation	5	55.4*		258.0**		93.4**	
a	1	198.7**	71.7	529.0**	41.0	2.2	0.5
d	1	0.0	0.0	0.7	0.1	62.6*	13.4
aa	1	1.2	0.4	4.8	0.4	19.1	4.1
ad	1	1.5	0.5	141.5*	11.0	81.4**	17.4
dd	1	0.0	0.0	0.6	0.0	51.6*	11.0
Error	14	12.4		11.7		6.5	

* and ** indicate significance at the 005 and 0.01 levels of probability, respectively.

Table A-20. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T222 x Ky226 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	2.7		3.7		33.8	
Generation	5	37.8**		71.6**		151.0	
a	1	128.8**	68.2	310.3**	86.7	534.8**	70.8
d	1	14.7	7.8	0.3	0.1	4.1	0.5
aa	1	16.7	8.8	3.1	0.9	0.1	0.0
ad	1	56.2*	29.8	113.4**	31.7	165.4	21.9
dd	1	21.3	11.3	0.2	0.1	4.3	0.5
Error	13	5.6		8.2		38.9	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-21. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T222 x PI217413 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	8.5		17.4		2.8	
Generation	5	69.6**		24.3		34.4	
a	1	148.0**	42.5	2.6	2.1	9.5	5.5
d	1	51.6	14.8	2.9	2.4	0.1	0.1
aa	1	65.1*	18.7	0.8	0.7	0.8	0.5
ad	1	11.1	3.2	51.1	42.1	84.3*	49.0
dd	1	52.6	15.1	9.4	7.7	1.0	
Error	12	7.2		9.8		10.8	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-22. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T224 x T115 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	24.3		1.5		2.6	
Generation	5	7.9		25.1*		100.4**	
a	1	14.4	36.6	62.9**	50.2	367.9**	73.3
d	1	0.7	1.8	4.0	3.1	24.8	4.9
aa	1	0.1	0.3	0.9	0.7	5.5	1.1
ad	1	12.9	32.8	3.7	2.9	38.5	7.7
dd	1	3.2	8.1	1.8	1.4	25.8	5.1
Error	13	6.1		4.0		7.0	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-23. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T224 x Mo18W cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	27.5		10.0		47.7	
Generation	5	259.6**		372.8**		533.0**	
a	1	801.4**	61.7	138.5**	7.4	1116.8**	41.9
d	1	37.4	2.9	36.1	1.9	12.7	0.5
aa	1	6.6	0.5	0.1	0.0	3.3	0.1
ad	1	21.3	1.6	50.0	2.7	16.6	0.6
dd	1	31.3	2.4	15.4	0.8	4.2	0.1
Error	13	21.8		10.7		20.8	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-24. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T224 x Ga209 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	7.0		12.5		6.7	
Generation	5	22.4		201.3**		110.6**	
a	1	98.9*	88.4	478.7**	47.6	369.3**	66.8
d	1	0.8	0.7	77.7	7.7	0.8	0.1
aa	1	1.5	1.3	42.9	4.3	10.1	1.8
ad	1	22.0	20.0	5.1	0.5	220.0**	39.8
dd	1	0.0	0.0	45.1	4.5	0.7	0.1
Error	12	11.6		10.8		7.4	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-25. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T224 x Ky226 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	13.8		10.0		49.9	
Generation	5	34.7		206.1**		121.3*	
a	1	65.4*	37.7	331.9**	32.2	23.8	3.9
d	1	1.7	1.0	1.9	0.2	6.1	1.0
aa	1	4.1	2.3	14.0	1.4	0.2	0.0
ad	1	7.8	4.4	17.9	1.7	12.2	2.0
dd	1	4.0	2.3	6.2	0.6	3.6	0.6
Error	12	8.5		5.9		20.2	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-26. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T224 x PI217413 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	14.9		6.7		2.3	
Generation	5	64.4**		123.5**		151.9**	
a	1	245.9**	76.3	6.6	1.0	558.5**	73.5
d	1	18.4	5.7	11.1	1.8	6.1	0.8
aa	1	30.4	9.4	0.0	0.0	0.1	0.0
ad	1	1.1	0.3	1.2	0.2	79.9**	10.5
dd	1	12.2	3.8	2.4	0.4	6.2	0.8
Error	12	9.2		12.2		5.6	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-27. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T115 x Mo18W cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	8.2		11.4		11.9	
Generation	5	286.3**		427.0**		812.1**	
a	1	1231.6**	86.0	431.5**	20.2	3241.1**	79.8
d	1	20.0	1.3	20.0	0.9	3.2	0.1
aa	1	10.9	0.8	0.0	0.0	0.5	0.0
ad	1	29.8	2.1	38.8	1.8	9.2	0.2
dd	1	10.4	0.7	1.8	0.1	0.1	0.0
Error	14	16.4		11.4		36.6	

*Indicates significance at the 0.01 level of probability.

Table A-28. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T115 x Ga209 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	0.8		13.9		1.3	
Generation	5	58.1**		131.1**		6.6	
a	1	226.1**	77.8	237.6**	36.2	1.3	3.9
d	1	4.6	1.6	11.6	1.8	4.2	12.6
aa	1	0.5	0.1	10.1	1.5	6.6	19.8
ad	1	7.4	2.5	7.7	1.2	16.8	50.6
dd	1	15.2	5.2	0.1	0.0	1.4	4.2
Error	12	5.7		6.7		4.8	

**Indicates significance at the 0.01 level of probability.

Table A-29. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T115 x Ky226 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	2.2		29.7		11.5	
Generation	5	50.4*		195.3**		123.4*	
a	1	154.6*	61.4	685.4**	70.2	464.9**	75.4
d	1	1.0	0.4	13.9	1.4	5.3	0.9
aa	1	2.6	1.0	2.1	0.2	0.2	0.0
ad	1	2.4	1.0	113.3*	11.6	53.2	8.6
dd	1	3.4	1.4	4.5	0.5	1.6	0.3
Error	13	11.2		10.8		29.1	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-30. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the T115 x PI217413 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	2.5		7.5		2.8	
Generation	5	40.2**		100.4**		18.5**	
a	1	154.9**	77.1	118.3*	23.6	34.8**	37.7
d	1	12.9	6.4	14.7	2.9	3.3	3.6
aa	1	20.5	10.2	12.3	2.4	1.1	1.2
ad	1	2.2	1.1	7.8	1.6	4.1	4.4
dd	1	10.9	5.4	42.9	8.5	1.9	2.1
Error	14	3.3		9.6		1.2	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-31. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the Mo18W x Ga209 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	4.0		13.6		9.6	
Generation	5	138.6		362.3**		760.0**	
a	1	396.7*	57.3	1289.7**	71.2	3152.3**	83.0
d	1	3.4	0.5	14.7	0.8	184.6	4.9
aa	1	11.6	1.7	29.0	1.6	176.7	4.7
ad	1	9.3	1.3	16.6	0.9	11.1	0.3
dd	1	7.0	1.0	1.0	0.1	145.5	3.8
Error	11	30.4		12.9		69.4	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-32. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the Mo18W x Ky226 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	22.8		18.2		157.3	
Generation	5	278.5**		293.7**		585.3**	
a	1	346.5**	24.9	65.9	4.5	644.6	22.0
d	1	50.5	3.6	7.5	0.5	243.6	8.3
aa	1	36.6	2.6	3.4	0.2	239.4	8.1
ad	1	67.6	4.8	5.5	0.4	326.6	11.2
dd	1	17.3	1.2	0.0	0.0	125.0	4.3
Error	14	24.9		11.1		91.4	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-33. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the Mo18W x PI217413 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	50.5		24.6		28.6	
Generation	5	528.4**		92.3**		960.5**	
a	1	2073.7**	78.5	86.8*	18.8	3440.9**	71.6
d	1	4.3	0.2	32.1	7.0	8.7	0.2
aa	1	3.2	0.1	7.5	1.6	5.6	0.1
ad	1	54.7	2.1	38.1	8.3	275.2**	5.7
dd	1	5.3	0.2	42.8	9.3	10.2	0.2
Error	12	10.3		9.1		19.8	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-34. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the Ga209 x Ky226 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	20.3		7.5		25.7	
Generation	5	54.1*		332.8**		109.0	
a	1	3.2	1.1	1557.5**	93.6	513.5**	94.3
d	1	8.8	3.2	17.8	1.1	0.2	0.0
aa	1	12.4	4.6	20.3	1.2	4.6	0.8
ad	1	1.7	0.6	1.5	0.1	10.1	1.9
dd	1	0.2	0.1	17.1	1.0	11.7	2.1
Error	14	14.8		47.3		27.4	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

Table A-35. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the Ga209 x PI217413 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	3.7		26.6		0.3	
Generation	5	147.1**		219.8**		14.0	
a	1	682.2**	92.0	620.3**	56.4	25.8	36.9
d	1	3.3	0.4	7.3	0.7	4.7	6.7
aa	1	11.7	1.6	11.5	1.0	9.3	1.3
ad	1	8.3	1.1	9.1	0.8	2.1	0.3
dd	1	2.0	0.3	10.0	0.9	0.1	0.1
Error	15	14.9		7.8		5.8	

**Indicates significance at the 0.01 level of probability.

Table A-36. Analysis of variance of three ear characteristics and percent of generation means attributable to different genetic effects in the Ky226 x PI217413 cross.

Source of variation	d.f.	Depth of penetration		Husk extension		Depth of blank tip	
		M.S.	Percent of genetic variance	M.S.	Percent of genetic variance	M.S.	Percent of genetic variance
Block	3	4.2		19.0		30.3	
Generation	5	108.8**		89.8**		224.9**	
a	1	515.2**	94.7	246.2**	54.8	656.6**	58.4
d	1	20.5*	3.8	2.5	0.6	38.1	3.4
aa	1	20.6*	3.8	1.8	0.4	74.9	6.7
ad	1	32.1**	5.9	39.3	8.8	31.6	2.8
dd	1	15.3	2.8	9.5	2.1	45.5	4.0
Error	12	2.3		9.3		24.1	

* and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively.

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John R. Attewell was born in Zanesville, Ohio, on June 16, 1953. He attended elementary and secondary schools in South Milwaukee, Wisconsin, and was graduated in June 1971. He attended Marquette University as a biology major in September 1971 and later transferred to the University of Wisconsin in Eau Claire.

He was drafted by the Army in May 1972 and toured Southeast Asia as a specialist with a United States Army Communications, Logistics, and Security Unit. He was honorably discharged in August 1974 and immediately resumed his education in Eau Claire.

He completed a Bachelor of Science degree in May 1978. Shortly afterward he married his fiancee, Deborah, and was employed by Universal Foods Corporation as a laboratory technician. In November 1978 he joined the staff of the Medical College of Wisconsin-Cancer Research Center as a research technologist.

In the spring of 1983 he and his wife were blessed with their first son, Michael.