# INHERITANCE OF LODGING RESISTANCE
# IN CERTAIN OAT CROSSES

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Donald Alsop Wheeler

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# IN CERTAIN OAT CROSSES

By

Donald Alsop Wheeler

AN ABSTRACT

Submitted to the College of Agriculture of Michigan
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# INHERITANCE OF LODGING RESISTANCE IN CERTAIN OAT CROSSES

Genetically weak straw is one of the common causes of lodging in small grains. The inheritance of lodging resistance and lodging susceptibility in oats was studied in the hope of finding a practical method of improving lodging resistance.

The parents used were, from strongest to weakest, Craigs Afterlea, Clintland, Craig, and A587-10. Most of the possible combinations of these parents were obtained. Only seeds of Clintland x Craig, Clintland x A587-10, and A587-10 x Craigs Afterlea survived an excessive disinfectant treatment. The three $F_1$'s were grown in the greenhouse. The $F_2$'s were also grown in the greenhouse. The parents, the $F_2$'s, and the $F_3$'s of each cross were grown together in the field. Readings were made when the plants were in the soft dough stage. Following the method described by Grafius and Brown in the Agronomy Journal 46: 414-418, a chain of known weight was hung from the base of a panicle of each plant to determine resistance of the culm to external torque.

The distributions of the observations were skewed in the direction of lodging susceptibility. There was no reduction in skewness in the $F_3$, which indicated a problem in scaling. When natural logarithms of the data were used, the distributions approached much more closely to a normal distribution. Dominance relations were assessed by comparing $F_2$ and $F_3$ means to the mid-parent. Lodging resistance was dominant in the cross Clintland x Craig. Lodging susceptibility was dominant in the crosses Clintland x A587-10 and A587-10 x Craigs Afterlea.

Variations in the $F_2$ and the $F_3$ were separated, using the method proposed by Mather in <u>Biometrical Genetics</u> (Dover Publications Inc., New York, 1949), into heritable and non-heritable portions. The heritable variation was further divided into fixable genetic and non-fixable genetic components. These components of variation were calculated both from the observed numbers of links of chain supported and from the natural logarithms of these observations. Little fixable genetic variance could be demonstrated in the cross Clintland x A587-10. In the other two crosses the use of logarithms increased the proportion of fixable genetic variance. In these two crosses the fixable genetic variance calculated from the $F_2$ plant readings was approximately 15 per cent while that calculated from the $F_3$ means was approximately 35 per cent.

Selection for lodging resistance prior to the $F_3$ generation seems likely to be on the basis of non-fixable differences. Selection based on means of $F_3$ families utilized more fixable variation and seemed to be a good start toward isolating superior lines.

Logarithms were valuable in determining the effectiveness of selection in this study. Logarithms did not change the order of the data; therefore selection can be on the basis of the original measurements.

Lodging resistance was defined by Grafius and Brown as a ratio of torque resistance to height. When either factor is held constant a change in the other will change the lodging resistance. Selection for lodging resistance should be only on plants of similar heights. The quickest advances by hybridization would be made by crossing strong plants of the same height.

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# INTRODUCTION

Lodging of small grains is a problem of widespread occurrence on soils high in fertility. Lodging often occurs in low areas of a field, on fields receiving large amounts of nitrogen fertilizer, and on muck areas. The immediate cause of lodging is generally a windstorm accompanied by rain which pushes the plants over. Indirect or contributing causes include high fertility, high soil moisture, lack of sufficient light, high temperatures, and genetically weak straw. Grain which has lodged is difficult to harvest and losses in harvesting are increased. Often the yield and quality of the crop are lessened. The stage of development of the plant at the time of lodging determines the degree of damage.

Several common oat varieties have genetically weak straw, therefore they often lodge badly when grown on rich soil. It is desired that high-yielding varieties with genetically strong straw be obtained. In order to accomplish this it is desirable to understand the inheritance of the character. The aim of this study was to determine the method of inheritance of lodging susceptibility versus lodging resistance in oats. A further purpose was to ascertain whether lodging resistance could be improved by the ordinary oat breeding method of crossing and selecting within the segregating generations.

## REVIEW OF LITERATURE

Pendleton (8)* found that 90 degree lodging at heading time caused reduction in yield to 63 per cent of that of erect plants and a reduction in test weight to 79 per cent. The yield was reduced to about 85 per cent by 45 degree lodging at heading time or by 90 degree lodging 20 days after heading. Thus the time when lodging occurred determined its effect on yield.

Several methods have been proposed for measuring differences between strains in respect to lodging or lodging resistance. The standard method is to observe a nursery where lodging has occurred and to make notes of the percentage of plants not standing erect in each plot and to note the approximate number of degrees by which they depart from the vertical. This method can be used only on plots where lodging has already occurred.

The breaking strength of the straw has been used as a measure of lodging resistance. Several machines have been developed to measure breaking strength of straw. One type of machine was that described by Helmick (6).

* Numbers in parentheses refer to the "Literature Cited."

In this device a bucket was suspended from the straw and shot was added to the bucket until the total weight was enough to break the straw. The instrument described by Salmon (10) measured the pressure required to break the straw. In this case the pressure was applied from above; but the results of the machines were comparable. Atkins (2) stated that while lodging was not significantly correlated with breaking strength of straw at one station in one year, the two were highly correlated when considered over several stations in several years. Atkins (2) also found a high correlation coefficient between breaking strength of straw and weight per unit length of culm at the base of the plant. He advocated use of the latter measurement as being quicker.

Breaking strength of straw was only one factor contributing to lodging resistance. In view of this fact there have been recent attempts to find a more inclusive method of measuring lodging resistance. Hamilton (5) gave a lodging index based on a discriminate function whereby the relative value of root type, diameter of culm, and height were assessed. This function was approximately the sum of ten times the diameter of the culm in the second internode above the ground, less five times the root type on a scale of one to ten as given, less the height of the plant in inches.

Grafius and Brown (4) gave the definition of lodging as the extent of response to torque caused by external force. In order to determine this response, they hooked a chain to the base of the panicle and observed how many links of the chain were supported when the culm bent to an equilibrium point. They derived a formula for lodging resistance: $cLr = \frac{F}{b}$, where F, the force applied, was the grams of chain supported, b was the height of the plant to the base of the panicle, and c was a proportionality constant to convert b into a force, based on the assumption that external force would be roughly proportional to plant height.

Inheritance of lodging resistance in small grains was governed by many genetic factors in most cases. Ramiah and Dharmalingham (9) reported one case of single-factor inheritance of lodging versus non-lodging in rice, with the lodging factor dominant. Atkins (1), found that the character of weight per unit length was transmitted from a parent to its progeny. He cited correlation coefficients of .609 between $F_2$ and means of its $F_3$ progeny lines and of .623 between $F_3$ and means of its $F_4$ progeny lines.

## MATERIALS AND METHODS

Four parents were chosen for this study on the basis of past lodging history. Two were commercial oat varieties, Clintland and Craig. Of these, Clintland was more resistant to lodging. A third parent was the experimental strain A587-10 which was very susceptible to lodging. The fourth parent was the variety Craigs Afterlea, a very strong oat from Scotland.

Crossing was done in the field in the summer of 1954. Crosses were attempted among the four parents in all combinations. Several seeds were obtained as the result of crossing; however, most of them were killed by an overdose of fungicide and consequently only three $F_1$ plants were obtained. These three plants were from the following crosses: Clintland x Craig, Clintland x A587-10, and A587-10 x Craigs Afterlea.

The three $F_1$ seedlings were started in three-inch pots and then were transplanted into ten-inch pots filled with soil. These plants continued to grow in the greenhouse throughout the fall and winter of 1954-55. The pots were watered daily and were supplied with a complete nutrient solution at about ten-day intervals. Incandescent lights were used to maintain a day length of at least twelve hours throughout the winter and also for supplementary light on cloudy days. Under these treatments the $F_1$ plants continued to tiller from October until March. Each plant produced 25 to 50 culms. As each head ripened, it was cut from the plant. In early February all the seeds which had ripened thus far were planted in rows on the greenhouse bench in a mixture of sand and soil. Water and nutrient solution were applied as to the $F_1$ plants. This planting was made a little later than desirable, so, in order to mature seeds quickly, the $F_2$ plants were supplied with continuous illumination. The seeds borne later by the $F_1$ plants; that is, $F_2$ seeds and the seeds borne by the $F_2$ plants; that is, $F_3$ seeds were harvested for planting in the field.

The $F_2$'s, the $F_3$'s, and the parental varieties were planted in the field in the spring of 1955. The rows were two feet apart with plants three inches apart in the row. The three crosses were planted in separate, adjoining areas. The progeny of each $F_2$ plant was planted together. These $F_3$ families averaged about eight members. The $F_2$ seeds were divided into groups of ten and these were randomized among the $F_3$ families with a restriction of one $F_2$

group to each three to six $F_3$ families, depending on the ratio of seed available of the particular cross. The parents, in groups of eight, were planted with the progeny at eight row intervals. Clintland was planted as a uniform check variety throughout the area. Each other parent was planted, in alternate check rows, in the area with its progeny.

Lodging resistance readings were made when the plants were in the soft dough stage. The method used was that described by Grafius and Brown (4). The culms to be used were visually selected to be at the same stage of maturity. Some plants from seed which germinated slowly were so badly affected by red leaf that they produced only one culm; these were not studied. Neither were readings made on the few plants which had previously lodged. One culm of each plant was selected for study. The height to the base of the panicle was measured. A chain was attached to the base of the panicle by means of a hook. The weight of the chain caused the culm to bend over and the excess links of chain piled up on the ground. When the culm ceased bending the number of links of chain still being supported was determined. Figures 1 to 3 illustrate the differences that were shown by this method. In Figure 1, the chain attached to Craigs Afterlea caused it to bend only slightly from the vertical. The opposite extreme is illustrated in Figure 2. Here the plant has lodged from the base and is supporting very little weight. The most common reaction was between these extremes, as exemplified by Figure 3.

Figure 1. Chain attached to lodging resistant plant.

Figure 2. Chain attached to lodging susceptible plant.

Figure 3. Chain attached to plant showing typical lodging reaction.

# THE COMPONENTS OF VARIATION

Variation in a biometrical experiment, according to Mather (7), can be partitioned into three components. The first is non-heritable variation resulting from the action of environmental factors. The second portion of variation is due to differences in character expression between homozygotes for each gene pair involved. Heritable variation between true breeding strains is of this kind and in this sense such variation may be described as fixable. The third component of variation is comprised of differences between the expression of heterozygotes and the average of the corresponding homozygotes. Such variation may be described as unfixable in that it cannot be utilized in the selection of true breeding strains.

Fisher, Immer, and Tedin (3) developed a method of determining the contributions of each gene to the fixable and unfixable components of variation. Following the designation of these authors, let the average effects on the character in question due to the three genotypes for gene A-a[*] be:

$AA = d_a$ $\qquad$ $BB = d_b$

$Aa = h_a$ , $\qquad$ for B-b: $Bb = h_b$ , and so on.

$aa = -d_a$ $\qquad$ $bb = -d_b$

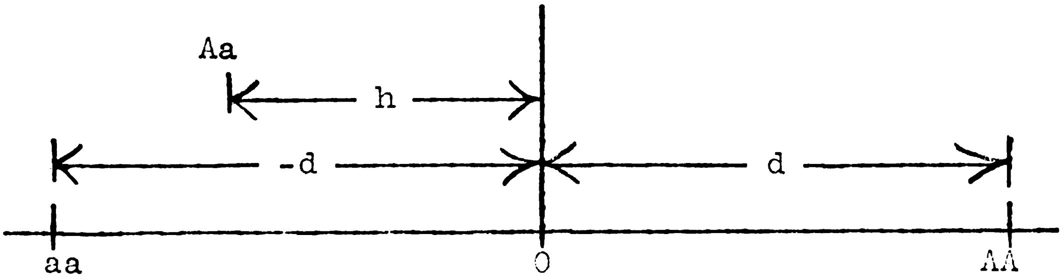

Figure 4. The d and h increments of the gene A-a. (after Mather)

Figure 4 represents the d and h increments of the gene pair Aa. The zero point is chosen mid-way between the homozygotes. Then d represents an increment in a constant direction along the scale of measurements, while h may be an increment in either direction.

The variation of the measurements of true breeding parents and of their $F_1$ is exclusively non-heritable. Therefore the variances of these measurements give estimates of the non-heritable portion of the variances of the $F_2$ and later generations. The heritable portion of

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[*] The A-a designation of allelomorphs here does not carry the conventional implication of dominance.

the variance of one of the later generations is the sum of the contributions due to the individual gene pairs providing that there is no linkage and no interaction of non-allelic genes.

In respect to any one segregating gene pair A-a, the $F_2$ is: $\frac{1}{4}$AA; $\frac{1}{2}$Aa; $\frac{1}{4}$aa. The mean measurement of $F_2$, expressed as a deviation from the mid-parent, for this locus, is $\frac{1}{4}d_a - \frac{1}{2}h_a - \frac{1}{4}(-d_a) = \frac{1}{2}h_a$. The contribution of A-a to the sum of squares of deviations from the mid-parent is $\frac{1}{4}d_a^2 - \frac{1}{2}h_a^2 - \frac{1}{4}(-d_a)^2$. Then the contribution to the sums of squares of deviations from the $F_2$ mean is $\frac{1}{2}d_a^2 - \frac{1}{2}h_a^2 - (\frac{1}{2}h_a)^2$ or $\frac{1}{2}d_a^2 - \frac{1}{4}h_a^2$. Summing over all genes contributing to the character being considered, total heritable variance in $F_2$ is $\frac{1}{2}S(d_a^2) - \frac{1}{4}S(h_a^2)$.

The $F_3$ families derived from $F_2$ individuals of the genotypes AA and aa contribute $d_a$ and $-d_a$ respectively to the $F_3$ means. One-half of the $F_3$ families are from $F_2$ individuals of the genotype Aa and in these families segregation is occurring in the same ratio as in the $F_2$, giving contributions of $\frac{1}{4}d_a - \frac{1}{2}h_a - \frac{1}{4}(-d_a) = \frac{1}{2}h_a$ to the mean.. Thus taking frequencies into account, the mean of $F_3$ means is $\frac{1}{4}h_a$ from the mid-parent. The variance of $F_3$ means is $\frac{1}{4}d_a^2 - \frac{1}{2}(\frac{1}{2}h_a)^2 - \frac{1}{4}(-d_a)^2 - (\frac{1}{4}h_a)^2$ or $\frac{1}{2}d_a^2 - h_a^2$

and, summing, the total heritable variance of $F_3$ means is $\frac{1}{2}S(d_a{}^2) + \frac{1}{16}S(h_a{}^2)$.

The variance of $F_3$ families can be represented by $\frac{1}{4}0 + \frac{1}{2}(\frac{1}{2}d_a{}^2 + \frac{1}{4}h_a{}^2) + \frac{1}{4}0 = \frac{1}{4}d_a{}^2 + \frac{1}{8}h_a{}^2$ since only the families derived from A-a individuals are segregating. Summing, the mean variance of $F_3$ families is $\frac{1}{4}S(d_a{}^2) + \frac{1}{8}S(h_a{}^2)$.

In each case, these formulae contain a part $S(d_a{}^2)$ due to fixable variation and a part $S(h_a{}^2)$ contributed by non fixable variation. Denoting these by D and H respectively, and remembering that observed variances also contain a non-heritable portion, we have the equations given in Table 1.

Table 1: Components of Variation in $F_2$ and $F_3$

| | | |
|---|---|---|
| $V_{F_2}$ | $F_2$ variance | $1/2\ D + 1/4\ H + E_1$ |
| $V_{\overline{F_3}}$ | Variance of means of $F_3$ families | $1/2\ D + 1/16\ H + E_2$ |
| $\overline{V}_{F_3}$ | Mean variance of $F_3$ families | $1/4\ D + 1/8\ H + E_1$ |

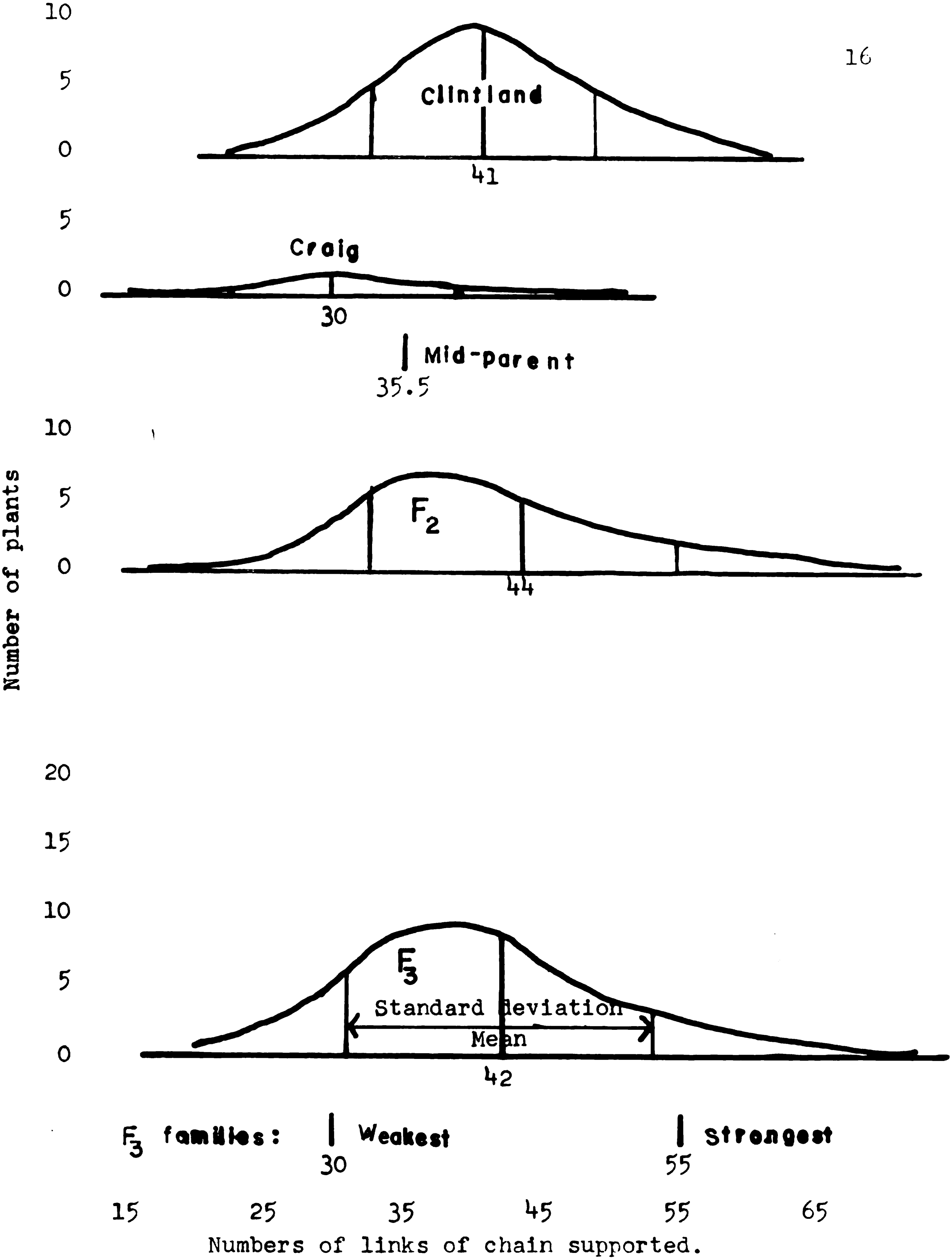

Figure 5. Frequency distribution based on number of links of chain supported for parents, $F_2$, and $F_3$ of Clintland x Craig cross.

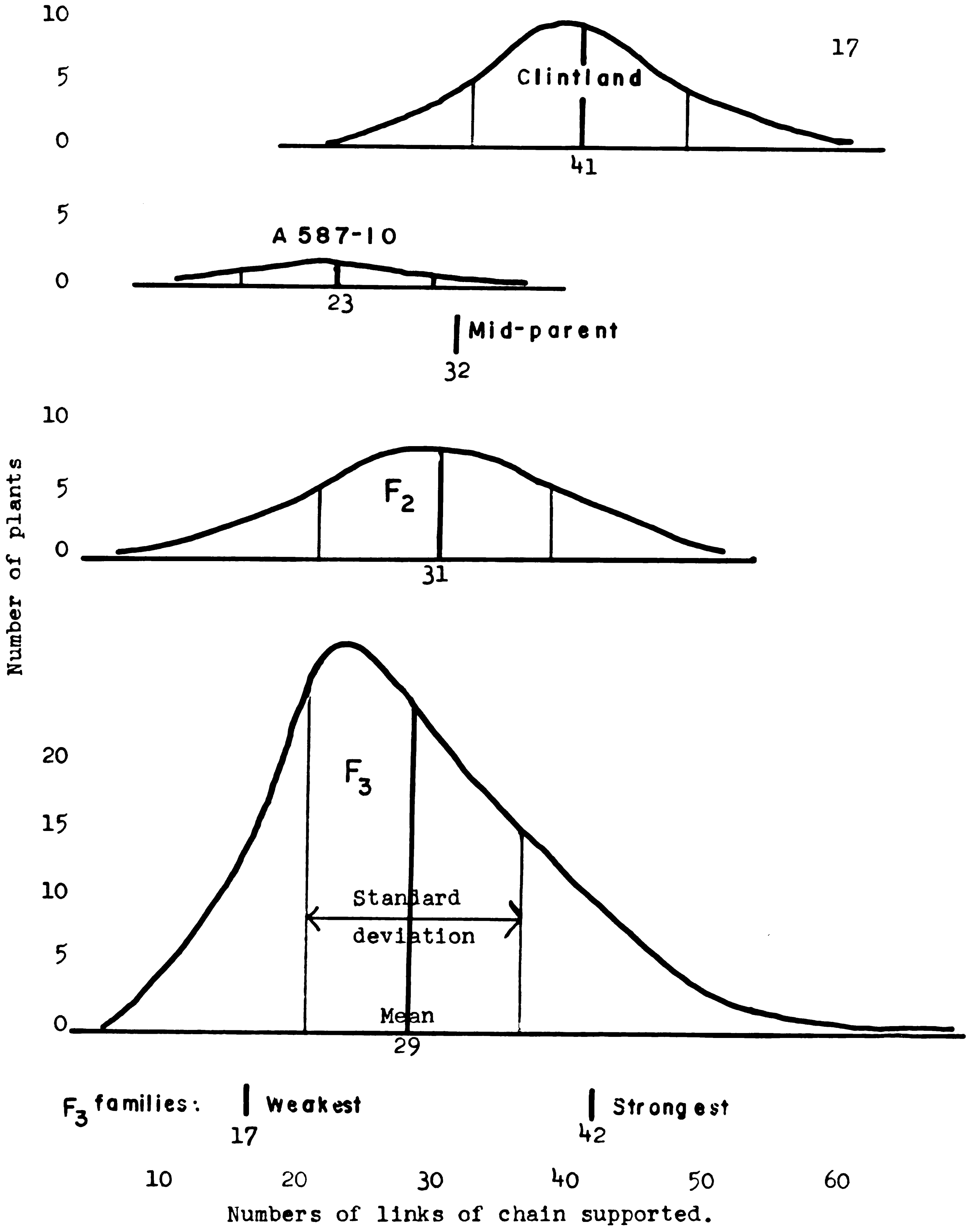

Figure 6. Frequency distribution based on number of links of chain supported for parents, $F_2$, and $F_3$ of Clintland X A587-10 cross.

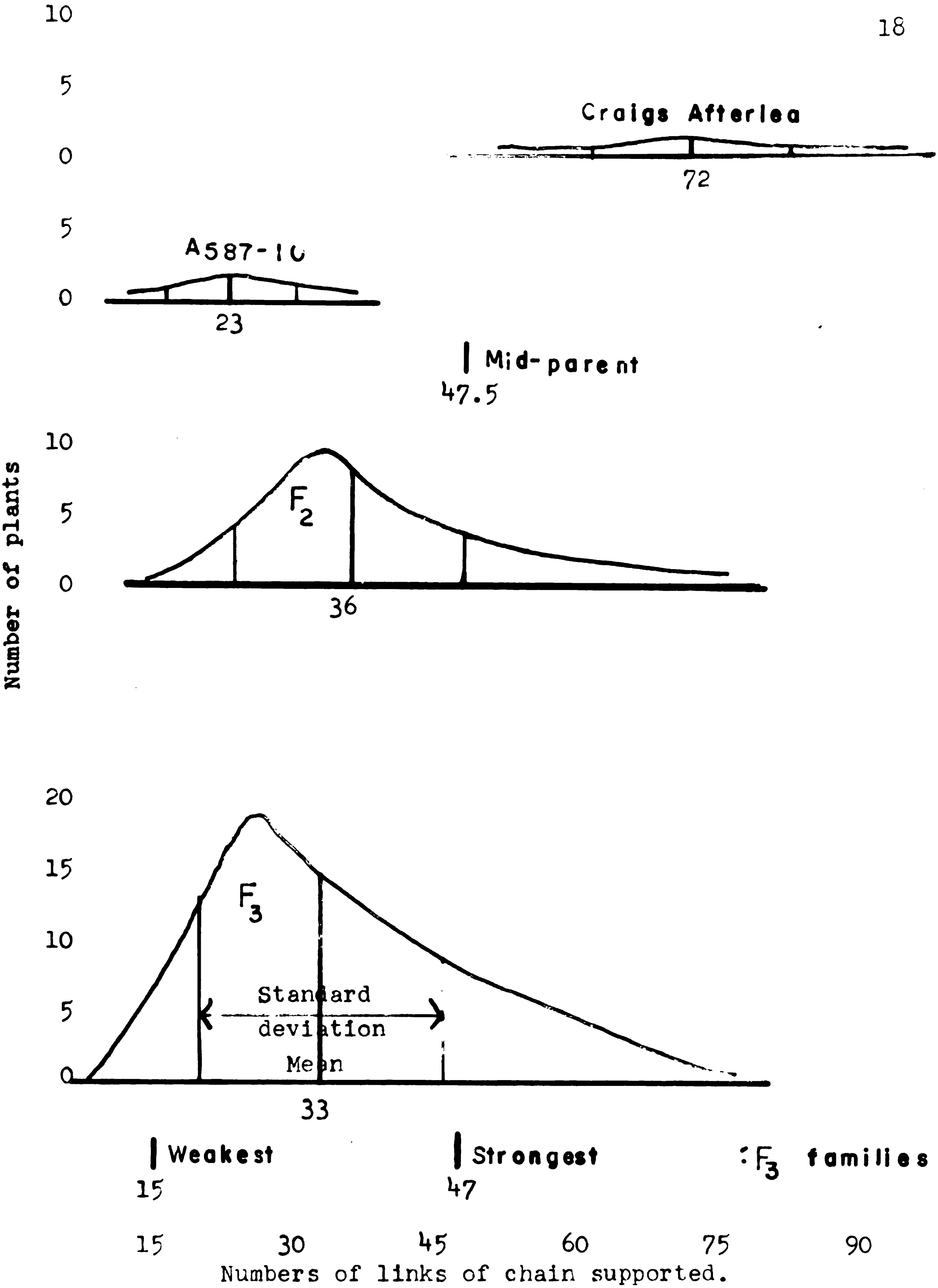

Figure 7. Frequency distribution based on number of links of chain supported for parents, $F_2$, and $F_3$ of A 587-10 x Craigs Afterlea cross.

# RESULTS

Figures 5, 6, and 7 show the means, standard deviations, ranges, and approximate distributions of the observed values for the number of links supported in these three crosses. Most of the original curves appear to be skewed toward the low side. In order to eliminate this condition a transformation of the data might be useful. The taking of logarithms would tend to shorten the upper end of the scale; therefore this would be a good transformation. In accordance with these considerations, natural logarithms of the data were taken and several statistics were computed from both the original data and the data transformed to logarithms. Table 2 presents the number of plants and also the means and standard deviation for each generation of each cross. The transformation to logarithms has reduced the coefficient of variability (the standard deviation expressed as a percentage of the mean) for each of the generations.

In order to find the components of variation several variances were required. Variances were computed for the $F_2$, means of $F_3$ families, and mean variance of $F_3$ families in each segregating population. Each of these variances

Table 2. Number of plants, means, and standard deviations for parents and progenies

| Variety or generation | No. of groups or families | Mean no. of individuals per group | No. of links supported: Mean | No. of links supported: Standard deviation | No. of links supported: Coefficient of variability | Natural logarithms of no. of links supported: Mean | Natural logarithms of no. of links supported: Standard deviation | Natural logarithms of no. of links supported: Coefficient of variability |
|---|---|---|---|---|---|---|---|---|
| Clintland | 21 | 6.9 | 41.1 | 8.2 | 20.0% | 3.69 | 0.21 | 5.7% |
| Craig | 4 | 6.3 | 29.7 | 9.1 | 30.6 | 3.35 | 0.09 | 2.7 |
| A587-10 | 4 | 6.0 | 23.1 | 7.1 | 30.8 | 3.09 | 0.11 | 3.4 |
| Craigs Afterlea | (3) | 5.7 | 71.8 | 10.6 | 14.8 | 4.26 | 0.15 | 3.5 |
| Clintland x Craig: $F_2$ | 14 | 8.1 | 43.8 | 11.0 | | 3.75 | 0.26 | |
| Clintland x Craig: $F_3$ | 21 | 6.4 | 41.9 | 11.0 | | 3.71 | 0.16 | |
| Clintland x A587-10: $F_2$ | 18 | 5.6 | 30.6 | 8.6 | | 3.31 | 0.31 | |
| Clintland x A587-10: $F_3$ | 59 | 7.9 | 28.9 | 8.2 | | 3.28 | 0.19 | |
| A587-10 x Craigs Afterlea: $F_2$ | 25 | 7.4 | 35.6 | 13.0 | | 3.51 | 0.37 | |
| A587-10 x Craigs Afterlea: $F_3$ | 63 | 7.4 | 33.3 | 13.5 | | 3.43 | 0.23 | |

contained a non-heritable component. Since the parental groups, $F_2$ groups, and $F_3$ groups were of approximately the same sizes, the variance within parental groups can be taken as an approximation of the non-heritable component in $F_2$ and $F_3$ variances. The non-heritable component of the variance of $F_3$ means can be estimated from the variance of parental group means.

Many of the $F_3$ families contained only a few plants. In order to obtain a fairly good sample of the potential of a particular family, only families consisting of five or more members were considered in calculating $F_3$ variances. It would be desirable to have larger families, but, if a larger number had been required, the Clintland x Craig cross would have been eliminated from the study. This same requirement of five members per group was applied to the parents in determining the estimates of error variances. Since the parental variety Craigs Afterlea was badly damaged by red leaf disease, only two groups were usable. This was too few, so Craigs Afterlea was not considered in determining the error variances. In its place, a pooling of the variances of the other three parents was used. In the crosses involving Clintland the estimates of error were obtained by pooling the variances of the two parents.

## Clintland x Craig

The variances calculated from the original data on the number of links supported in the segregating cross, Clintland x Craig, are as given in the following five equations.

$$V_{F_2} = 1/2\ D + 1/4\ H + E_1 = 121.9$$

$$V_{\overline{F_3}} = 1/2\ D + 1/16\ H + E_2 = 43.6$$

$$\overline{V}_{F_3} = 1/4\ D + 1/8\ H + E_1 = 93.4$$

$$V \text{ within parental groups} = E_1 = 47.7$$

$$V \text{ parental group means} = E_2 = 22.0$$

The first step in obtaining the least squares estimates of the four components of variation was to multiply through each equation by the coefficient of D which it contained. The new equations thus obtained were summed. Where D did not appear the equation was omitted. Thus the following equations were obtained.

$$1/4\ D + 1/8\ H + 1/2\ E_1 = 60.95$$

$$1/4\ D + 1/32\ H + 1/2\ E_2 = 21.8$$

$$1/16\ D + 1/32\ H + 1/4\ E_1 = 23.35$$

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$$(1) \quad 9/16\ D + 3/16\ H + 3/4\ E_1 + 1/2\ E_2 = 106.1$$

Similarly multiplying through the original equations by the coefficients of H, $E_1$, and $E_2$ and summing the following were obtained.

(2) $3/16\ D + 21/256\ H + 3/8\ E_1 + 1/16\ E_2 = 44.8$

(3) $3/4\ D + 3/8\ H + 3\ E_1 = 263.2$

(4) $1/2\ D + 1/16\ H + 2\ E_2 = 65.6$

The solution of these four simultaneous equations gave estimates of D, H, $E_1$, and $E_2$. Mather (7) presented a method for solving these equations using a matrix of multipliers. For the purpose of this study, these equations were solved by the standard method of solving simultaneous linear equations in more than one unknown. That is, each equation was added to or subtracted from each of the other three in order to eliminate one unknown. The remaining three equations in three unknowns were compared and another unknown was eliminated. This process was repeated until a solution was obtained for one unknown. Then the other equations were solved by substituting known values.

Solution of these equations gave the following values for the components of variance in the cross Clintland x Craig.

$D = 10.7$

$H = 271.5$

$E_1 = 51.1$

$E_2 = 21.6$

Upon substituting these values in the original equations the expected values given in Table 3 were obtained.

Table 3: Variances of number of links supported in Clintland x Craig cross

| | Components | Variances computed from number of links | | |
|---|---|---|---|---|
| | | observed | expected | deviation |
| $V_{F_2}$ | $1/2\ D + 1/4\ H + E_1$ | 121.9 | 124.3 | -2.4 |
| $V_{\overline{F_3}}$ | $1/2\ D + 1/16\ H + E_2$ | 43.6 | 44.0 | -0.4 |
| $\overline{V}_{F_3}$ | $1/4\ D + 1/8\ H + E_1$ | 93.4 | 87.7 | 5.7 |
| V within parental groups | $= E_1$ | 47.7 | 51.1 | -3.4 |
| V parental group means | $= E_2$ | 22.0 | 21.6 | 0.4 |

| | Components | Variances computed from logarithms | | |
|---|---|---|---|---|
| | | observed | expected | deviation |
| $V_{F_2}$ | $1/2\ D + 1/4\ H + E_1$ | .066 | .064 | .002 |
| $V_{\overline{F_3}}$ | $1/2\ D + 1/16\ H + E_2$ | .025 | .026 | -.001 |
| $\overline{V}_{F_3}$ | $1/4\ D + 1/8\ H + E_1$ | .052 | .052 | .000 |
| V within parental groups | $= E_1$ | .039 | .041 | -.002 |
| V parental group means | $= E_2$ | .014 | .013 | .001 |

The variances calculated from the natural logarithms of the number of links are as given in the "observed" column of Table 3. Least squares estimates of the four components of variation were obtained by the same procedure used previously. It should be noted that the left sides of equations (1) to (4) on pages 22 and 23 remain constant for all experiments of the same design. Thus only the right sides were calculated, and these equations became

$$\begin{aligned}
&\text{(1a)} \quad 9/16\ D + 3/16\ H + 3/4\ E_1 + 1/2\ E_2 = .058 \\
&\text{(2a)} \quad 3/16\ D + 21/256\ H + 3/8\ E_1 + 1/16\ E_2 = .024 \\
&\text{(3a)} \quad 3/4\ D + 3/8\ H + 3\ E_1 = .157 \\
&\text{(4a)} \quad 1/2\ D + 1/16\ H + 2\ E_2 = .039\ .
\end{aligned}$$

Solution of these simultaneous equations gave the following values for the components of variance in the cross Clintland x Craig.

$$\begin{aligned}
D &= .020 \\
H &= .051 \\
E_1 &= .041 \\
E_2 &= .013
\end{aligned}$$

Taking the logarithms of the data has greatly reduced the relative value of H and has increased the relative value of D in relation to the values for these components computed from the original data.

An estimate of the fixable genetic variation in the $F_2$ generation was obtained by dividing the portion of total variation due to D by the total expected variation; that is, using the original data

$\frac{1/2\ D}{\text{expected}} = \frac{5.35}{124.3} \times 100 = 4.3\%$ fixable genetic variation in $F_2$.

Similarly,

$\frac{1/2\ D + 1/4\ H}{\text{expected}} = \frac{73.22}{124.3} \times 100 = 59\%$ total genetic variation in $F_2$.

$\frac{1/2\ D}{\text{expected}} = \frac{5.35}{44.0} \times 100 = 12\%$ fixable genetic variation in $F_3$ means.

$\frac{1/2\ D + 1/16\ H}{\text{expected}} = \frac{22.32}{44.0} \times 100 = 51\%$ total genetic variation in $F_3$ means.

Using the components of variation computed from the logarithms of the data, these values become

$\frac{1/2\ D}{\text{expected}} = \frac{.010}{.064} = 15.6\%$ fixable genetic variation in $F_2$.

$\frac{1/2\ D + 1/4\ H}{\text{expected}} = \frac{.023}{.064} = 35.9\%$ total genetic variation in $F_2$.

$\frac{1/2\ D}{\text{expected}} = \frac{.010}{.026} = 38.5\%$ fixable genetic variation in $F_3$ means.

$\frac{1/2\ D + 1/16\ H}{\text{expected}} = \frac{.013}{.026} = 50\%$ total genetic variation in $F_3$ means.

## Clintland x A587-10

For convenience the calculations for both the original data and the logarithmic transformation were carried through at the same time. The variances calculated from the segregating cross Clintland x A587-10 were as follows:

| | using no. of links | using logarithms |
|---|---|---|
| $V_{F_2} = 1/2\,D + 1/4\,H + E_1$ = | 74.1 | .094 |
| $V_{\overline{F_3}} = 1/2\,D + 1/16\,H + E_2$ = | 27.7 | .035 |
| $\overline{V}_{F_3} = 1/4\,D + 1/8\,H + E_1$ = | 70.4 | .091 |
| V within parental groups $= E_1$ = | 44.6 | .036 |
| V parental group mean $= E_2$ = | 20.8 | .018 |

Least squares estimates of the components of variance were obtained by the same method used in the previous cross. Thus were obtained equations similar to (1) to (4) on pages 22 and 23.

| | using no. of links | using logarithms |
|---|---|---|
| (1b) $9/16\,D + 3/16\,H + 3/4\,E_1 + 1/2\,E_2$ = | 68.5 | .087 |
| (2b) $3/16\,D + 21/256\,H + 3/8\,E_1 + 1/16\,E_2$ = | 29.1 | .037 |
| (3b) $3/4\,D + 3/8\,H + 3\,E_1$ = | 189.1 | .222 |
| (4b) $1/2\,D + 1/16\,H + 2\,E_2$ = | 48.5 | .053 |

Solution of these simultaneous equations gave the following values for the components of variance in the cross Clintland x A587-10.

|  | Using no. of links | Using logarithms |
|---|---|---|
| $D$ = | -1.6 | .006 |
| $H$ = | 121.2 | .208 |
| $E_1$ = | 48.3 | .046 |
| $E_2$ = | 20.9 | .018 |

Since D is a sum of squares, it cannot be negative. However, the small negative value obtained for D cannot be considered as different from zero nor from the small positive value obtained for D using logarithms. As the data stand it is not possible to demonstrate any fixable genetic variance in this cross. In this cross, logarithms increased rather than decreased the relative value of H. Table 4 shows the observed and expected values for the several variances using the components as given above.

Table 4: Variances of number of links supported in Clintland x A587-10 cross

| Components | | Variances computed from no. of links | | |
|---|---|---|---|---|
| | | observed | expected | deviation |
| $V_{F_2}$ | $1/2\ D + 1/4\ H + E_1$ | 74.1 | 77.8 | -3.7 |
| $V_{\overline{F_3}}$ | $1/2\ D + 1/16\ H + E_2$ | 27.7 | 27.7 | 0 |
| $\overline{V}_{F_3}$ | $1/4\ D + 1/8\ H + E_1$ | 70.4 | 63.1 | 7.3 |
| V within parental groups | $= E_1$ | 44.6 | 48.3 | -3.7 |
| V parental group means | $= E_2$ | 20.8 | 20.9 | -0.1 |

| Components | | Variances computed from logarithms | | |
|---|---|---|---|---|
| | | observed | expected | deviation |
| $V_{F_2}$ | $1/2\ D + 1/4\ H + E_1$ | .094 | .101 | -.007 |
| $V_{\overline{F_3}}$ | $1/2\ D + 1/16\ H + E_2$ | .035 | .034 | .001 |
| $\overline{V}_{F_3}$ | $1/4\ D + 1/8\ H + E_1$ | .091 | .074 | .017 |
| V within parental groups | $= E_1$ | .036 | .046 | -.010 |
| V parental group means | $= E_2$ | .018 | .018 | .000 |

## A587-10 x Craigs Afterlea

The variances calculated from the segregating cross A587-10 x Craigs Afterlea were as follows:

| | Using no. of links | Using logarithms |
|---|---|---|
| $V_{F_2} = 1/2\ D + 1/4\ H + E_1 =$ | 172.1 | .137 |
| $V_{\overline{F_3}} = 1/2\ D + 1/16\ H + E_2 =$ | 53.8 | .052 |
| $\overline{V}_{F_3} = 1/4\ D + 1/8\ H + E_1 =$ | 148.2 | .140 |
| V within parental groups $= E_1 =$ | 47.1 | .041 |
| V parental group means $= E_2 =$ | 20.5 | .018 |

The least squares estimates of the four components were obtained from the following equations which were derived in the same manner as those used in the preceding two crosses.

| | Using no. of links | Using logarithms |
|---|---|---|
| (1c) $9/16\ D + 3/16\ H + 3/4\ E_1 + 1/2\ E_2 =$ | 150.0 | .129 |
| (2c) $3/16\ D + 21/256\ H + 3/8\ E_1 + 1/16\ E_2 =$ | 64.9 | .055 |
| (3c) $3/4\ D + 3/8\ H + 3\ E_1 =$ | 367.3 | .317 |
| (4c) $1/2\ D + 1/16\ H + 2\ E_2 =$ | 74.3 | .070 |

When these simultaneous equations were solved, the following values were obtained for the components of variance.

| | Using no. of links | Using logarithms |
|---|---|---|
| $D$ = | 6.2 | .020 |
| $H$ = | 487.2 | .349 |
| $E_1$ = | 60.0 | .057 |
| $E_2$ = | 20.4 | .019 |

The expected values given in Table 5 were obtained by substituting these values for D, H, $E_1$, and $E_2$ in the original equations. It should be noticed that the deviations between the observed and the expected values were quite large due chiefly to a difference in the values of D and H between the $V_{F_2}$ and $\bar{V}_{F_3}$. Such a difference might have resulted from the effects of linkage.

In the case of linkage, the heritable portion of variance was no longer simply the sum of the contributions due to the individual gene pairs but also involved a factor derived from the recombination or crossover values. Mather (7) derived certain formulae for D and H when linkage was present. With linkage, the values for D and H in the $F_2$ differed from those for D and H in the $F_3$. To test for the presence of linkage, then, it must be determined whether this difference in D and H between $F_2$ and $F_3$ existed.

In the experiments here being reported, D and H of the $F_2$ generation were estimated from $V_{F_2}$ and $V_{\overline{F}_3}$ while D and H

Table 5. Variances of number of links supported in A587-10 x Craigs Afterlea cross

| Components | Observed | Uncorrected |  | Corrected for linkage |  |
|---|---|---|---|---|---|
|  |  | Expected | Deviation | Expected | Deviation |
| Variances computed from no. of links |  |  |  |  |  |
| $V_{F_2}$ $1/2\ D + 1/4\ H + E_1$ | 172.1 | 184.9 | −12.8 | 172.1 | 0 |
| $V_{\overline{F_3}}$ $1/2\ D + 1/16\ H + E_2$ | 53.8 | 53.9 | − 0.1 | 53.8 | 0 |
| $\overline{V}_{F_3}$ $1/4\ D + 1/8\ H + E_1$ | 144.2 | 122.4 | 21.8 | perfect fit |  |
| V within parental groups$=E_1$ | 47.1 | 60.0 | −12.9 | 47.1 | 0 |
| V parental group means $= E_2$ | 20.5 | 20.4 | 0.1 | 20.5 | 0 |
| Variances computed from logarithms |  |  |  |  |  |
| $V_{F_2}$ $1/2\ D + 1/4\ H + E_1$ | .127 | .144 | −.017 | .125 | .002 |
| $V_{\overline{F_3}}$ $1/2\ D + 1/16\ H + E_2$ | .052 | .051 | .001 | .054 | −.002 |
| $\overline{V}_{F_3}$ $1/4\ D + 1/8\ H + E_1$ | .140 | .106 | .034 | perfect fit |  |
| V within parental groups$=E_1$ | .041 | .057 | −.016 | .043 | −.002 |
| V parental group means $= E_2$ | .018 | .019 | −.001 | .017 | .001 |

of the $F_3$ generation were estimated from $\overline{V}_{F_3}$. If $D_{F_3}$ and $H_{F_3}$ differed from $D_{F_2}$ and $H_{F_2}$ respectively, a perfect fit could have been obtained for $F_3$ by adjustment of D and H. As a result of this perfect fit in $\overline{V}_{F_3}$, the sum of squares of the observed variances from their expectation would have been reduced by this adjustment of D and H. The estimation of D and H from the complete data for the cross A587-10 x Craigs Afterlea has previously been done. The next step was to estimate D and H from $V_{F_2}$ and $V_{\overline{F_3}}$, assuming the perfect fit in $\overline{V}_{F_3}$. The variances required are:

| | Using no. of links | Using logarithms |
|---|---|---|
| $V_{F_2} = 1/2\,D + 1/4\,H + E_1 =$ | 172.1 | .137 |
| $V_{\overline{F_3}} = 1/2\,D + 1/16\,H + E_2 =$ | 53.8 | .052 |
| $E_1 =$ | 47.1 | .041 |
| $E_2 =$ | 20.5 | .018 |

Equations for least squares estimates of the four components of variance were obtained by a method analogous to that used previously. Each equation was multiplied through by the coefficient of D which it contained and the resulting equations were summed, and so on for H, $E_1$, and $E_2$. This gave the following equations:

| | Using no. of links | Using logarithms |
|---|---|---|
| (5) $1/2\ D + 5/32\ H + 1/2\ E_1 + 1/2\ E_2 =$ | 112.95 | .094 |
| (6) $5/32\ D + 17/256\ H + 1/4\ E_1 + 1/16\ E_2 =$ | 46.39 | .037 |
| (7) $1/2\ D + 1/4\ H + 2\ E_1 =$ | 219.2 | .178 |
| (8) $1/2\ D + 1/16\ H + 2\ E_2 =$ | 74.3 | .070 |

Solving these simultaneous equations the following estimates were obtained for the components of variance in the cross A587-10 x Craigs Afterlea.

| | Using no. of links | Using logarithms |
|---|---|---|
| $D =$ | 5.4 | .038 |
| $H =$ | 489.3 | .293 |
| $E_1 =$ | 47.6 | .043 |
| $E_2 =$ | 20.5 | .017 |

The expected values given under the headings "corrected" in Table 5 were obtained by substituting these values for D, H, $E_1$, and $E_2$ in the original equations. It was observed that the relative values of D and H had been changed when $\overline{V}_{F_3}$ was omitted, which gave strong evidence that linkage was involved in this cross. However, there was no more recovery of parental types than expected. This indicated the presence of several linkage groups on different chromosomes with random combinations between groups. In a wide cross such as this it was expected that there would be linkage of factors from each of the diverse parents.

Estimates of fixable genetic variation obtained from the original data, uncorrected and corrected for linkage, were about the same. However, the percentage of fixable genetic variation was increased by using the logarithms of the data and was further increased by the correction for linkage. The proportion of variation due to heredity is presented in Table 6.

Table 6: Genetic variation expressed as percent of total variation in A587-10 x Craigs Afterlea cross

| | Using no. of links | | Using logarithms | |
|---|---|---|---|---|
| | uncorrected | corrected for linkage | uncorrected | corrected for linkage |
| Fixable genetic variation in $F_2$ | 1.7% | 1.6% | 6.4% | 14.1% |
| Total genetic variation in $F_2$ | 68 | 72 | 63 | 68 |
| Fixable genetic variation in $F_3$ means | 5.6 | 5.0 | 19.6 | 35.0 |
| Total genetic variation in $F_3$ means | 59 | 63 | 63 | 69 |

## Consideration of Linkage in Clintland x A587-10

Consideration of linkage in the calculations from the cross A587-10 x Craigs Afterlea was shown to increase the proportion of fixable genetic variation in relation to total variation. The deviation of observed from expected variances was also fairly high in the cross Clintland x A587-10, especially when logarithms were taken. Therefore a test should also be made for linkage in Clintland x A587-10, using logarithms. Least squares estimates of the components of variance were obtained by the same method used previously. The left sides of equations (5) to (8) on page 26 apply in this case. When the right sides of the equations were computed, the following equations were obtained.

(5a) $1/2\ D + 5/32\ H + 1/2\ E_1 + 1/2\ E_2 = .065$

(6a) $5/32\ D + 17/256\ H + 1/4\ E_1 + 1/16\ E_2 = .026$

(7a) $1/2\ D + 1/4\ H + 2\ E_1 = .130$

(8a) $1/2\ D + 1/16\ H + 2\ E_2 = .053$

The following estimates for the components of variance were obtained when these simultaneous equations were solved.

$D = .004$

$H = .234$

$E_1 = .035$

$E_2 = .018$

These values are only slightly changed from those obtained by using the mean variance of $F_3$ families. Therefore evidence of linkage is lacking.

# DISCUSSION

Mather (7) gave a method for calculating the standard errors of D, H, $E_1$, and $E_2$ from the sum of squares of deviations of observed from expected values of the several variances. This method involved use of multipliers which were not calculated in the present study. Lacking these standard errors, there was no reliable way of telling whether the values observed were significant or not. It seemed that the high values of H in the three crosses indicated dominance. Changing the data to logarithms changed the value of H in the cross Clintland x Craig enough that, lacking its standard error, the preceding statement was not certain.

Dominance relations could also be assessed by comparing the $F_1$ and its derivatives to the mid-parent value. No $F_1$'s were grown in the field, so the $F_2$ and the $F_3$ were utilized in determining dominance. The following observations were based on the data presented in Figures 5, 6, and 7. In the cross Clintland x Craig there was dominance of the factors favoring lodging resistance. In the cross A587-10 x Craigs Afterlea there was dominance of the factors favoring lodging susceptibility. In the cross Clintland x A587-10 there was dominance, to a lesser extent, of factors favoring lodging susceptibility. This reduction in degree of dominance was probably due to a balancing of some dominant susceptibility factors from A587-10 by dominant resistance factors from Clintland.

In plant breeding work it is desired that individuals selected for any trait be able to transmit the trait to their progeny. Selection is accomplished on the basis of individual readings or on the basis of family means. These individual readings or means are subject to variation and this variation will be composed of D, H, and E portions. In order to increase the heritability or ability to transmit the trait to progeny, it is desired to increase the proportion of the variance due to difference between homozygotes represented by D. The best way to increase the proportion of D is to decrease the proportion of H. and E.

In self -pollinated crops the D component of means remains constant while the H component decreases by one-half in each generation. Thus selection in later generations becomes more and more effective. Economy of time suggests making selections in as early a generation as possible. The D component which was calculated for the cross Clintland x A587-10 was very small. The greatest proportion of fixable genetic variation was nine per cent fixable genetic variation in $F_3$ means. This low value indicated that selection might not be successful in this cross. In the other two crosses, Clintland x Craig and A587-10 x Craigs Afterlea corrected for linkage, the proportion of fixable genetic variation to total variation was about 15 per cent in the $F_2$ and about 35 per cent in the $F_3$ means. This 15 per cent of variation due to fixable genetic differences in the $F_2$ was low enough that selection might be inefficient. However, by the $F_3$ generation, the figure for fixable genetic variation had risen and selection might be more effective. Furthermore, this increase in fixable genetic variation increased the probability of retaining the best progeny. The statistics utilized were not sensitive in determining the size of population to save.

Another way to increase the proportion of variation due to D would be to reduce the proportion due to E. In these calculations values of 30 to 60 per cent of the total variation have been found for non-heritable variation. Replication would have helped greatly in removing or accounting for much of the non-heritable variation encountered in the experiment.

In the formula, $cLr = \frac{F}{b}$, given by Grafius and Brown (4) lodging resistance was a function of both the weight supported and the height. The weight supported, but not the height, has been considered in this study. Height of the plant is inherited separately from the factors determining torque resistance. When either height or torque resistance is held constant, a change in the other factor will cause a change in lodging resistance. Selection for lodging resistance should, on a practical basis, be made only on plants of similar heights. Similarly, if it were desired to improve lodging resistance by hybridization, the quickest advances would be made by crossing strong plants of the same height. Crossing of strong plants of considerably different heights would give a wider range of heights compounded on the range of torque resistance. Then the desired combination may not be found in a small sample.

Conversion of the data by taking logarithms changed the proportion of fixable genetic variance. The original H figure might have included a part due to interaction of genes due to improper scaling. The order of the original data was not affected by logarithms; therefore selection should be done on the basis of the field measurements. If it were desired to make any predictions concerning advances under selection, it would be necessary to consider whether the original scale was adequate. The logarithmic transformation used in this paper was, in effect, equal to hanging a heavy chain on strong plants and progressively lighter chains on the weaker plants so that all plants might bend to the same distance above the ground.

## SUMMARY

Inheritance of lodging resistance versus lodging susceptibility was studied in three oat crosses involving the parents Clintland, Craig, A587-10, and Craigs Afterlea. Crosses were obtained for most of the possible combinations of these parents but several seeds were killed by excessive disinfectant treatment. The parents, the $F_2$'s, and the $F_3$'s for each cross were grown together in the field. A chain of known weight was used to determine resistance of each plant to external torque.

Lodging resistance was found to be dominant in the cross Clintland x Craig and was found to be recessive in the crosses Clintland x A587-10 and A587-10 x Craigs Afterlea.

Variations in the $F_2$ and the $F_3$ were separated into heritable and non-heritable portions. The heritable variation was further divided into fixable genetic and non-fixable genetic components according to the method proposed by Mather (7). The distributions of the original observations were skewed toward the low side. There was no reduction in skewness in the $F_3$, which indicated that the problem was in scaling. When natural logarithms of the data were used, the distributions approached much more closely to a normal distribution. Conversion of the data had an important effect in increasing the proportion of fixable genetic variance in the calculations on the crosses Clintland x Craig and A587-10 x Craigs Afterlea.

The fixable genetic variance, in the two crosses where it could be calculated, was approximately 15 per cent when the $F_2$ plant readings were used and 35 per cent when the $F_3$ means were used. Selection for lodging resistance prior to the $F_3$ generation seems likely to be on the basis of non-fixable differences. Selection on the basis of means of $F_3$ families seemed to give a good start toward isolating superior lines. Logarithms were valuable in this study in determining the effectiveness of selection but were not necessary for selection as they did not change the ranking of plants.

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