AN ESTIMATION OF GENETIC COMPONENTS OF VARIANCE IN BULKED F_6 PROGENIES OF BARLEY

By

Balwant Singh Jogi

AN ABSTRACT

Submitted to the School of Graduate Studies of Michigan
State College of Agriculture and Applied Science
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Farm Crops

Year 1954

Approved Kenyon T. Payne

BALWANT SINGH JOGI

ABSTRACT

An estimate of the genetic components of variance in the F_6 generation was made on two barley crosses, Stewart x Bay, and Kindred x Bay. Seed was drawn from a bulked F_4 at random from the two crosses. Stewart and Kindred are rough awned varieties and Bay is a smooth awned variety. Cross Stewart x Bay was designated as A 272 and Kindred x Bay was identified as A 267.

Twenty families from each cross were selected and 18 F_4 seeds from each family were taken at random. The seed so taken were grown for increase in the green house in fall, 1952. In the spring of 1953, the F_5 seeds were planted for increase in the field. A group of F_5 rows tracing to a designated F_3 row was called a family.

The yield trials were conducted in the F_6 generation at two locations in Ingham and Tuscola counties. In all, there were three experiments, two in Ingham County and one in Tuscola. A lattice design was used. Ingham Experiments I and II consisted of Stewart x Bay and Kindred x Bay crosses, respectively. Tuscola Experiment III included only the Kindred x Bay cross. Ingham Experiments I and II consisted of 100 plots each, and Tuscola Experiment III contained 90 plots. Environmental variance was determined from

parental check plots. The tests were on a four-row, single-plot basis. It was impossible to replicate subfamilies using this plot size because of limited seed. The four subfamilies in each family were treated as replicates.

Notes were taken on disease reactions and agronomic characters. The diseases concerned were powdery mildew (Erysiphe graminis hordei) and spot blotch (Helminthosporium sativum). The agronomic characters studied were date of heading, height of the plants, percent of lodged plants, lodging resistance, test weight, and awn type. Efforts were made to obtain additional information about these characters to determine the estimation of components of variance. The components of variance were also estimated from the yield data, and the effects of each character on seed yield per plot were calculated. Various class ratings were given to the effects of each character and each class was compared with the other for statistically significant differences.

On a single gene basis if the original F_4 seed chosen were AA or aa, the resulting plot mean will remain unchanged after any number of generations of selfing. On the other hand, if seed chosen were Aa, then the plot mean will change with each generation of

selfing. This was illustrated with an algebraic model. Let the mean effects of AA, Aa, and aa equal d_{λ}, h_{λ}, and $-d_{\lambda}$. The model assumes only the additive action of genes and no epistasis. The value H equals dominance deviation from the additive scheme and may be positive or negative. In the F_6 generation the mean square expectation was calculated between the families:

$$1/2D + \frac{1}{1024} H \cdots\cdots \sigma^2_F \cdots\cdots \text{(a)}$$

and mean square expectation for within the families was:

$$3/8D + \frac{6}{1024} H \cdots\cdots \sigma^2_W \cdots\cdots \text{(b)}$$

D is 3/4 of the size for within the families as compared to the size for between the families. The coefficient in both the cases is extremely low so that it approaches zero. Having both the values for environmental error and for the additive genetic fraction, the heritability values can be easily determined. The formula used here to calculate heritability percentages in each experiment was as follows:

$$\text{Heritability} = \frac{\sigma^2_F}{\sigma^2 + \sigma^2_F} \times 100$$

σ^2_F is equal to variance due to additive genetic effects.

σ^2 is the environmental variance calculated from parents only.

The environmental error, additive genetic fractions, and heritability percentages were calculated in all three experiments. The heritability percentages for yield are 31, 37, and 32 percent, with a mean of 33 percent in the F_6 generation. The high heritability values in the F_6 generation indicates that homozygosity has reached practically a maximum. Delay later than this will be a waste of time on the part of the plant breeder.

The components of variance were calculated for powdery mildew, H. sativum, date of heading, height of the plants, percent of lodged plants, lodging resistance (cLr), factor and awn type. The heritability values for each character is given below for all the three experiments.

Mildew	84%	80%	40%
H. sativum	4%	33%	36%
Date of Heading	76%	83%	-
Height	49%	40%	35%
Lodging	16%	35%	-
Lodging Resistance	62%	17%	60%
Test Weight	87%	55%	78%

Lodging resistance factor cLr is equal to $\frac{F}{b}$ where F is equal to force applied and b is the height of the plant.

These heritability values are relatively high and provide information as to possible genetic progress through selection.

AN ESTIMATION OF GENETIC COMPONENTS OF VARIANCE IN BULKED F_6 PROGENIES OF BARLEY

By

Balwant Singh Jogi

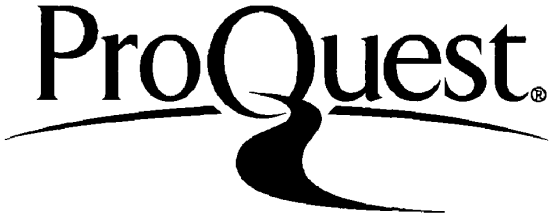
A THESIS

Submitted to the School of Graduate Studies of Michigan State College of Agriculture and Applied Science in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Farm Crops

1954



ACKNOWLEDGMENTS

This study was carried out under the guidance of Dr. K. T. Payne, Head and Professor of Farm Crops, Dr. J. E. Grafius, Associate Professor of Farm Crops, and Dr. K. J. Frey, at present Associate Professor of Farm Crops at Iowa State College, Ames, Iowa. I take this opportunity to express my sincere gratitude to these three men.

Appreciation is extended to Dr. W. D. Baten and Professor H. M. Brown for help with the statistical analysis. Grateful acknowledgment is given to the Midwest Barley Improvement Association and Michigan Brewers Association for their financial assistance.

I also express a special note of gratitude to my brother, Bachitter Singh Bassi, for his assistance and encouragement throughout the entire program of studies. To all others who contributed to the study, but go unmentioned, I am deeply grateful.

TABLE OF CONTENTS

INTRODUCTION

Information is now available on the use of early generation testing in small grains as a means of determining those crosses which would most likely produce the greatest number of high yielding segregates. From these studies the concept has been developed that it is possible to obtain the highest yielding segregates from the highest yielding parental varieties.

As a result of genetic studies with small grains, various models have been constructed for separating the components of variance. Such models have been applied to the segregating populations and to a large number of bulked F_2 and F_3 progenies.

The present paper is a report of a study in which an attempt was made to estimate the genetic components of variance involving two crosses in bulked F_6 progenies of barley. Efforts have also been made to obtain additional information on the genetic components of variance for disease reaction, date of heading, plant height, percent of lodged plants, lodging resistance, and awn type.

REVIEW OF LITERATURE

Estimation of Variance Components

Fisher (17) in 1925 introduced the analysis of variance and suggested its use in the following ways:

1. To obtain tests of significance of treatments.
2. To estimate variance components.

The analysis of variance to estimate variance components has been widely used in the field of genetics and in selection for efficient sampling designs. Excellent discussions of these applications are found in Cochran (11), Yates and Zazopany (80), and Youden and Mehlich (81).

Fisher (16) first separated genetic variance into three components: that due to additive effects of genes, that due to dominance deviations from the additive scheme, and that due to deviations from the additive scheme attributable to interallelic interactions.

Mather (47) suggested that the components of variance can be partitioned into two components; namely, (1) non-heritable, and (2) heritable, which in turn may be subdivided into fixable and unfixable genetic variance.

Charles and Smith (8) separated genetic from total variance by the use of estimates of environmental variance based on non-segregating populations and possible relations between means and variance.

Griffing (26) in a study on tomatoes, calculated the components in analysis of variance and covariance of non-segregating populations for the P_1, P_2, and F_1. This analysis was found to give a simple, direct and probably the most accurate method of obtaining estimates of phenotypic and environmental correlations and relationships developing from these estimates. Genotypic correlations were calculated making use of genotypic covariance and the geometric means of the two parental genotypic variances. Of more immediate interest are the error (within varieties) variance and covariance which he used as environmental variance and covariance.

Wright (79) developed formulae for the mean and variance of squared deviations from an optimum for the cases of no dominance and of complete dominance, first assuming no environmental complications but later removing this restriction. The variance in each case was split into contributions due to:

1. Additive genetic effects.
2. Dominance deviations.
3. Epistatic deviations.
4. Environmental effects
5. Non-additive joint effects of heredity and environment.

He further developed the formulae which apply to epistatic relations in case of complete dominance. He also proposed formulae for the correlations between parent and offspring and between two offspring. He concluded that in a

population in which the mean of some measurable character is at the optimum, the parent-offspring and fraternal correlations in adaptive value are approximately the squares of the corresponding correlations with respect to the character itself, whatever environmental complications there may be. Where the mean is not at the optimum there is less difference between the correlations in adaptive value and corresponding ones with respect to the character itself.

The study of hereditary and environmental components of variation had its beginnings in the work of Johannsen (37), who first demonstrated that both heritable and nonheritable agencies contributed to somatic variation in a segregating population and that variation in pure lines was entirely environmental. East (15) further confirmed the work of Johannsen and demonstrated how such results conformed with the concept of Mendelian genetics.

Fisher, Immer, and Tedin (18), Mather (47), Lush (41), Panse (58) and others have studied heritable variation and have further subdivided it into that portion attributable to additive genetic effects and that due to deviations from the additive scheme.

In a discussion of heritability of characters in animals, Lush (42) defines heritability and describes its usage in the broad and narrow aspects. In a broad sense, heritability refers to the functioning of the whole genotype as a unit and is used in contrast with environmental effects. In

the narrow sense heritability includes only the average effects of genes transmitted additively from parent to progeny.

Lush and Panse (43) proposed the use of the ratio of the additive genetic component of variance to total variance as a measure of the degree of heritability.

Robinson, Comstock, and Harvey (66) used a method involving estimates of components of variance through study of biparental progenies to measure heritability in corn. They further compared this method with heritability as calculated from parent-offspring regressions.

Grafius (22) developed a model for the estimation of the components of genetic variance between self-fertilized, bulked progenies from crosses of isogenic lines. He presented in detail the mathematical basis for the method of estimation.

Grafius, Nelson and Dirks (24) studied the heritability of yield in barley as measured by early generation bulked progenies. They reported that the non-heritable fraction comprised the major portion of the genetic variance in the F_2. In the F_3, with increased homozygosity, the non-heritable fraction decreased in comparison to the additive (heritable) fraction of the genetic variance.

Mahmud and Kramer (50) made estimates of heritability for yield and plant height in a soybean cross. They utilized the F_2 segregates as the total variance and the square root of the product of the parental variances as the environmental variance. They found heritabilities of 43 and 41 percent for

yield and height respectively, using this method.

Weber (75) in an interspecific cross of soybeans, made use of the cube root of the product of the variance of P_1, P_2, and F_1 as the best estimation of environmental variance. Calculation of genetic and environmental correlations involved the use of reciprocal regression coefficients between F_2 and their F_3 progenies. Genetic correlations were generally higher than the observed correlations in F_2 and F_3.

Weber and Moorthy (76) in three soybean crosses, studied seed yield, flowering time, maturity date, period from flowering to maturity, plant height, seed weight and oil content on an individual plant basis. The estimates of the genotypic and environmental variances in these seven characters were made. They noted transgressive segregation for most of the characters in all of these crosses. The highest heritability was noted in flowering time (75.7 percent) and the lowest seed weight (54.3 percent). Oil content was 54.7 percent heritable. The heritability of seed yield was erratic due to a large environmental variance.

Date of Heading

Griffee (25) found an association between heading date and two-row versus six-row characteristic. He suggested that the inheritance of date of heading in barley was due to one factor pair.

Neatby (54) reported that the inheritance of earliness in barley is due to three factor pairs. When these factors

are in the homozygous recessive condition, the plants develop winter habits of growth. He further suggested that there is a linkage between the earliness and short versus long outer glume.

Hehn (31) investigated linkage in barley in connection with many characteristics. He concluded that three factor pairs determined the earliness of heading in barley.

Wexelsen (78) reported two factor pairs determining date of heading in barley. He suggested that heading date was associated with the two versus six-row characteristic, rough versus smooth awn and the number of barbs on the nerves of the lemma.

Griffee (25) also reported that earliness in barley is linked with the factor for short versus long outer glume.

Frey (20) investigated the heading date in four crosses of barley in the F_2 generation and the parents and progenies of F_2 plants of seven other barley crosses. He found that the Ogalitsu variety of barley differs from Harlan by one factor for date of heading. Jet and Anodium differ from Harlan by two genes. Both Jet and Anodium contain the same gene pairs for determining heading date. Date of heading was found to be associated with the rough versus smooth awn characteristic in a three way cross, Moore x (Dorsett x M49001), and with the black versus white hull character in a cross of Harlan x Jet.

Spot Blotch (*Helminthosporium sativum*) (Pam) King

Spot blotch disease of barley was reported by Pammel (56) in 1909 and was attributed to *Helminthosporium sativum*. Pammel, King and Bakke (57), and Christensen (9) have reviewed previous studies relating to the pathogenecity of *H. sativum* and suggested that the parasite is responsible for leaf spot, root rot, foot rot and seedling blight of wheat, barley, rye and many other grass species.

Hayes et al (30) studied the inheritance of reaction to *H. sativum* and its association with botanical characters in a Manchuria and Lion cross. Manchuria is a resistant variety and Lion is susceptible to the disease. One hundred twenty-four F_3 lines were grown in rows of 25 plants each and sprayed with spore suspensions of *H. sativum*. Every tenth line was planted as a check, alternating the Manchuria and Lion parents. From this, the resistant and susceptible lines were separated and tested in the F_4 generation. Eight lines were found to be as susceptible as Lion in F_3 and F_4 and six lines were as resistant as Manchuria. The correlation coefficient for degree of infection in F_3 and in F_4 of 36 hybrid lines of Lion x Manchuria was $0.256 \pm .105$. This is significant at the 5 percent point. They concluded that resistance to *H. sativum* is an inherited character although apparently dependent on more than a single genetic factor.

Griffee (25) studied the reaction of F_3 lines to H. sativum in relation to other characters. He concluded that at least three factors are concerned in the resistance of the type possessed by the variety Svanhal. One factor was linked with the factor for two-rows, one with the factor of rough awn and one with the factor of white glume. The linkage of the factor susceptibility to H. sativum with the factor of earliness is much closer than that with the factor for six-rowed. It is also suggested that earliness in itself may predispose the plant to attack by the pathogen.

Powdery Mildew (Erysiphe graminis Hordei)

Briggs (6) suggested that in an inheritance study of resistance to any disease in plants the following points are of interest:

1. The number of factors for resistance present in each variety.
2. The identity of each factor.
3. The effect of each factor acting alone.

The inheritance of resistance to barley mildew was studied in hybrids involving three resistant varieties, Arlington, Chinerme, Nigrate and a susceptible variety, Atlas. The three resistant varieties differ from susceptible Atlas in two independent major factors for resistance to this disease. Susceptibility was recessive.

Stanford and Briggs (72) reported that there are seven

different factors for mildew resistance, six dominant and one recessive. The number of factors in a single variety varies from one to three. Of the seven identified, two are definitely linked. The other five appear to be independent.

Ray et al (62) studied eleven wheat crosses in the F_2 generation for the inheritance of mature plant resistance to natural infection with powdery mildew in the field. They also examined ten crosses under green house conditions for seedling resistance to infection by four races of the mildew fungus. The seedling reaction appears to be conditioned by a single dominant factor in three crosses. One cross segregated for two factor differences for seedling resistance. It was reported that under field conditions the gene controlling the expression of glume pubescence appeared to be closely linked with the major factor for seedling resistance to one race of powdery mildew.

Mains and Martini (45) tested a number of varieties against mildew and found that varieties differed considerably in their reactions. Some showed differences in type and stability of reaction and others exhibited marked differences in reaction to the three physiologic forms of mildew.

Lodging Resistance

Garber and Olson (21) reported that lodging in cereals is associated with many characters but that no one character

seems to be correlated closely with lodging.

Atkins (1) suggested that no one lodging index can be considered reliable since lodging is dependent on a number of factors that vary greatly from year to year. He suggested that the character of straw strength is an inherited one.

Ramiah and Dharmalingam (61) found in crosses between two typically lodging and non-lodging varieties of rice that there is only a single factor pair difference. There seems to be genetic association between the character of the straw on one hand and such characters as tillering and flowering duration in days on the other hand. The non-lodging nature of the straw is linked with poorer tillering and longer duration. There apparently is no relationship between plant height and straw character nor between straw character and floret sterility.

Clark et al (10) studying the linkage relation in barley found that the factor pairs of awnedness and lodging are linked.

Bose et al (5) found that at least two genes were responsible for the development and distribution of sclerenchyma tissue. These characters were reported to be associated with lodging resistance. They also found weak straw to be dominant.

In an inheritance study of weight per unit length of culm and other characters in a cross of Kanred and Coppei, Atkins (2) reported the following significant correlation

coefficients of F_2 parent plants and their F_3 progeny lines: diameter of culm 0.582, height of the plant 0.830, length of the head 0.830. On the basis of these results, he suggested that selection for these characters can be made in early generations and that the continued selection will lead to desired type.

Grafius and Brown (23) defined lodging resistance (Lr) as the ratio of the additional torque (over and above the torque caused by the weight of the culm, leaves and head) a culm is capable of resisting (Tr) to the torque (Ta) applied by external forces, such as wind and rain. They proposed the lodging resistance factor (cLr) and suggested the following formula for its calculation:

$$cLr = \frac{F}{b}$$ where F is equal to force applied and b is the height of the plant.

EXPERIMENTAL PROCEDURE

This problem is a continuation of a barley project which had been in progress at the Michigan Experiment Station, East Lansing since 1949. It consists of a study of advanced generation selections from two crosses which include three varieties. The material used in the experiment was from the F_3 bulked rows which had been allowed to self for two additional generations in order to obtain sufficient seed to conduct a yield trial in the F_6 generation.

In the fall of 1949 two barley crosses, Steward x Bay and Kindred x Bay were made in the green house. Stewart and Kindred varieties are rough awned and Bay is smooth awned. Selections from Stewart x Bay were designated A272 and Kindred x Bay crosses were identified as A267. During the spring of 1950, the F_1 seeds were space planted in the field. Each plant was harvested and threshed separately. The F_2 seeds from individual plants were grown in separate rows in 1951 and at harvest each row was bulked. Yield trials were conducted with F_3 seed in 1952. In the fall of 1952, out of the F_3 bulk rows, F_4 seeds were taken at random from both selections. Twenty families from each cross were selected. Eighteen seeds were taken from each family, making a total of 720.

The F_4 seeds taken at random from individual F_3 rows were grown for increase in the green house in the fall of

1952. In the spring of 1953, the F_5 seeds were planted for increase in the field. Each F_5 row in the field was numbered so as to be able to trace its pedigree to a single F_3 row. A group of the F_5 rows tracing to a designated F_3 row was called a family.

Of 720 original F_4 seeds, 228 produced at least 40 grams of F_6 seed, which is necessary for yield trials planted at the calculated rate of approximately five pecks per acre, as is shown in Table 1.

TABLE I. THE NUMBER OF FAMILIES AND SUB-FAMILIES IN SELECTIONS FROM TWO BARLEY CROSSES IN WHICH SUFFICIENT SEED WAS AVAILABLE FOR YIELD TRIALS IN THE F_6 GENE-RATION

Selections	Cross	Families	Sub-families in each family	Total
A272	Stewart x Bay	19	4	76
A267	Kindred x Bay	19	8	152
			Grand Total	228

On the basis of seed supply as indicated in Table 1, three experiments were arranged. The location and total number of plots in each may be seen in Table 2.

TABLE II. THE NAME AND NUMBER OF EXPERIMENTS WITH THE TOTAL NUMBER OF PLOTS IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES, 1954

Experiment	Cross Number	Cross	Location	Number of Plots		Total
				Sub-families	Parents	
Ingham I	A272	Stewart x Bay	East Lansing (Ingham Co.)	76	24	100
Ingham II	A267	Kindred x Bay	East Lansing (Ingham Co.)	76	24	100
Tuscola III	A267	Kindred x Bay	Tuscola Co.	70	20	90

In Ingham Experiments I and II, 12 check plots of each parental variety are included. In Tuscola Experiment III, there were nine Bay plots and eleven Kindred plots as check. The total number of sub-families was 70. In Tuscola Experiment III, ten plots were eliminated due to insufficient space.

The bulked F_6 seed from each F_5 row was used to seed an yield plot in 1954. In all three experiments each individual plot was a sub-family. It was impossible to replicate the sub-families using this plot size because of limited seed. The four sub-families in each main family were treated as 4 replicates in all three experiments. In order to determine the environmental effects in each experiment the parent plots were used as checks.

The check plots were grown at random in all three experiments and analysis of variance for the parents was calculated separately. The mean square for error was used as environmental variance to test the statistically significant differences between and within the families in all three experiments.

A simple lattice design was used at both locations. Each plot was four rows wide, 18 feet long with a one foot spacing between rows. At maturity the 12 foot central portion of the two inner rows was harvested for yield.

2-4-D (2-4-Dichlorophenoxyacetic acid) was used for weed control when the barley plants were in the four-leaf stage. After threshing the individual plot seed lots were weighed, cleaned and test-weighed.

During the growing season observations on disease reaction and other agronomic characters were recorded. The diseases concerned were powdery mildew (Erysiphe graminis hordei) and spot blotch (Helminthosporium sativum).

Agronomic characters studied were: date of heading, height of plant, percent of lodged plants, lodging resistance and smooth versus rough awn.

DISEASE REACTIONS

Powdery Mildew

The attack of mildew was severe and the first four leaves of ten random plants per plot were examined for mildew infection and readings were recorded on a direct percentage basis. The average of the ten readings provided the plot rating.

The sub-families were grouped on the basis of amount of infection into four categories. They are 0-25%, 26-50%, 51-75% and 76-100%. In each experiment the average yield of seed from the sub-families falling within each of the above categories was compared with average from the other catagories to determine whether seed yield was directly related to mildew reaction.

Spot Blotch (H. sativum)

Ten to twenty plants were pulled from the two outer rows just prior to harvest and the roots and stems were examined from the first to the fifth basal nodes. The amount of infection on each plant was noted. The rating scale used was zero to five with five indicating complete infection.

The sub-families were grouped according to H. sativum

reaction into four catagories. There were none in classes zero or one, so all fell in classes two, three, four or five. The average seed yield of each category was compared with that in the other categories to determine the effects, if any, of H. sativum on yield.

AGRONOMIC CHARACTERS

Date of Heading

Nearly all of the plots at both locations headed in the month of June. Based on date of heading, the sub-families were grouped into four classes as follows: June 10 to June 15; June 16 to June 20; June 21 to June 25; and June 26 or after. The average seed yield for each of the four classes was compared with the others to determine whether statistically significant differences existed between their mean yields.

Height of Plant

Height notes were taken on 15 to 20 plants in each plot and averaged. On the basis of height classification, the sub-families were divided into three groups. The first group includes those sub-families which were 20 to 25 inches tall, the second group included those from 26 to 30 inches in height, and the third group was made up of those 31 inches or taller. The average seed yields of these groups were compared to determine whether yield was associated with plant height.

Lodging

The amount of lodging was estimated and recorded in percent at harvest time. The sub-families were grouped into four categories: 0-25%, 26-50%, 51-75% and 76-100%. The average yields of seed of these categories were compared to determine whether or not lodging was a significant factor in seed yields.

Lodging Resistance

Two weeks prior to maturity, readings were taken on lodging resistance. A special chain of 150 links was used, each link weighing one gram. A hook was attached to one end of the chain. The hook was fastened to the rachis at the base of the head, and the culm was allowed to bend until a portion of the links were on the ground and the remainder were supported by the culm. The readings were taken by counting the links from the ground to the hook. Five readings were taken in each plot and the average was used as an indication of lodging resistance. This average was divided by the plant height of each respective plot prior to statistical anlysis. The lodging resistance (cLr) factor is equal to $\frac{F}{b}$ where F is equal to force supplied and b is equal to plant height.

In Ingham Experiments I and II readings were recorded two weeks prior to maturity and again shortly after maturity. The number of culms that broke with the weight of the chain and the type of curve created in the culm by the weight of

the chain were also recorded but are not being presented as a part of this thesis.

Smooth Versus Rough Awn

In Ingham Experiment I, no segregation was noted. Apparently the smooth awned segregate in the F_6 generation was used as the Stewart parent.

In Ingham Experiment II and Tuscola III, the sub-families were grouped into smooth and rough awn. The average seed yield of each group was calculated and compared for possible statistically significant differences.

Test-Weight

Test-weights of each sub-family and the parental plots were taken.

Yield

Yield of plots was determined in grams and plots were compared for statistically significant differences.

EXPERIMENTAL RESULTS

The Components of Variance

Assume that k seeds were taken at random from F_3 bulk rows and selfed j generations. The F_6 lines used were random samples of k seeds from each of m F_3 bulk rows. Each of the k seeds was increased for two generations. Hence, each plot was the result of a random sample of seeds from bulk F_3 rows which were allowed to self for two additional generations. For example, on a single gene basis if the seed chosen were AA or aa, the resulting plot means will remain unchanged after j generations of selfing. On the other hand, if the seed chosen were Aa then the plot mean will change with each generation of selfing. This can best be illustrated with an algebraic model.

Following Mather (47), let the mean effects of AA, Aa, aa equal d_i, h_i and $-d_i$, respectively, as may be seen in Tables III and IV, etc. The model assumes only the additive action of genes and no epistasis. The value h equals the dominance deviation from the additive scheme and may be positive or negative.

TABLE III. DISTRIBUTION OF GENOTYPES AND THEIR MEAN EFFECTS IN AN F_2 POPULATION

Genotype of F plants	Frequency	Mean effect
AA	$\frac{1}{4}$	d_i
Aa	$\frac{1}{2}$	h_i
aa	$\frac{1}{4}$	$-d_i$

From Table III, one may calculate the F_2 variance which will be:

$$\tfrac{1}{4}\, d_i^2 + \tfrac{1}{4}\, d_i^2 + \tfrac{1}{2}\, h_i^2 - (\tfrac{1}{2}h_i)^2 =$$
$$\tfrac{1}{2}d_i^2 + \tfrac{1}{4}\, h_i^2$$

Summing over n such loci gives:

$$= \sum_{n=1}^{n} (\tfrac{1}{2}\, d_i^2 + \tfrac{1}{4}\, h_i^2)$$
$$= \tfrac{1}{2}\, D + \tfrac{1}{4}\, H$$

The distribution of genotypes at a single locus in the F_3 is given in Table IV. It is to be noted that the center class represents a single F_3 row with a mean of $h_i/2$. In this experiment seeds were drawn at random from each F_3 row giving the distribution shown in Table V. The three classes in the left hand column of Table V represent individual F_4 plants in all possible types of families.

TABLE IV. DISTRIBUTION OF GENOTYPES AND THEIR MEAN EFFECTS IN AN F_3 POPULATION

Expected genotype of F_3 row		Frequency	F_3 row mean effect
AA	d_i	$\frac{1}{4}$	$+ d_i$
$\frac{1}{4}$AA $\frac{1}{2}$Aa $\frac{1}{4}$ aa	$(\frac{1}{4}\, d_i + \frac{1}{2}\, h_i - \frac{1}{4}\, d_i)$	$\frac{1}{2}$	$\frac{h_i}{2}$
aa	$-d_i$	$\frac{1}{4}$	$-d_i$

TABLE V. DISTRIBUTION OF GENOTYPES AND THEIR MEAN EFFECTS IN AN F_4 POPULATION

Expected genotypic families of selected plants in F_4	Frequency	Family mean effect
AA	$\frac{1}{4}$	d_i
$\left[\frac{3}{8}\ AA + \frac{2}{8}\ Aa + \frac{3}{8}\ aa\right]$	$\frac{1}{2}$	$\frac{h_i}{4}$
aa	$\frac{1}{4}$	$-d_i$

TABLE VI. DISTRIBUTION OF GENOTYPES AND THEIR MEAN EFFECTS IN AN F_5 POPULATION

Expected genotypic families of F_5 rows from F_4 plants in Table III	Frequency	Family mean effect
AA	$\frac{1}{4}$	d_i
$\left[\frac{3}{8}\ AA + \frac{2}{8}\ (\frac{1}{4}AA + \frac{1}{2}\ Aa + \frac{1}{4}aa) + \frac{3}{8}\ aa\right]$	$\frac{1}{2}$	$\frac{h_i}{8}$
AA	$\frac{1}{4}$	$-d_i$

It will be noted in Tables V and VI that the family mean effect for the center class is halved in each generation. This is the expected result under selfing and if continued, the total family mean effect approaches zero. By the time the selections had reached F_6 the family mean effect for the heterozygous family had been reduced to $\frac{h_i}{16}$ as shown in Table VII.

TABLE VII. DISTRIBUTION OF GENOTYPES AND THEIR MEAN EFFECTS IN AN F_6 POPULATION

Expected genotype of yield plots in F_6	Frequency	Family mean effect
AA	$\frac{1}{4}$	d_i
$\left[\frac{3}{8}\ AA + \frac{2}{8}\ (\frac{3}{8}\ AA + \frac{2}{8}\ Aa + \frac{3}{8}\ aa) + \frac{3}{8}\ aa\right]$	$\frac{1}{2}$	$h_i/16$
aa	$\frac{1}{4}$	$-d_i$

Field Experiments

As has been noted in Ingham Experiment I, there were 19 families each with four sub-families which were treated as replicates. Inasmuch as the sub-families were sampled at random, the replicate total should show no genetic bias. Twelve plots of each of two parents were planted at random throughout the experiment and were analyzed separately in order to obtain an estimate of the environmental variance.

Ingham Experiments I and II were composed as follows:

Total number of families.....19

Total number of sub-families in each main family..... 4

Total number of plots for families 19 x 4...76

Total number of plots for two parents 12 x 2.....24

Grand total.....100

In Tuscola Experiment III ten plots were eliminated due to a lack of adequate space. At this location there were seventy plots for families and twenty for parents, making a total of 90.

Analysis of variance components may be seen in Table VIII.

TABLE VIII. THE ANALYSIS OF VARIANCE WITH MEAN SQUARE EXPECTATIONS OF NUMBER OF m BULK ROWS IN k REPLICATION USED IN A CROSS WITH 1 PARENTS.

Sources of variation	D.F.	M.S.	Mean square expectation
Between families	m-1	M_1	$\sigma^2 + k\,\sigma^2_F$
Reps	k-1		
Families x Reps	(m-1)(k-1)	M_2	$\sigma^2 + \sigma^2_W$
Parents	1	M_3	σ^2

It is necessary to determine σ^2_F and σ^2_W (See Table IX).

TABLE IX. MODEL FOR THE ANALYSIS OF VARIANCE INVOLVING A SINGLE LOCUS

Frequency of families	Genotype of original F_3 row	Total possible categories of plots			Family mean effect
		d_i	h_i	$-d_i$	
$\frac{1}{4}$	AA	d_i			d_i
$\frac{1}{2}$	Aa	$\frac{3}{8} d_i$	$\frac{1}{4}(\frac{3}{8} d_i + \frac{1}{4}h - \frac{3}{8} d_i)$	$-\frac{3}{8}d_i$	$\frac{h_i}{16}$
$\frac{1}{4}$	aa			$-d_i$	$-d_i$

The total sum of squares will then be:

$$= \sum_{i=1}^{n} (\tfrac{1}{4}d_i^2 + \tfrac{1}{4}d_i^2 + 3/8d_i^2) + \tfrac{1}{2}\left(\frac{h_i^2}{64}\right) - \left(\frac{h_i}{32}\right)^2$$

$$= (\tfrac{1}{2} \quad 3/8)d_i^2 + \frac{h_i^2}{128} - \frac{h_i^2}{1024}$$

$$= 7/8d_i^2 + 7/1024\ h_i^2$$

Total S.S. $= 7/8D + 7/1024\ H$

The sum of squares due to families $= \frac{2}{F}$

$$= \sum_{i=1}^{n} \left\{\tfrac{1}{4}d_i^2 + \tfrac{1}{4}d^2 + 1/512\ h_i^2 - 1/1024h_i^2\right\}$$

$$= \tfrac{1}{8}\ D + 1/1024\ H$$

The remainder (Total S.S.-S.S. due to families)$=\sigma^2_W$.

$$\sigma^2_W = (7/8\ D + 7/1024\ H) - (1/2\ D + 1/1024\ H)$$

$$= 3/8\ D + 6/1024\ H$$

At this point it can be seen that the coefficient of H is so small that it can safely be ignored. The coefficient of D within families is 3/4 of that between families.

Estimation of Genetic Components of variance from F_6 Bulked Yield Trials

In the F_6 generation the genetic components of variance may be calculated as follows:

1/2 D + 1/1024 H	σ^2_F.....(a)
3/8 D + 6/1024 H	σ^2_W.....(b)

In these two equations the coefficient of H is so low in the F_6 generation that it approaches zero. The additive genetic variance within families in equation (b) is only 3/4 the size of that between families.

In Table 10, the analysis of variance for yield of all three experiments is given and differences significant at the one percent level were obtained between families. Significant differences were not obtained within families.

The heritability values given in Table 11 were calculated from the following formula:

$$\text{Heritability} = \frac{\sigma^2_F}{\sigma^2 + \sigma^2_F}$$

The heritability values are 31, 37, 32 percent for Ingham Experiments I and II and Tuscola Experiment III respectively. These relatively high heritability figures indicate that selection for yield at this stage of homozygosity would be successful.

TABLE X. THE ANALYSIS OF VARIANCE FOR YIELDS OF F_6 BULK PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

Sources of variance	CROSSES						
	Stewart x Bay			Kindred x Bay		Kindred x Bay	
	Ingham Exp. I			Ingham Exp.II		Tuscola Exp. III	
	D.F.	MS	F	MS	F	MS	F
Total	75						
Families	18	6197.10	2.77**	6346.36	3.30**	9280.58	2.90**
Fam x Reps.	54	2377.89	1.06	3705.18	1.93	5190.83 1/	1.62
Error (Parents) 3/	18	2238.88		1924.44		3196.95 2/	

** F value exceeds the 1% level of significance.

1/ For Tuscola D.F. 48

2/ For Tuscola D.F. 14

3/ Environmental error calculated from the analysis of variance of parents only.

TABLE XI. THE CALCULATED VALUES OF E, 1/2 D AND HERITABILITY PERCENTAGES FOR YIELD FROM F_6 BULK PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

Experiment	Cross	E 1/	1/2 D	Heritability %
Ingham I	Stewart x Bay	2238.88	989.55	31
Ingham II	Kindred x Bay	1924.44	1105.48	37
Tuscola III	Kindred x Bay	3196.95	1520.91	32

1/ Where E is the estimate of environmental variance and 1/2 D is the estimate of additive genetic variance.

The Estimation of Genetic Components of Variance of Other Characters Observed From F_6 Bulked Progenies

The results of studies of other characteristics observed in the field are presented under the following two sub-heads:

Disease reaction

1. Powdery Mildew (*E. graminis hordei*)
2. Spot Blotch (*H. sativum*)

Agronomic characters

1. Date of heading
2. Percent of lodged plants
3. Height of plant

4. Straw strength
5. Smooth versus rough awn

Disease Reaction

Powdery Mildew

There were statistically significant differences in amount of mildew present between the families in all three experiments. The analysis of variance may be seen in Table 12. The results given in Table 13 indicate no significant differences in the average seed yields of the different quartile classes. It may be interpreted that the pathogen did not have a differential effect on yield of seed. In a further attempt to determine whether mildew infection was affecting seed yield, the families were grouped in 10 percentile classes rather than quartiles. Analysis indicated no significant difference between class seed yield averages, which further substantiates that severe mildew infection was not affecting seed yield any more than mild infection.

TABLE XII. ANALYSIS OF VARIANCE FOR MILDEW DATA OBSERVED FROM F_6 BULK PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

Sources of variance	CROSSES						
	Stewart x Bay			Kindred x Bay		Kindred x Bay	
	Ingham Exp. I			Ingham Exp. II		Tuscola Exp. III	
	D.F.	MS	F	MS	F	MS	F
Total	75						
Families	18	650.22	22.56**	963.33	16.99**	469.47	3.60**
Fam. x Reps	54	175.81	6.10**	98.02	1.78*	152.25 1/	1.17
Error (Parents) 3/	18	28.83		55.11		130.27 2/	

* F values exceeds 5% level of significance.

** F values exceeds 1% level of significance.

1/ For Tuscola 48

2/ For Tuscola 14

3/ Environmental error.

TABLE XIII. THE EFFECT OF MILDEW ON THE AVERAGE YIELD OF FAMILIES CLASSIFIED IN PERCENT FROM F_6 BULK PROGENIES IN TWO CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

Experiment	Crosses	Mildew rating classes in percent 0-25 (Mean yield in grams per plot)	26-50	51-75	76 above	F values
Ingham Exp. I	Stewart x Bay	436.18	427.79	431.25	-	0.11
Ingham Exp. II	Kindred x Bay	415.28	411.06	438.40	-	0.38
Tuscola Exp. III	Kindred x Bay	490.27	461.34	449.44	-	1.26

Spot Blotch (*H. sativum*)

The spot blotch reaction in Table 14 indicates no significant difference between families. In addition, statistically significant differences were not noted in the average yields between the four different classes of *H. sativum* reaction. This indicates that the pathogen had not produced a differential effect in regard to average seed yields of different classes of families.

TABLE XIV. ANALYSIS OF VARIANCE FOR H. SATIVUM DATA OBSERVED FROM F6 BULK PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

		CROSSES					
		Stewart x Bay Ingham Exp. I		Kindred x Bay Ingham Exp. II		Kindred x Bay Tuscola Exp. III	
Sources of variance	D.F.	MS	F	MS	F	MS	F
Total	75						
Families	18	0.82	0.92	0.63	0.15	1.43	0.35
Fam. x Reps	54	0.91	1.32	0.48	0.91	0.41 1/	0.91
Error (Parents) 3/	18	0.69		0.53		0.45 2/	

1/ D. F. for Tuscola is 48

2/ D. F. for Tuscola is 14

3/ Environmental error

TABLE XV. THE EFFECT OF H. SATIVUM ON THE AVERAGE SEED YIELD OF FAMILIES IN THE F_6 BULK PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

		H. sativum rating classes				
		2	3	4	5	F values
Experiment	Crosses	Mean yield per plot in grams				
Ingham Exp. I	Stewart x Bay	442.72	443.09	407.57	433.91	1.21
Ingham Exp. II	Kindred x Bay	435.91	416.29	411.59	340.50	1.08
Tuscola Exp. III	Kindred x Bay	418.71	465.00	462.77	500.00	1.44

Agronomic Characters

Highly significant differences between the families in date of heading in all three experiments may be seen in Table 16. There were no significant differences in the average yields of the families at different heading dates, as shown in Table 17. It may be considered that the date of heading had no significant effect on the average yields of the families.

Significant differences at the one percent level were obtained between the families for lodging (Table XX) in Ingham Experiment II, whereas there was no significant difference in Ingham Experiment I between the families. The average yields in both Ingham experiments classified under lodging in Table 19 show no significant difference between the catagories.

Highly significant differences in height existed between families, as may be seen in Tables 20 and 21. This may be interpreted to mean that there were differences in the average yields of the families due to height.

The anlysis of variance for lodging resistance (cLr) presented in Table 22 indicates significant differences between families at the 1% level in Ingham Experiment II.

The average yields of smooth and rough awned families are given in Table 23. This indicates that there are no significant differences between families in Ingham Experiment II and Tuscola Experiment III. As has been stated, families in Ingham Experiment I did not segregate for awn character.

TABLE XVI. ANALYSIS FOR DATE OF HEADING OBSERVED IN F_6 BULKED PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

		CROSSES			
		Stewart x Bay Ingham Exp. I		Kindred x Bay Ingham Exp. II	
Sources of variance	D.F.	MS	F	MS	F
Total	75				
Families	18	21.20	13.59**	30.66	20.86**
Fam. x Reps	54	6.80	4.36**	3.03	2.06
Error (Parents) 1/	18	1.56		1.47	

* F values exceeds 5% level of significance

** F values exceeds 1% level of significance

1/ Environmental error

TABLE XVII. THE EFFECT OF DATE OF HEADING ON THE AVERAGE SEED YIELD OF FAMILIES IN F_6 BULKED PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

Experiment	Crosses	Heading date June				F values
		10-15	16-20	21.25	26 above	
		Mean yield in grams per plot				
Ingham Exp. I	Stewart x Bay	414.65	430.48	450.77	-	1.94
Ingham Exp. II	Kindred x Bay	424.15	409.72	420.58	-	0.27
Tuscola Exp. III	Kindred x Bay	-	424.08	500.72	447.50	0.52

TABLE XVIII. ANALYSIS OF VARIANCE FOR HEIGHT OF PLANT IN F_6 BULK PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

		CROSSES					
		Stewart x Bay Ingham Exp. I		Kindred x Bay Ingham Exp. II		Kindred x Bay Tuscola Exp. III	
Sources of variance	D.F.	MS	F	MS	F	MS	F
Total	75						
Families	18	14.93	4.91**	12.09	3.92**	5.58	3.00**
Fam. Reps	54	5.08	1.67	3.50	0.90	3.49 1/	1.88
Error (Parents) 3/	18	3.04		3.88		1.86 2/	

** F exceeds 1% level of significance

1/ D.F. for Tuscola 48

2/ D.F. for Tuscola 14

3/ Environmental error

TABLE XIX. THE EFFECT OF HEIGHT OF PLANTS ON THE AVERAGE YIELDS OF FAMILIES IN F_6 BULKED PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

Experiment	Crosses	Height in inches: 20-25	26-30	31 above	F values
		Mean yield per plot in grams			
Ingham Exp. I	Stewart x Bay	408.94	447.00	520.00	5.56**
Ingham Exp. II	Kindred x Bay	373.58	417.13	455.30	4.74**
Tuscola Exp. III	Kindred x Bay	447.55	529.93		7.63**

** F value exceeds 1% level of significance

TABLE XX. ANALYSIS OF VARIANCE OF LODGING AT MATURITY IN F_6 BULK PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

		CROSSES			
		Stewart x Bay Ingham Exp. I		Kindred x Bay Ingham Exp. II	
Sources of variance	D.F.	MS	F	MS	F
Total	75				
Families	18	1048.54	1.76	164.55	3.12**
Fam. x Reps	54	515.16	0.86	117.82	2.23*
Error (Parents) 1/	18	596.53		52.72	

** F exceeds 1% level of significance

* F exceeds 5% level of significance

1/ Environmental error

TABLE XXI. THE EFFECT OF LODGING ON THE AVERAGE SEED YIELD OF FAMILIES IN F_6 BULKED PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

		Classes in lodging percentage				
		0-25	25.50	51.75	76-above	
Experiment	Cross	Mean yield per plot in grams				
Ingham Exp. I	Stewart x Bay	423.68	442.88	440.20	491.50	1.60
Ingham Exp. II	Kindred x Bay	405.30	411.22	429.45	404.45	0.60

TABLE XXII. ANALYSIS OF VARIANCE FOR LODGING RESISTANCE RECORDED TWO WEEKS BEFORE MATURITY IN F_6 BULK PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

		CROSSES					
		Stewart x Bay Ingham Exp. I		Kindred x Bay Ingham Exp. II		Kindred x Bay Tuscola Exp. III	
Sources of variance	D.F.	MS	F	MS	F	MS	F
Total	75						
Families	18	106694.69	7.58**	29697.00	1.82*	73411.28	7.13**
Fam. x Reps	54	35356.01	1.83	19964.00	1.22	33532.85 1/	3.26**
Error (Parents) 3/	18	19349.37		16335.00		10299.07 2/	

** F exceeds 1% level of significance

* F exceeds 5% level of significance

1/ D.F. for Tuscola 48

2/ D.F. for Tuscola 14

3/ Environmental error

TABLE XXIII. THE EFFECT OF AWN TYPE ON THE AVERAGE YIELDS OF FAMILIES IN F_6 BULKED PROGENIES IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

		Awn types		
		Smooth	Rough	
Experiment		Mean yield per plot in grams		F values
Ingham Exp. II	Kindred x Bay	412.46	420.87	0.40
Tuscola Exp. III	Kindred x Bay	473.59	448.69	1.76

TABLE XXIV. CALCULATED VALUES OF E, D/2 AND HERITABILITY PERCENTAGES OF DISEASE REACTION AND AGRONOMIC CHARACTERS OBSERVED IN F6 BULKED POPULATION IN TWO BARLEY CROSSES GROWN IN INGHAM AND TUSCOLA COUNTIES

		CROSSES								
		Stewart x Bay						Kindred x Bay		
		Ingham Exp. I			Ingham Exp. II			Exp. III		
No.	Characters	E	1/2 D	Her.%	E	1/2 D	Her.%	E	1/2D	Her.%
1	Date of Heading	1.56	4.91	76%	1.47	7.29	83%			
2	Mildew	28.83	155.35	84%	55.11	220.30	80%	130.27	87.88	40%
3	Lodging	596.53	113.00	16%	52.72	27.96	35%			
4	Height	3.04	2.97	49%	3.88	2.97	40%	1.86	1.01	35%
5	Lodging resistance (cLr)	19349.37	31836.30	62%	16335.00	3341.00	17%	10299	16350	61%
6	Test Weight	15.17	97.49	87%	27.11	33.11	55%	11.27	40.97	78%
7	H. sativum	0.69	0.03	4%	.528	.27	33%	0.45	0.25	36%

Lodging resistance = cLr = $\frac{F}{b}$ where F is equal to force applied

and b is height of the plant.

DISCUSSION

It is evident that the genetic components of variance are composed of additive and non-additive gene effects. In order to support this concept the following approaches to the problem will be discussed:

1. The genetic components of variance as determined from the algebriac model.
2. The genetic components of variance determined from the F_6 bulk yield test.
3. The genetic components of variance as determined from disease reaction and other agronomic characters.

In the algebriac model, the capital letters D for additive effects and H for non-additive effects were used to indicate summation over all loci. The expected genotypes with their frequencies and mean effects were shown from the F_2 to the F_6 generation, this experiment being conducted in F_6. From this model the following two equations were developed, showing the frequency of D and H in the F_6 generation:

$$1/2\ D + 1/1024\ H = \sigma^2 F \quad \text{.....(a)}$$

$$3/8\ D + 6/1024\ H = \sigma^2 F \quad \text{.....(b)}$$

Equation (a) represents the mean square expectation

for genetic effects between the families and equation (b) is the mean square expectation for genetic effects within the families. We have seen that the coefficient of D between families remains constant from generation to generation. The coefficient of D within the families is 3/8. This is equal to 3/4 of the value for between families. In the heterozygous families, the coefficient of H goes down one-half in each subsequent generation and it becomes so low that it can be ignored at the end of F_6 generation. The coefficient of H within families is six times larger than that between families. The reduction in the non-additive effects is an indication that the families are almost homozygous at the end of the F_6 generation. Due to the increase in homozygosity, it is possible to select effectively from the progenies at this stage. Moreover, the values of D and H also facilitate the calculation of the heritability percentages.

With the help of the algebraic model, the components can be divided into additive and non-additive effects in any selected generation. In this report the F_6 yield data was used. The environmental variance was subtracted first from between family mean squares (Table 10). The values of k were determined in Ingham Experiments I and II and Tuscola Experiment III. The value of k is 4.00 in the first two experiments, whereas the value of k in the Tuscola Experiment III is 3.68. The value of k in the latter experiment

is smaller since six fewer families were contained in this test. The heritability values were determined from the following formula:

$$\text{Heritability} = \frac{\sigma^2_F}{\sigma^2 + \sigma^2_F}$$

The heritability for yields are 31, 37 and 32 percent for Ingham Experiments I and II and Tuscola Experiment III respectively, with a mean value of 33 percent. The heritability values in F_6 generations are relatively high, which confirms the viewpoint that selection in F_6 generation will be very effective for yield.

From the anlysis of yield data (Table 10), it may be seen that the F value exceeds the one percent level of significance for differences between families in both crosses in all three experiments.

The estimate of genetic components of variance due to disease and other agronomic characters provide additional heritability estimates.

The amount of mildew recorded indicate statistically significant differences between families (Table 12) in all three experiments, but significant differences did not exist between the different classes (Table 13) when the classes, based on degree of infection, were compared for average yields of seed. This apparently was due to the fact that

the pathogen etc., was not affecting seed yield appreciably.

The anlysis of variance (Table 14) for H. sativum infection shows no statistically significant difference between the families in any of the three experiments; and when these families were grouped into classes of infection and compared for average seed yields, no significant differences were obtained. This indicates that the pathogen had no differential effect on yield.

Five agronomic characters, date of heading, height of plant, percent of lodged plants, lodging resistance (cLr), and smooth versus rough awn, were included which provide estimates of heritability.

Date of heading (Table 16) and height data (Table 18) indicate highly significant differences existing between the families. The families were classified into four groups on the basis of date of heading and average seed yields of each group were compared. No statistically significant difference between these groups was found (Table 17). The height, however, was associated with significant differences in the average yields of the families (Table 19). The taller families tended to produce greater yields of seed.

Significant differences in lodging percent existed between families (Table 20) and within families in the Kindred x Bay cross, but statistically significant differences were not detected in the Stewart x Bay cross. The families

were grouped into four classes on the basis of percentage of lodged plants and these classes were compared for the average yields of seed (Table 21). No significant differences were noted.

It is concluded that lodging did not effect the seed yield. This may be due to the fact that the lodging occurred only shortly before the plants matured and the harvesting methods used permitted the recovery of the lodged as well as the erect plants.

Differences between families were highly significant for lodging resistance (cLr) factor in Ingham Experiment I and Tuscola Experiment III. In Ingham Experiment II, the differences were significant at the 5 percent level.

The average yields of smooth and rough awn families were compared and no significant differences between families existed in the Kindred x Bay cross.

The estimates of heritability in all the disease and agronomic characters are given in Table 24 along with the values of environmental variances and additive genetic effects. The heritability of heading date between families ranges from 76% to 83%, with an average of 84%. In line with Frey's results (20), this high heritability estimate was not unexpected.

The estimates of heritability for mildew indicate a range from 40% to 84%, with a mean of 68% for the three experiments.

Lodging heritability estimates for the two crosses range from 16% to 35%. The contrasting estimates are undoubtedly due to differences in the two crosses. In the Stewart x Bay cross, both parents are relatively stiff strawed. In Kindred x Bay cross, Kindred is a weak-strawed parent and Bay a strong-strawed parent, resulting in a higher genetic variance.

Height data indicates relatively uniform heritability percentages in both the crosses and the range is from 35% to 49%.

The heritability range for lodging resistance is 17% to 62%, with a mean of 48% in both the crosses; whereas, in test weight, the range is 55 to 87 percent, with a mean of 74 percent. The heritability estimates for H. sativum are 18 to 38 percent.

These estimates of heritability are relatively high, and it is possible to make an effective selection in the F_6 generation because homozygosity is approaching a maximum. Delay later than this undoubtedly would be a waste of time on the part of the plant breeder.

CONCLUSIONS

In all segregating generations the additive genetic fractions remain one-half and the non-additive genetic fraction between families is halved in each succeeding generation. The non-additive genetic fractions in the F_6 generation approach zero. From this it is concluded that with the reduction of non-additive genetic fraction the homozygosity in F_6 has reached a practical maximum.

The heritability percentages for yield data are 31, 37 and 32 for the three reported experiments. These values are relatively high and suggest that selection for yield is most effective in F_6 generation.

From powdery mildew data it can be concluded that the pathogen was affecting the seed yields in all families the same. There was not a high type of resistance as a large proportion of the families had more than 25 percent infection.

H. sativum infection did not produce differential effects on the average seed yields of the families.

There was no effect of date of heading on the average yield of the families. However, the height seems to be associated with yield, as taller families produced greater yields.

Seed yields of different families were not affected by the lodging which occurred in this experiment.

No differences in yield were noted which might have been associated with rough or smooth awn character.

The heritability values of these disease reaction and agronomic characters confirm the viewpoint reached for heritability of yield; namely, that by the F_6 generation, genetic gain from selection will be approaching a maximum.

SUMMARY

To conduct yield trials in the F_6 generation, twenty bulked families from two barley crosses, Stewart x Bay and Kindred x Bay, were selected in the F_4 generation. Eighteen F_4 seeds were taken at random from each of the 40 F_3 bulked rows increased for two generations in the green house in 1952 and the field in 1953. The pedigrees of families and sub-families were maintained.

Three experiments, two in Ingham County and one in Tuscola County, were conducted. The tests were on a single, four-row plot basis in a lattice design.

Environmental error was calculated from the parental checks. The following characters were studied in addition to yield: powdery mildew, spot blotch, date of heading, height of plant, percent of lodged plants, lodging resistance, and awn type. The effect of each of these characters on seed yield of families was studied.

An algebraic model for the estimation of σ^2_F and σ^2_W was included. The heritability values from seed yield and other characters were calculated from the following formula.

$$\text{Heritability} = \frac{\sigma^2_F}{\sigma^2 + \sigma^2_F} \times 100.$$

These heritability percentages for yield and other characters were relatively high and indicated that effective selection can be practiced in the F_6 generation.

LITERATURE CITED

1. Atkins, I. M. Relation of certain plant characters to strength of straw and lodging in winter wheat. Jour. Agr. Res. 56: 99-120. 1938.

2. Atkins, I. M. Inheritance of straw strength per unit length of culm and other characters in Kanred x Coppei wheat. Jour. Agr. Res. 76: 53-72. 1948.

3. Atkins, R. E. and H. C. Murphy. Evaluation of yield potentialities of oat crosses from bulk hybrid tests. Agron. Jour. 41: 41-45. 1949.

4. Bakke, A. L. The late blight of barley (Helminthosporium teres sacc). Proc. Iowa Acad. Sci. 19: 93-102. 1912.

5. Bose, R. D., M. A. Aziz, and M. P. Bhatnagar. The inheritance of some anatomical characters responsible for lodging and some ear head characters in an interspecific cross between two pusa barleys. Ind. Jour. Agr. Sci. 7: 48-88. 1937.

6. Briggs, N. F. The inheritance of resistance of mildew. Am. Nat. 72: 34-41. 1938.

7. Brown, A. R. and J. H. Miller. A comparative study of Helminthosporium sativum Pam, King and Bakke and H. victoriae Meehan and Murphy on oats. Agron. Jour. 46: 63-68. 1954.

8. Charles, D. R. and H. H. Smith. Distinguishing between two types of gene action in quantitative inheritance. Genetics 24: 34-38. 1939.

9. Christensen, J. J. Studies in the parasitism of H. sativum. Minn. Agr. Expt. Sta. Tech. Bul. 11: 42-pp. 1922.

10. Clark, R. E. and H. K. Wilson. Lodging in all grains. Jour. Amer. Soc. Agron. 25: 561-572. 1933.

11. Cochran, W. G. Long term agricultural experiments. Jour. Roy. Stat. Soc. Supp. 6: 104-148. 1949.

12. Comstock, R. E. and H. E. Robinson. The components of genetic variance in population of bi-parental progenies and their use in estimating the average degree of dominance. Biometrics 4: 254-266. 1948.

13. Comstock, R. E., H. E. Robinson and P. H. Harvey. A breeding procedure designed to make maximum use of both general and specific combining ability. Agron. Jour. 41: 360-367. 1949.

14. Crump, S. L. The estimation of variance components in anlysis of variance. Biometrics Bul. 2: 7-11. 1946.

15. East, E. M. Studies on size inheritance in Nicotiana. Genetics 1: 164-176. 1916.

16. Fisher, R. A. The correlation among relatives on the supposition of Mendelian inheritance. Trans. Royal Soc. Edinburgh. LII: 399-433. 1918.

17. Fisher, R. A. Statistical methods for research workers. Oliver and Boyd, Edinburgh (1925-1944).

18. Fisher, R. A., F. R. Immer, and O. Tedin. The genetical interpretation of statistics of the third degree in the study of quantitative inheritance. Genetics 17: 107-124. 1932.

19. Florell, V. H. Studies on the inheritance of earliness in wheat. Jour. Agr. Res. 29: 333-347. 1924.

20. Frey, K. J. Inheritance and heritability of heading date in barley. Agron. Jour. 46: 226-228. 1954.

21. Garber, R. J. and P. J. Olson. A study of the relationship of some morphological characters to lodging in cereals. Jour. Amer. Soc. Agron. 11: 173-186. 1919.

22. Grafius, J. E. A statistical model for estimating components of genetic variance in bulk yield tests of self pollinated small grains. South Dak. Agr. Exp. St. Tech. Bul. No 9. 1952.

23. Grafius, J. E., and H. M. Brown. Lodging resistance in oats. Agron. Jour. 46: 414-418. 1954.

24. Grafius, J. E., W. L. Nelson and V. A. Dirks. The heritability of yield in barley as measured by early generation bulked progenies. Agron. Jour. 44: 253-257. 1952.

25. Griffee, F. Correlated inheritance of botanical characters in barley and manner of reaction to H. sativum. Jour. Agr. Res. 15: 915-935. 1925.

26. Griffing, J. B. Statistical analysis of gene action in components of tomato yield.

Unpublished PH.D. thesis. Iowa State College Library, Ames, Iowa. 1948.

27. Harlan, H. V., M. L. Martini and S. A. Harland. A study of method in barley breeding. U.S.D.A. Tech. Bul. No 720. 1940.

28. Harrington, J. B. Predicting the value of a cross from an F_2 analysis. Can. Jour. Res. 6: 21-37. 1932.

29. Harrington, J. B. Yielding capacity of wheat crosses as indicated by bulk hybrid tests. Can. Jour. Res. 18: 578-584. 1940.

30. Hayes, H. K., E. C. Stakeman, F. Griffee and J. J. Christensen. Reaction of barley varieties to Helminthosporium sativum. Minn. Agr. Expt. Sta. Tech. Bul. 21: 47 pp. 1923.

31. Hehn, E. The inheritance of agronomic characters in barley. Unpublished PH. D. thesis. 1952. Iowa State College Library. Ames, Iowa.

32. Hor-Kven, S. Interaction of genetic factors in barley. Genetics 9: 151-180. 1924.

33. Hull, H. Recurrent selection for specific combining ability in corn. Jour. Am. Soc. Agron. 37: 134-145. 1945.

34. Immer, F. R. Relation between yielding ability and homozygosis in barley crosses. Jour. Amer. Soc. Agron. 33: 200-206. 1941.

35. Immer, F. R. Relation between yielding ability and homozygosis in barley crosses. Jour. Amer. Soc. Agron. 34: 844-850. 1942.

36. Jenkins, M. T. The segregation of genes affecting yield of grain in maize. Jour. Amer. Soc. Agron. 32: 55-63. 1940.

37. Johannson, W. Elemente der exakten Erbbehkestslehre gene. Gustav. Fisher. 1909.

38. Kalton, R. R. Breeding behavior at successive generations following hybridization in soybeans. Iowa Expt. Sta. Res. Bul. 358. 1948.

39. Lerner, J. Population genetics and animal improvement. Cambridge at the Uni. Press. 1950.

40. Love, H. H. A program for selecting and testing small grains in successive generations following hybridization. Jour. Amer. Soc. Agron. 19: 705-712. 1927.

41. Lush, J. L. Animal breeding plans. The Collegiate Press Inc. Ames, Iowa. 2nd Edition pp 76-79. 1943.

42. Lush, J. L. Heritability of quantitative characters in farm animals. Proc. Eighth. Int. Cong. Gene. 1948. Hereditas Suppl. Vol. 356-375. 1949.

43. Lush, J. L. and V. G. Panse. The inheritance of quantitative characters and plant breeding. Jour. Genetics. 40: 283-302. 1940.

44. Luttrell, E. S. A comparison of H. sativum and H. victoriae (Abs) Phytopath. 42: 469-475. 1952.

45. Mains, E. B. and M. L. Martini. Susceptibility of barley to leaf rust (Puccinia anomal) and to powdery mildew (Erisiphe graminis hordei)

46. Martin, G. W., C. R. Weber and R. R. Kalton. Early generation testing in soybeans. Amer. Soc. Agron. 39: 791-812. 1947.

47. Mather, K. Biometrical genetics. London. Methuen & Co. 162 pp. 1949.

48. Meehan, F. and H. C. Murphy. A new Helminthosporium blight of oats. Science, 104: 413-414. 1946.

49. Murphy, H. C. and F. Meehan. Reaction of oat varieties to a new species of Helminthosporium. Phytopath. 36: 407 pp. 1946.

50. Muhmud, Imam and H. H. Kramer. Segregation for yield, height and maturity following a soybean cross. Agron. Jour. 43: 605-609. 1951.

51. Myler, J. L. Awn inheritance in barley. Jour. Agr. Res. 65: 405-512. 1942.

52. Neatby, K. W. Inheritance of quantitative and other characters in barley crosses. Sci. Agr. 7: 77-84. 1926.

53. Neatby, K. W. An anlysis of quantitative characters and linkage in barley. Sci. Agr. 6: 701-718. 1926.

54. Neatby, K. W. An analysis of the inheritance of quantitative characters and linkage in barley. Sci. Agr. 9: 701-717. 1929.

55. Newton, Margaret and W. J. Cherewick. Erysiphe graminis in Canada. Can. Jour. Res. (C) 25: 73-93. 1947.

56. Pammel, L. H. Wheat blight and browning of barley. Breeders' Gazette. 56-155. 1909.

57. Pammel, L. H., C. M. King and A. L. Bakke. Two barley blight with a comparison of species of Helminthosporium upon cereals. Iowa Agr. Exp. Sta. Bul. 116. 1910.

58. Panse, V. G. Application of genetics to plant breeding. Jour. Genetics 40: 283-302. 1940.

59. Powers, Leroy. The nature of the series of environmental variances and the estimation of the genetic variance and the geometric means of crosses involving species of Lycopersicon. Genetics 27: 561-575. 1942.

60. Powers, Leroy, L. F. Locke and J. C. Garrett. Partitioning method of genetic analysis applied to quantitative characters of tomato crosses. U.S.D.A. Tech. Bul. 998. 56 pp. 1950.

61. Ramiah, K. and S. Dharmalingam. Lodging of straw and its inheritance in rice. Indian Jour. Agr. Science 4: 880-894. 1934.

62. Ray, D. A., T. T. Herbert and G. K. Middleton. Inheritance of resistance to powdery mildew in wheat. Agron. Jour. 46: 379-383. 1954.

63. Robertson, D. W. Linkage studies in barley. Genetics 14: 1-36. 1929.

64. Robertson, D. W., G. A. Wiebe and F. R. Immer. A summary of of linkage studies in barley. Jour. Amer. Soc. Agron. 33: 47-64. 1941.

65. Robertson, D. W., G. A. Wiebe and F. R. Immer. A summary of linkage studies in barley. Supp. I 1940-1946. Jour. Amer. Soc. Agron. 39: 464-473. 1947.

66. Robinson, H. F., R. E. Comstock and P. M. Harvey. Estimates of heritability and the degree of dominance in corn. Agron. Jour. 41: 353-359. 1949.

67. Satterthwaite, F. E. An approximate distribution of variance components. Biometrics Bul. 2: 110-114. 1946.

68. Sprague, G. F. and A. A. Bryan. The segregation of genes affecting yield, prepotency, lodging and disease resistance in F_3 lines of corn. Jour. Amer. Soc. Agron. 33: 207-214. 1941.

69. Sprague, G. F., L. A. Tatum. General V/S specific combining ability in single crosses of corn. Jour. Amer. Soc. Agron. 34: 923-932. 1942.

70. Sprague, G. F. Early testing of inbred lines of corn. Jour. Amer. Soc. Agron. 38: 108-117. 1946.

71. Snedecor, G. W. Statistical methods. Ames, Iowa. The Collegiate Press Inc. Ed. 4. 1946.

72. Stanford, H. E. and N. F. Briggs. Two additional factors for resistance to mildew in barley. Jour. Agr. Res. 61: 231-236. 1940.

73. Suneson, C. A. and G. A. Wiebe. Survival of barley and wheat varieties in mixtures. Jour. Amer. Soc. Agron. 34: 1052-1056. 1942.

74. Weaver, J. C. American barley production. Burgess Publishing Co. Minneapolis. 1950.

75. Weber, C. R. Inheritance and interaction of some agronomic and chemical characters in an interspecific cross in soybeans. Glycine max X G. ussuriensis. Iowa Agr. Expt. Sta. Res. Bul. 374: 765-816. 1950.

76. Weber, C. R. and B. R. Moorthy. Heritable and nonheritable relationships and variability of oil content and agronomic characters in the F_2 generation of soybean crosses. Agron. Jour. 44: 202-209. 1952.

77. Weiss, M. G., C. R. Weber and R. R. Kalton. Early generation testing in soybeans. Jour. Amer. Soc. Agron. 39: 791-811. 1947.

78. Wexelsen, H. Quantitative inheritance and linkage in barley. Hereditas 18: 307-348. 1933.

79. Wright, Sewall. The analysis of variance and correlations between relatives with respect to deviations from an optimum. Jour. Genetics. 30: 243-256. 1935.

80. Yates, F. and I. Zacopanay. The estimation of the efficiency of sampling for yield in cereal experiment. Jour. Agr. Sci. 25: 545-577. 1935.

81. Youden, W. J. and A. Mehlich. Selection of efficient methods for soil sampling. Contributions from Boyce Thompson Institute 9: 59-70. 1937.