THE INHERITANCE OF SEVERAL CHARACTERISTICS IN CELERY AND TOMATO

Thesis for the Degree of Ph. D.

MICHIGAN STATE UNIVERSITY
JOHN C. BOUWKAMP

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of the requirements for

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ABSTRACT

THE INHERITANCE OF SEVERAL CHARACTERISTICS IN CELERY AND TOMATO

By

John C. Bouwkamp

Studies were carried out on celery to determine the inheritance of vernalization response, pinnae number, and leaf shape.

It was found that vernalization response was due to a single dominant major gene, Vr (which resulted in easy bolting). Cytoplasmic effects on the response to vernalization were also noted. Pinnae number was effected by two genes which segregated in the F_2 giving a 13:3 ratio. Leaf shape was determined by a single gene pair, dt, with shallow toothed leaves dominant to deeply toothed leaves.

Studies on tomatoes were conducted to determine the mode of inheritance and linkage relationships of sepal length, sepal shape, fruit shape, beaked fruit, and pedicel length.

It was found that fruit shape was determined by two genes, designated o^{rf} and Lc^{rf} with additive effects. These two genes were located 40 recombination units apart. Beaked fruit was conditioned by a single dominant gene designated Bk-2. This gene was located approximately midway between the loci of the two fruit shape genes, o^{rf} and

Lc^{rf}. Sepal shape was determined by a single gene pair designated en for ensiform sepals. The dominant allele causes acuminate sepals. The gene en was located at 34 recombination units from Bk-2 and 16 units from the nearest fruit shape gene. Sepal length was determined by a single gene pair with incomplete dominance and designated sx; Sx Sx conditioned long sepals; sx sx, short; and Sx sx, intermediate. Sx was located 20 recombination units from en, 39.4 units from Bk-2, and 24 units from the nearest fruit shape gene. Pedicel length was found to be quantatively inherited.

Correlation analysis substantiated the gene order postulated from the recombination data.

THE INHERITANCE OF SEVERAL CHARACTERISTICS IN CELERY AND TOMATO

By

John C. Bouwkamp

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DEDICATION

To my father, mother, and Ellen

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THE INHERITANCE OF SEVERAL CHARACTERISTICS IN CELERY AND TOMATO

I

THE INHERITANCE OF VERNALIZATION RESPONSE, PINNAE NUMBER, AND LEAF SHAPE IN CELERY (*Apium graveolens* L. var. *dulce*)

INTRODUCTION

Exposure to a period of cold temperature is known to be a prerequisite for flower initiation in many biennial species. This phenomenon, referred to as vernalization, is commonly defined as the acquisition by a plant of the ability to hasten or promote flowering by exposure to low temperature. This definition will be used in this study. Celery (Apium graveolens L. var. dulce) set in the field without protection early in the spring or exposed to cold temperatures in the greenhouse prior to transplanting, often bolts before reaching marketable size. The occurrence of bolters varies depending on the duration of the cold period during the growing season. This results in a considerable loss to the growers since the bolted plants are not marketable and the cost of production is high for early celery. One solution to this problem is the use of paper or plastic coverings. The cost of these protective coverings is high, and the results are not entirely satisfactory. Although they provide some protection, they are not adequate for long dark cool periods.

A more satisfactory solution to this problem is through the use of varieties resistant to bolting. Although genetic control of bolting has been known for some time, no study to determine the mode of inheritance of the response to vernalization has been reported in celery. The objectives of the following study were:

1. To identify the factors controlling the inheritance of pinnae number, leaf shape, and response to vernalization.
2. To establish linkage relationships of these three characters as well as the factor conditioning yellow petiole color.

REVIEW OF LITERATURE

Vernalization

There have been several recent review articles and books on the subject of vernalization and flower induction (7, 20, 26, 46, 72). No attempt will be made to summarize and compile all of the literature on vernalization, however, those articles pertinent to this study will be included.

Bolting has been known in biennial vegetable crops for many years. Krasan, as reported by Thompson (64) in 1890 called attention to the importance of temperature in the initiation of flowering in many species. Starring (51) and Thompson (63) reported that bolting in celery could be induced by a two to three week treatment at 40 - 60° F. Several factors which check growth (such as frost, drought, poor soil conditions and crowding the plants in the seed bed) were also studied. Both researchers concluded that in celery prolonged exposure of the plants to cold temperature was responsible for premature seed stalk development.

Several investigators have shown that all stages of plant growth are not equally responsive to the vernalizing stimulus. Pawar and Thompson (35), working with celery,

concluded that the age of the plant was more important than plant size. Sarkar (47) reported that, in the biennial Hyoscyamus niger, seedlings less than ten days old could not be vernalized. The sensitivity to vernalization increased until the plants were thirty days old. Older plants showed no increase in sensitivity over the thirty day old plants.

Wellensiek (72) proposed that some biennials have a "juvenile phase" and, during this phase, plants were insensitive to the vernalization stimulus. Cheiranthus allioni (3) and Arabidopsis thaliana (32) also show differences in response to vernalization at the various stages of development. Chouard (7) concluded that sensitivity generally increased with age.

Several workers (8, 38, 63) have reported that the receptive site for vernalization was the stem apex. Curtis and Chang (13), working with celery, cooled the growing point by circulating cold water in tubing wrapped around the plant at the base of the petioles. The cooled plants grown in a warm greenhouse bolted while the uncooled control plants remained vegetative. Plants with their apices warmed by circulating warm water failed to bolt while the control plants bolted when grown in a cool greenhouse.

Wellensiek (72), working with Lunaria biennis, concluded that mitosis was necessary for vernalization. He based his conclusions on the fact that leaf cuttings from

vernalized plants regenerated a flowering plant only if the leaves were quite young. Older leaves from a vernalized plant regenerated vegetative plants. His findings, however, do not preclude the possibility that vernalization is dependent on young, undifferentiated cells and not mitosis as such.

Although several authors (28, 34, 50, 73) noted varietal differences in response to vernalization, there are few studies concerning the genetics of the response. Hall (17) reported that bolting was not simply inherited but that non-bolting appeared to be dominant in sugar beets, mangolds and leeks. Van Heel (67), working with sugar beets, concluded that bolting was recessive and was controlled by a single gene. Sutton (60) found that bolting in cabbage was conditioned by recessive factors.

Barber (2) concluded that in peas a single gene, Sn, was conditioned for the response to vernalization. Response was dominant to non-response. It might be noted, however, that peas do not require vernalization in order to flower but that vernalization only makes peas flower sooner.

Nilsson-Ehle (33) and Cooper (10), studying crosses of winter and spring wheat, found that the spring type was dominant to the winter type giving a 3:1 ratio. Cooper also reported a 13:3 ratio using another winter wheat parent. Takahashi (61) reported that the spring type was dominant to the winter type in barley giving a 3:1 ratio.

Gaines (16), however, reported a 13:3 ratio of spring to winter types in barley. Tschermak (66) found a 3:1 ratio of spring to winter types in rye but noted a difference in reciprocal F_2 populations. Purvis (37) reported similar results with rye.

Elmsweller (15) demonstrated a difference in bolting response among inbred lines of celery and suggested that bolting resistance was quantative and recessive. Thompson (63) also concluded that varieties and strains differed in their response with reference to bolting. Starring (52) made similar observations and suggested that it was possible to select and breed for resistance to bolting.

Leaf Shape

The existence of genes controlling shape was demonstrated with cucurbit fruits by Sinnott (48, 49) who noted that "shape" genes did not control individual dimensions but controlled the correlations between growth rates in different dimensions or planes.

Several genetic studies of leaf shape have been reported. Tedin (62) found leaf shape in Camelina to be controlled by two genes. The pinnatified parent was designated as AABB while the entire-leafed parent was aabb. There were also two true breeding intermediate types which were designated AAbb and aaBB.

Imai (22) reported more than twenty genes affected the leaf shape in Pharbitis nil, the Japanese morning

glory. Joyner and Pate (24) found in Hibiscus cannabinus that deeply lobed leaves were due to a single gene which was dominant to the gene conditioning shallowly lobed leaves. Ryder (45) reported three genes affecting leaf shape in lettuce.

Extensive genetic studies on leaf shape have been made in the genus Gossypium (18, 19, 54, 55, 56, 57, 58). Stephens (54) has shown that leaf shape is controlled by a system of four alleles in amphidiploid cotton. In this system, the allele for the more deeply lobed form is always dominant to the allele for the less deeply lobed form. Rhyne (40) demonstrated that phenocopies of the amphidiploid, New World cottons could be produced by combinations of alleles for leaf shape in the diploid and the Asiatic series. Thus the four allelic leaf shapes in the amphidiploid cotton might have arisen from combinations of two leaf types in each of the progenitors of the amphidiploid.

Several genes have been reported which affect leaf shape in tomato. They are potato leaf, c (5), entire leaf, e (5), curl, Cu (76), trifoliate, tf (44), mouse ear, Me (42) and lanceolate, La (29, 30, 59).

MATERIALS AND METHODS

In 1960 a program was started at the Michigan Agricultural Experiment Station to obtain materials to study the mode of inheritance of bolting in celery. The general plan was to establish diverse lines so that the characters could be readily identified in the segregating population.

The easy bolting line was obtained by exposing the yellow petioled variety Golden Plume to two weeks of vernalizing temperatures (40° F) and selecting plants that bolted. These plants were selfed in the greenhouse and were again subjected to the same treatment. After five generations, a line which bolted after two weeks of vernalization was established which henceforth will be referred to as Golden Plume.

The hard-to-bolt line was obtained from a cross between Early Fortune and Emerson Pascal. The F_2 generation was exposed to six weeks of vernalizing temperatures and green petioled plants that failed to bolt after this treatment were selected, given additional cold treatment, and selfed in the greenhouse. Plants resulting from selfing were again subjected to the same treatment; this was repeated (four generations) until a line that would not

bolt after six weeks of cold treatment was established. This line is henceforth referred to as MSU 130.

Reciprocal crosses were made between one plant of Golden Plume and one of MSU 130 according to the method outlined by Honma (21). The plants were also selfed in the greenhouse to obtain parental seeds for use in the study. The F_1 plants were grown in the field, lifted, vernalized, and selfed in the greenhouse to obtain the F_2 seeds. The F_2 seed from the cross MSU 130 x Golden Plume was labelled 980 and its reciprocal, 981. The importance of including the F_1 and back cross populations was realized; however, celery crosses are difficult to make and if successful only a few seeds are obtained per cross (21).

Seeds from the parents and the two F_2 populations were sown in vermiculite. At the first true leaf stage, the seedlings were planted in flats on 1 1/2 inch centers into a sterilized soil mixture of 1/2 muck, 1/2 sand. Cold treatments were started when the plants were at the five to seven true leaf stage.

The experiment consisted of seven treatments with three replications of each treatment. Each replication consisted of 24 plants of each parent and 72 plants of each of the F_2 populations. The treatments consisted of different durations of exposure to a constant 40° F temperature and a 12 hour day length. The shortest

exposure was 20 days and the exposure time increased at five day intervals to 50 days. In addition, extra seedlings of MSU 980 were given a ten and fifteen day exposure.

After the cold treatment, the plants were kept in a greenhouse at 70° - 75° F for a week in order to stabilize the vernalization. The plants were then transplanted to a plot at the MSU Muck Experimental Farm near Bath, Michigan. The transplanting was delayed until July 15 in order to eliminate the possibility of the plants receiving an exposure to natural cold temperatures. During the growing season, the plants were fertilized and irrigated as necessary.

Records were taken on the number of bolted and yellow petioled plants in the field. Plants with a long duration of treatment had a shorter normal growing season than plants with a shorter treatment time. In order to eliminate the variable of rate of seed stalk development, all plants without visible seed stalks were cut longitudinally to observe the apices. All plants with pointed apices were considered as bolters (Figure 1). One petiole from each plant from the 25 and 30 day treatments was sampled and the pinnae number was recorded. The terminal leaflets from these petioles were saved and pressed in an herbarium press for measurements.

The data on the length, weight, and leaf area of the terminal leaflets were taken when the samples were dried. The differences in leaf area were measured using

Figure 1.--Stages in seedstalk development. Left, not bolting; center and right, bolting; growing points outlined for ease of identification.

an apparatus similar to that described by Potter (36). The images of one hundred leaves were reproduced with a Xerox copying machine and their areas were measured with a planimeter. The data from the light meter apparatus and from the planimeter measurements were used to obtain a linear regression equation. A correlation coefficient of 0.968 was obtained between the measured leaf area and the units from the apparatus. Since the r-value was highly significant, the light meter reading of the leaflet samples was transformed using the linear regression equation (leaf area in cm^2 = 0.78 + 0.38 light units) prior to analysis.

The estimate of genetic differences of certain characters in this cross was based on the ratio obtained by apportionment of the F_2 data where separation was suggested by the bimodal distribution. Observed frequencies were compared with theoretical ratios using the Chi-square method.

Data from individual plants were assembled and entered on IBM cards. Means, variances, standard deviations, and correlations were obtained from individual plant data and calculated by the use of the Control Data Corporation 3600 computer. The results were statistically interpreted by using statistical tables in Steel and Torrie (53).

RESULTS AND DISCUSSION

Bolting

The results from the bolting experiment for the two F_2 populations studied are shown in Table 1. These results suggest that the character "bolting response" is not a simply inherited trait. The variance analysis computed for bolting is shown in Table 2. The significant F value for F_2 populations suggests a cytoplasmic difference in the inheritance of this character.

Cytoplasmic differences might be explained by the current theories on vernalization and gene action if one considers vernalization in celery to be an inducible genetic system. Such a system would require a change in concentration of some chemical or biochemical constituent in the cell which in turn would regulate the action of a gene.

Celery requires a prolonged (2-4 week) cold treatment for bolting. A short, very cold treatment (i.e., a frost) will not induce bolting, but a longer cool treatment causes bolting. This suggests that some accumulative chemical changes may be taking place.

TABLE 1.--Mean bolting percentages for various durations of cold treatment for celery plants from F_2 populations from reciprocal crosses of Golden Plume x MSU 130.

F_2 population	Days of cold treatment								
	50	45	40	35	30	25	20	15	10
980	94.1	81.5	88.3	90.9	87.2	78.8	78.7	77.4	29.2
981	97.4	88.1	91.3	95.7	88.7	86.3	78.3		

TABLE 2.--Variance analysis of bolting percentages in F_2 populations from reciprocal crosses of Golden Plume x MSU 130.

Source	SS	df	MS	F
Reps	0.002267	2	0.001134	0.632
Treatments	0.131368	6	0.021895	12.191***
Linear	0.071837	1	0.071837	39.988***
Other	0.059531	5	0.011906	
F_2 Populations	0.014935	1	0.014935	8.316***
Error	0.050547	32	0.001796	
Total	0.199117	41		

***Significant at 0.005 level.

Analysis of 20 through 50 day treatments inclusive.

An inducible system should be reversible. It is known (63) that vernalized celery can be devernalized by exposure to high temperatures. It is suggested that whatever substance was accumulated or depleted during vernalization may have been destroyed or replaced by devernalizing temperatures, thus restoring the plant to its pre-vernalized condition.

Assuming that the cytoplasm is the receptor of the vernalizing stimulus and that the chemical and biochemical changes take place in the cytoplasm, there are two possible sites for variability in bolting response. Since the action of the genetic makeup may be regulated by the cytoplasm, differences in sensitivity of the cytoplasm to cool temperatures or differences in the sensitivity of regulator genes to regulating substances may result in varying responses to vernalizing stimuli. Differences in sensitivity of the cytoplasm would be manifested as differences in reciprocal crosses, since the genetic makeup should be identical.

A graphical presentation of the bolting data may be seen in Figure 2. The ratio of bolters to non-bolters for the 20 day treatment was 311:83 which gave a good fit to a 3:1 ratio. The Chi-square value was 2.247 with a P value of 0.15-0.10. Since the reciprocal F_2 population showed similar bolting percentages for this treatment, it appears that the effect at 20 days was due to genetic

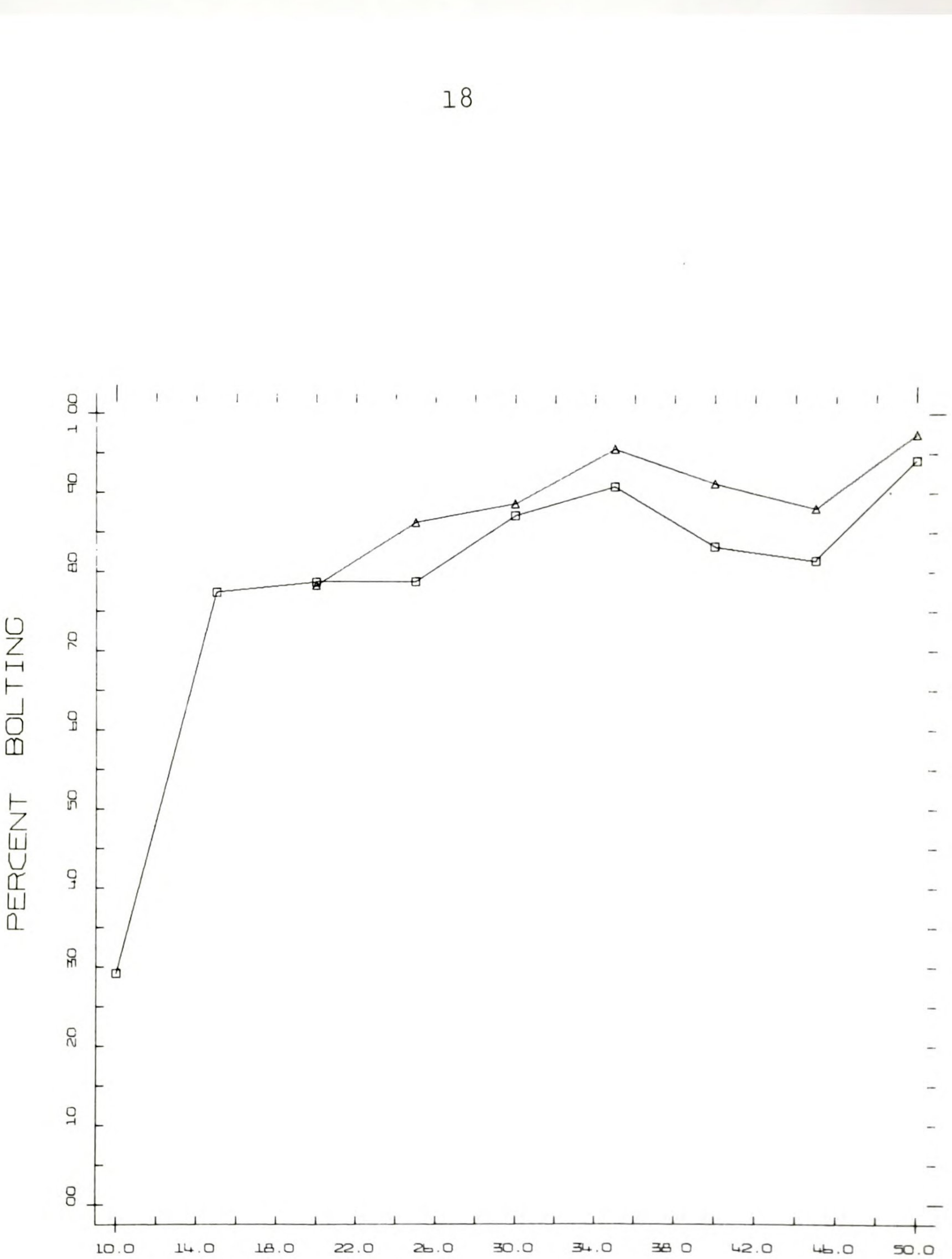


Figure 2.--Percentages of plants bolting after various days of treatment. Squares, 980 (MSU 130 x Golden Plume); triangles, 981 (Golden Plume x MSU 130).

variability. Therefore it appears that one dominant major gene, Vr (Vernalization response), controls the easy bolting response.

A plant with one or two dominant alleles bolts since the regulator is sensitive to small changes in concentration of the regulating substance. Homozygous recessive plants fail to bolt after 20 days treatment since the recessive alleles are insensitive to small changes in concentration.

The homozygous recessive plants can be made to bolt, however, if the concentration of the regulating substance is changed sufficiently. These changes in concentration could be obtained by subjecting recessive plants to longer cold periods. It may be concluded from the significant F value for the linear effects for treatments that this is the case. This net increase is probably due to expression of the minor genes influencing this character.

Petiole Color

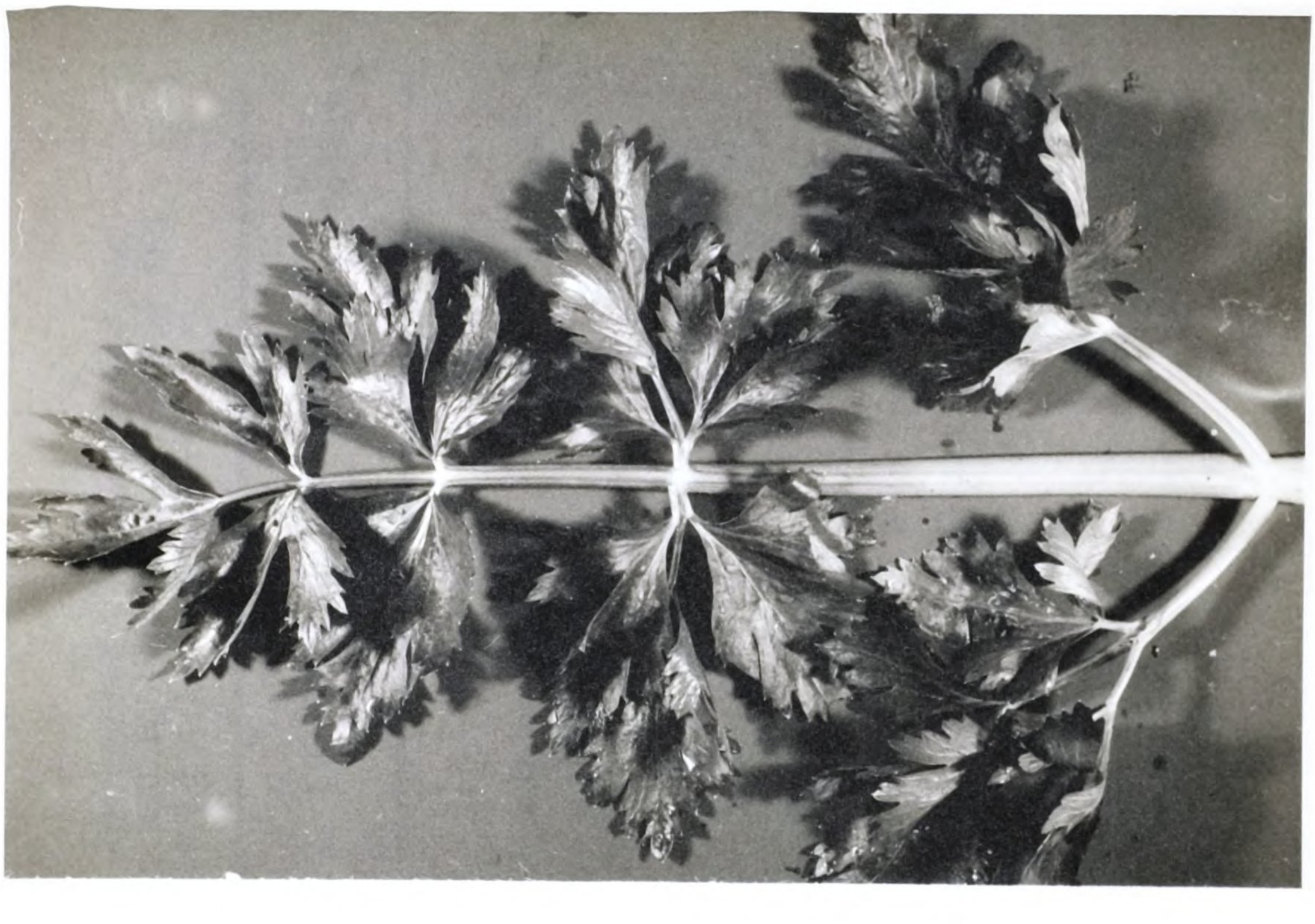
Yellow petiole color was reported by Townsend, et al. (65) to be conditioned by a single recessive gene. The ratio of green to yellow petioles was 3.0:0.8 for all treatments and for both F_2 populations. There was no difference between F_2 populations for the ratio of green to yellow petioles (Chi-square for heterogeneity is 0.107 with a P value of 0.7 - 0.6).

Since the percentage of green and yellow petioled bolters were nearly equal (1823/2072 or 88% of the green plants bolted while 464/549 or 85% of the yellow petioled plants bolted), it is apparent that there was no linkage between petiole color and vernalization response.

Pinnae Number

Figure 3 depicts differences in the number of pinnae per petiole. The upper petiole has eight pinnae while the lower has ten. The frequency distribution in per cent of individuals in each pinnae class for the parental and the pooled F_2 populations can be seen in Table 3. The F_2 was classified in the following manner: Plants with six pinnae were of the P_2 (Golden Plume) phenotype while those with ten and twelve pinnae were of the P_1 (MSU 130) phenotype. In the F_2 population 77.6% of the plants had eight pinnae. In the P_2 population 92% of the parental plants consisted of eight pinnae plants. Thus 92% of the F_2 eight pinnae class were added to the six pinnae class and were considered as the P_2 phenotype. Since 8% of the parental plants with eight pinnae were from the P_1 population, 8% of the eight pinnae class in the F_2 were added to the ten and twelve pinnae class and considered as the P_1 phenotype. The Chi-square test for goodness of fit to a 13:3 ratio shows a Chi-square value of 0.028 with a probability of 0.95 - 0.90, suggesting a good fit to this ratio.

Figure 3.--Number of pinnae per petiole; top eight, bottom ten.



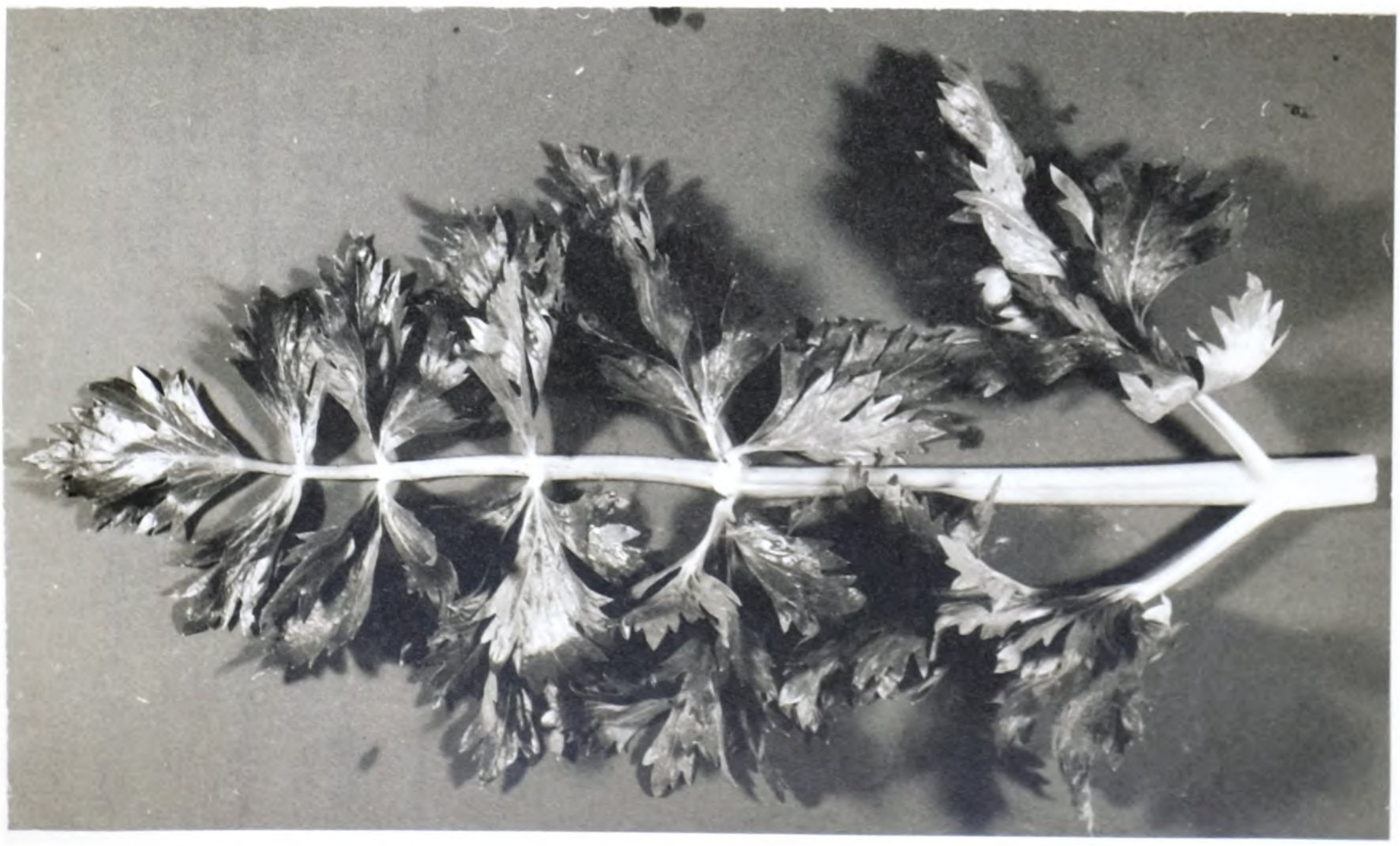


TABLE 3.--Frequency (in per cent) of parental and pooled F_2 populations from reciprocal crosses of Golden Plume x MSU 130 for pinnae number and a chi-square test for goodness of fit to a 13:3 ratio.

Pinnae Number	MSU 130 (P_1)	Golden Plume (P_2)	F_2	Observed	Expected	Chi-Square
6		20.7	10.2			
				81.6 (P_2)	81.8	0.004
8	6.6	79.3	77.6			
				18.4 (P_1)	18.2	0.024
						0.028
10	85.8		12.1			
12	7.6		0.1			

The hypothesis is further supported by Power's formula to estimate the number of gene pairs (36a). The formula used was:

$$(\overline{P_1})\ (3/16) \ + \ (\overline{P_2})\ (13/16) = \overline{F_2}$$

where: $\overline{P_1}$ is the mean of MSU 130 (P_1)

$\overline{P_2}$ is the mean of Golden Plume (P_2)

$\overline{F_2}$ is the theoretical mean of the F_2

The means of the P_1, P_2, and F_1 populations were 10.02 ± 0.76, 7.60 ± 0.80, and 8.04 ± 0.95, respectively. The theoretical mean of the F_2 was 8.04 ± 0.78 which is similar to the observed mean.

The pooled F_2 population was examined to determine if pinnae number and vernalization response were independent. The Chi-square test for heterogeneity (Table 4) shows that there was no linkage between these two characters.

Table 5 shows the Chi-square test of a 39:13:9:3 ratio for segregation of petiole color and pinnae number, assuming independence. The high Chi-square value and low probability suggests that one or more assumptions are incorrect. The Chi-square value can be divided into its component parts to determine which assumption is incorrect (Table 6). The Chi-square value for petiole color is due to deviation from a 3:1 ratio; for pinnae number, the result of deviation from a 13:3 ratio; and the interaction

TABLE 4.--Chi-square test of bolting and non-bolting groups for heterogeneity of pinnae number in pooled F_2.

Vernalization Response	Phenotypes		Chi-square
	P_1	P_2	
Bolting	171	740	0.165
Non-bolting	33	164	0.296
All	204	904	0.028

Chi-square for heterogeneity 0.423; $0.6 > p > 0.5$

TABLE 5.--Chi-square test of goodness of fit to a 39:13:9:3 ratio of green P_2:yellow P_2:green P_1:yellow P_1 assuming independence.

Petiole Color	Pinnae Type	Observed	Expected	Chi-square
Green	P_2	693	675	0.480
Yellow	P_2	211	225	0.871
Green	P_1	186	156	5.769
Yellow	P_1	18	52	22.231
				29.351

$P < 0.0001$

TABLE 6.--Components of Chi-square test for goodness of fit to a 39:13:9:3 ratio between petiole color and pinnae number.

Chi-square due to	df	Chi-square	Probability
Petiole color	1	10.633	0.001 - 0.002
Pinnae number	1	0.028	0.95 - 0.90
Interaction (linkage)	1	18.690	less than .0001

is due to linkage. The high Chi-square value for linkage suggests that linkage is present between petiole color and pinnae number.

Leaf Shape

The leaf shape of the two parents is shown in Figure 4. The MSU 130 parent on the right is deeply toothed, while the Golden Plume parent is shallowly toothed. Visual inspection of the two leaf shapes suggested that there was a difference in the area per units of length of the leaflet. For the leaf shape character regression analysis was used.

Figures 5 and 6 show the scatter diagrams of the parental types and their regression equations. The best equations in each case were the logarithmic functions expressing the log of the length of the leaflet in millimeters as a function of the log of the leaf area in square centimeters. The r-values of the lines are 0.87 and 0.84 for Golden Plume and MSU 130 respectively. The regression lines were tested for differences with a t-test using the formula of Steel and Torrie (53):

$$t = \frac{b_1 - b_2}{\sqrt{S_p^2 \left(1/\Sigma x_{1j}^2 + 1/\Sigma x_{2j}^2\right)}}$$

where: b_1 and b_2 are the regression coefficients of lines 1 and 2 respectively.

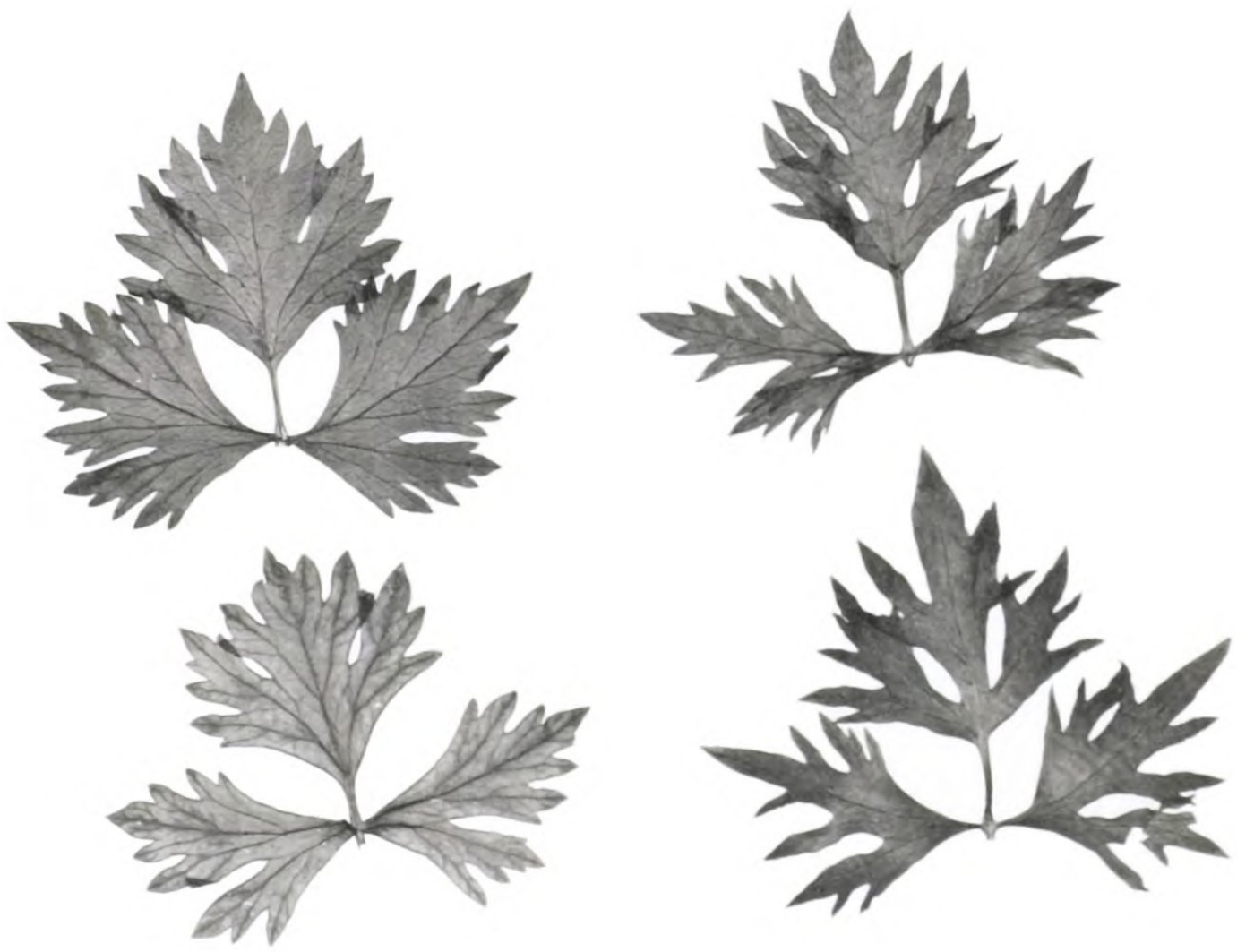


Figure 4.--Leaf shape of the two parental types. Left, Golden Plume (P_2) shallowly toothed; right, MSU 130 (P_1) deeply toothed.

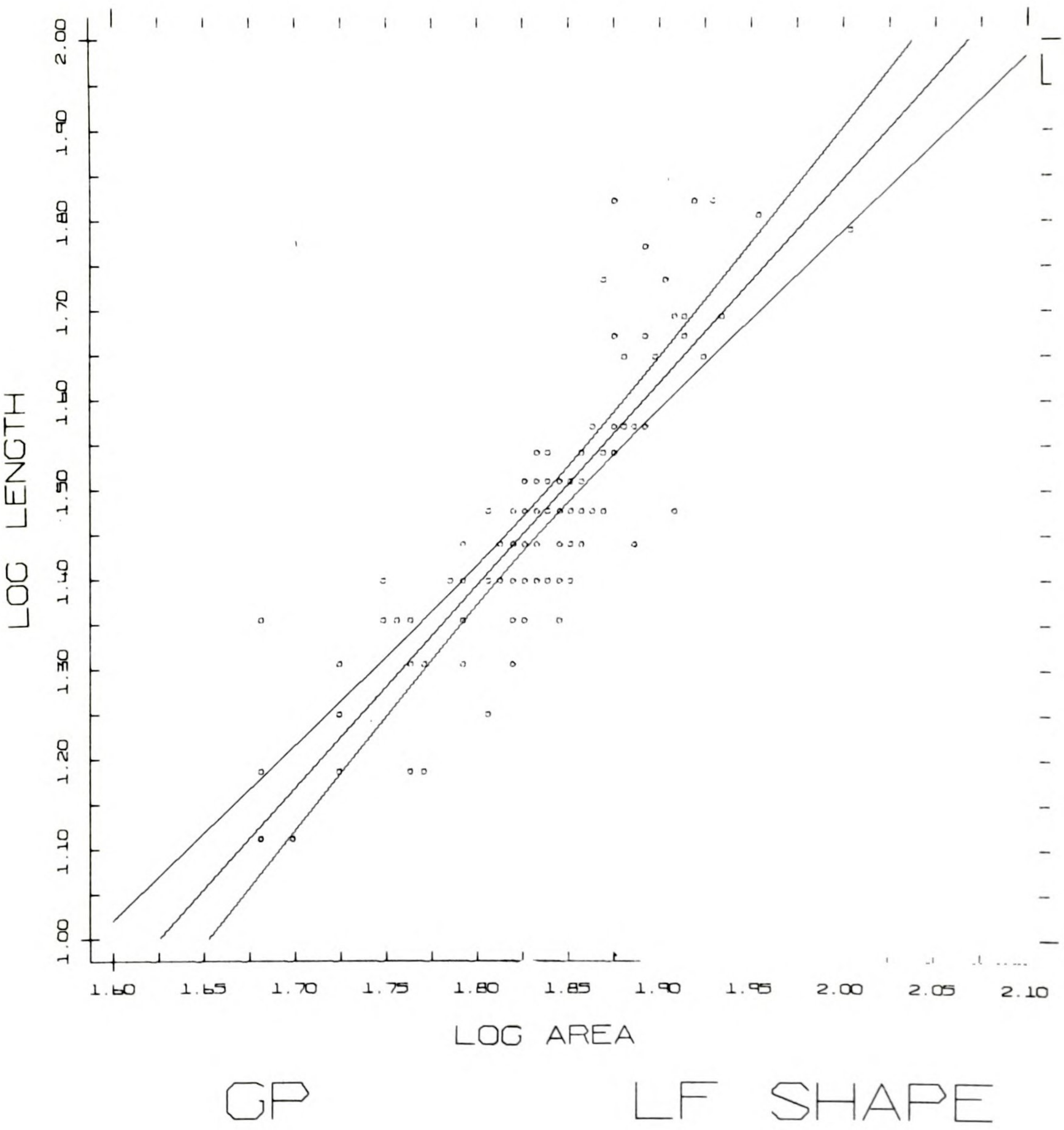


Figure 5.--Scatter diagram of leaf shape data, regression line (y = -2.6742 + 2.2602x), and 1% confidence belts about the regression line for the Golden Plume parent.

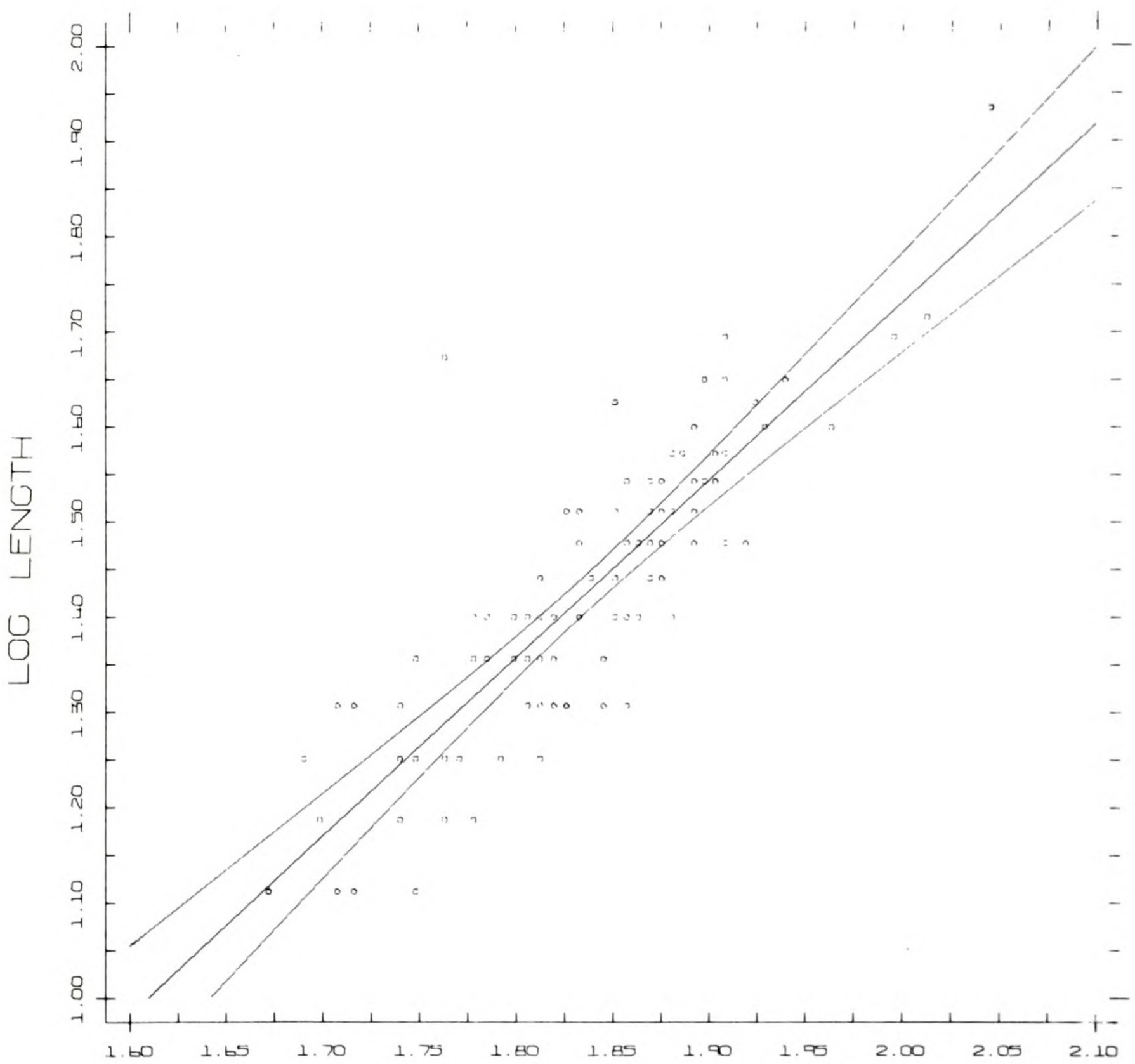


Figure 6.--Scatter diagram of leaf shape data, regression line (y = -2.0132 + 1.8718x), and 1% confidence belts about the regression line for the MSU 130 parent.

S_p^2 is the weighted average of the error sum of squares for each line divided by the sum of the error degrees of freedom.

Σx_{1j}^2 and Σx_{2j}^2 are the sum of the squared deviations from the mean of the x variable for lines 1 and 2 respectively.

The t-value was 7.27 which is significant at the 0.01 level indicating that the regression lines are different. Confidence belts about the regression lines were determined using the formula of Steel and Torrie (53):

$$\bar{y} + bx \pm t\alpha s_{y \cdot x} \sqrt{\frac{1}{n} \quad \frac{(X - \bar{x})^2}{\Sigma x^2}}$$

where: $\bar{y} + bx$ is the regression line.

t is Student's t for n-2 degrees of freedom.

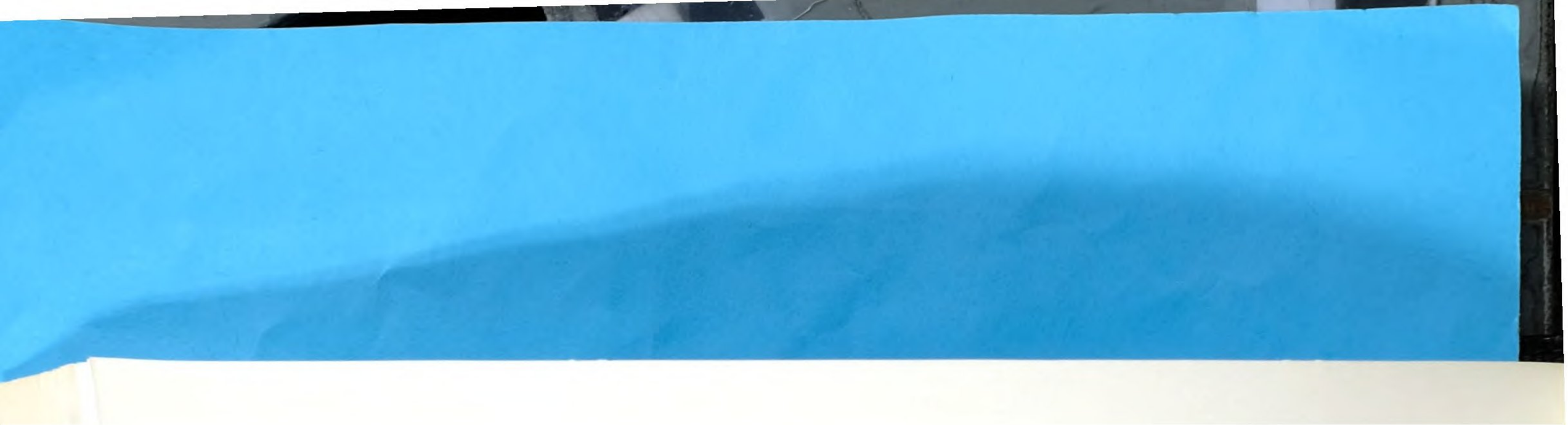
$s_{y \cdot x}$ is the square root of the error mean square of the regression line.

X is some value of the horizontal variable.

$\bar{x}$ is the mean of the horizontal variable.

Σx^2 is the sum of the squared deviations from the mean.

Division of the F_2 into classes was accomplished by use of the parental regression lines and their confidence belts. Figures 7 and 8 show the scatter diagrams of the two F_2 populations. The pooled F_2 population was divided into the various classes as shown in Figure 9. The number



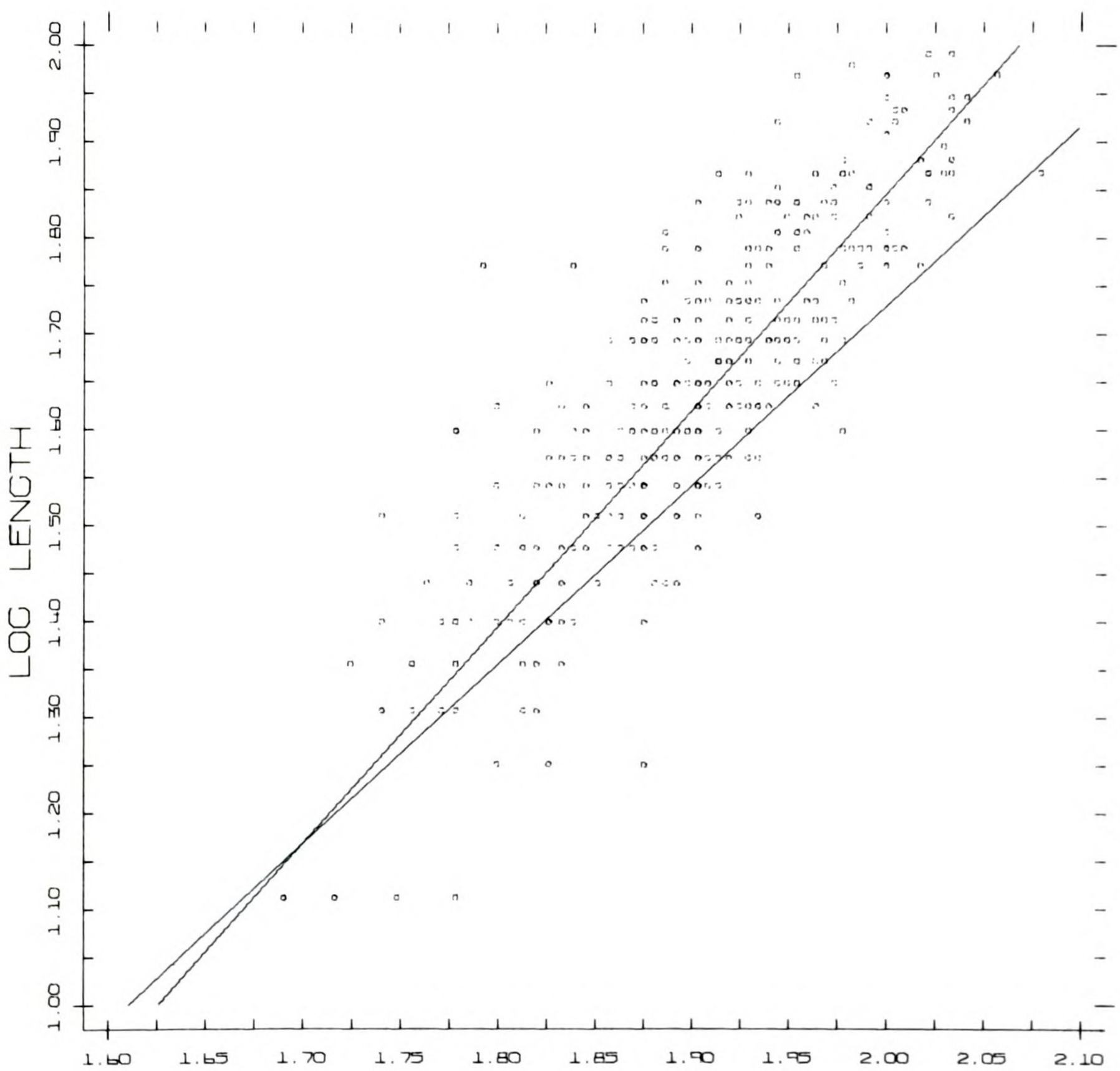


Figure 7.--Scatter diagram of leaf shape data for 980 (MSU 130 x Golden Plume) and parental regression lines.

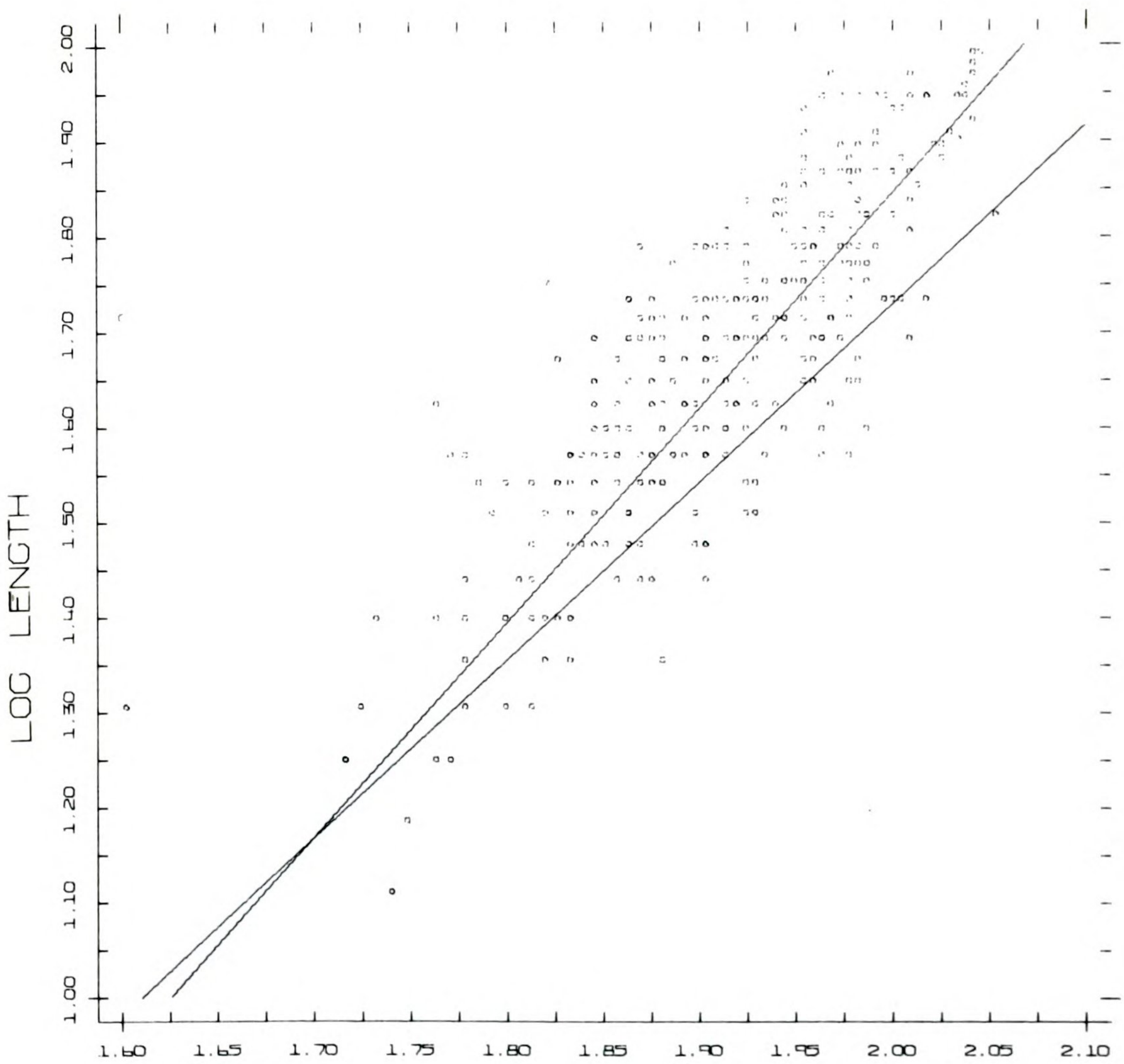


Figure 8.--Scatter diagram of leaf shape data for 981 (Golden Plume x MSU 130) and parental regression lines.

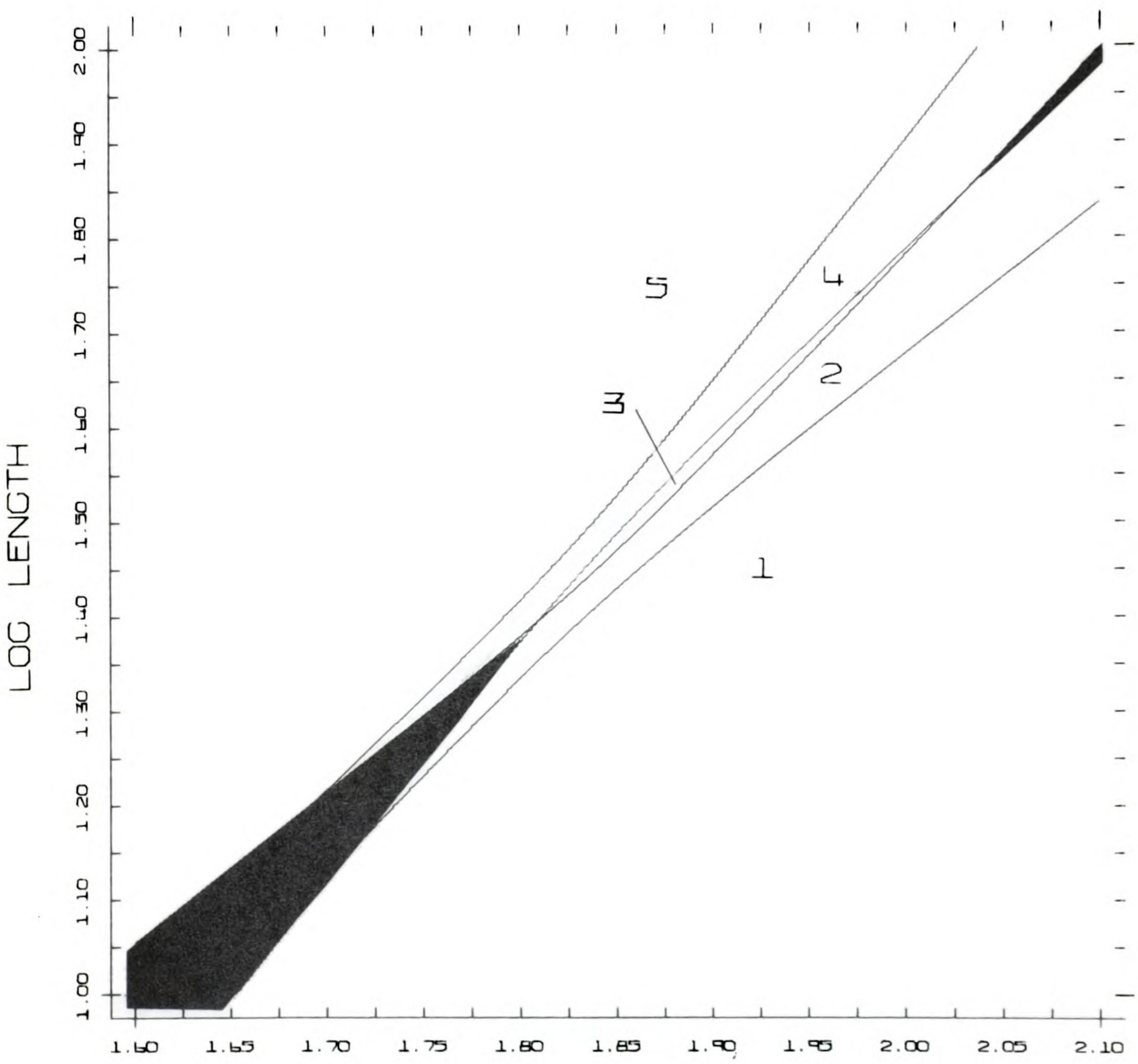


Figure 9.--1% confidence belts for both parents showing five leaf shape classes in the F_2 population. (All observations in overlapping confidence belts--shaded area--were dropped).

of F_2 individuals falling in each class is shown in Table 7. The F_2 populations were tested for homogeneity prior to pooling the data. A bimodal distribution was obtained when the class values were plotted against the frequencies in each class. The dividing point or separation class appears to be at class 3 since it contained the smallest number of individuals. Classes 1, 2, and half of class 3 are of the P_1 phenotype (MSU 130) and classes 4, 5, and half of class 3 are of the other parental phenotype (Golden Plume). The division into two parental phenotypes suggested a segregation characteristic of a single gene pair with a probability of 0.20 - 0.15, suggesting an acceptable fit. This character will be designated dt for deeply toothed; the other allele Dt, is the dominant form which results in shallowly toothed leaves.

Further genetic analysis of leaf shape data was made by means of discriminant analysis. Webber (69, 70, 71) suggested the use of discriminant analysis when the trait in question was complex and the character could best be described by more than one measurement. Since leaf shape cannot be described by a single measurement, it was felt that discriminant analysis might be useful. The method used was described by Miller (31). The discriminant function used was $X = .07107\ a + .49121\ b - .86813\ c$, where:

TABLE 7.--Chi-square test for goodness of fit for pooled F_2 populations from reciprocal crosses of MSU 130 x Golden Plume based on a one factor pair hypothesis for leaf shape.

Class	Observed	Leaf type	Expected	Chi-Square
1	52			
2	104	169 P_1(dt)	185.25	
3	26			
4	230	572 P_2(Dt)	555.75	0.475
				1.900
5	329			

0.20 > p > 0.15

a is the dry weight of the leaflet in milligrams.

b is the length of the leaflet in millimeters.

c is the area of the leaflet in square centimeters.

Application of this function to the parental and F_2 data gave the relative frequencies as shown in Figure 10. The frequency distribution of the F_2 populations showed a bimodal character when plotted against the discriminant values (X). This dip occurred at a value where the parental distributions showed a dip. The dip in the parental distributions occurred between 18 and 19. The separation point between 18 and 19 gave a 181:562 ratio in the F_2. A Chi-square of 0.165 with a P value of 0.70 - 0.60 gave a good fit to a 3:1 ratio.

Independence tests for leaf shape as determined by regression analysis showed that petiole color and vernalization response were independent of leaf shape.

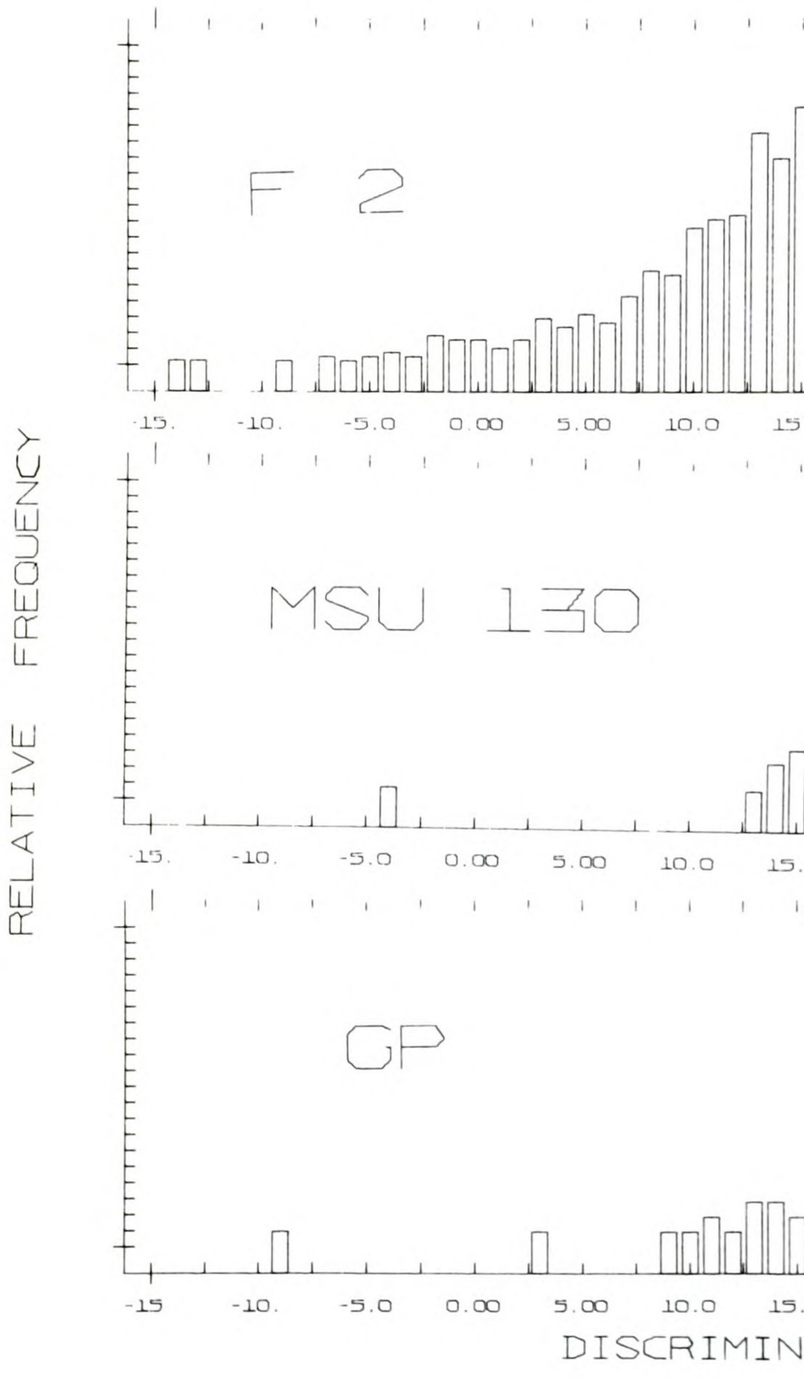


Figure 10.--Relative frequency of MSU
and pooled F_2 from the re
Golden Plume^2 x MSU 130 in
value classes.

SUMMARY

1. The progenies of reciprocal crosses between Golden Plume and MSU 130 together with the parents were evaluated to determine the mode of inheritance of vernalization response, petiole color, pinnae number, and leaf shape.

2. The "easy" bolting condition of the Golden Plume was effected by one major dominant gene, designated Vr for vernalization response, and minor genes affecting the action of the major gene. Cytoplasmic factors were also present.

3. Yellow petiole color was conditioned by a single gene which was recessive to green petiole, as previously reported. The factor for petiole color was independent of that for vernalization response.

4. Two genes controlling pinnae number were established which segregated in a 13:3 ratio. Six to eight pinnae is dominant to 10 to 12 pinnae. Pinnae number was independent of vernalization response but is thought to be linked with petiole color.

5. Leaf shape was conditioned by a single gene pair when the data were analyzed by either regression analysis

or discriminant analysis. This gene pair was designated _dt_ for deeply toothed. Shallowly toothed leaves (_Dt_) are dominant to deeply toothed. Leaf shape as determined by regression analysis was independent of vernalization response and petiole color.

THE INHERITANCE OF SEVERAL CHARACTERISTICS IN CELERY AND TOMATO

II

THE INHERITANCE OF FRUIT SHAPE, BEAKED FRUIT, SEPAL LENGTH, SEPAL SHAPE, AND PEDICEL LENGTH IN TOMATO (*Lycopersicon esculentum* Mill)

INTRODUCTION

Mechanical harvesting of tomatoes is increasing each year. One of the problems associated with mechanical harvesting is fruit damage. One type of fruit damage is punctured fruit which may occur when a pedicel from one fruit punctures another fruit. These punctures are sites for rot infestation and, if soiled, are difficult to wash, thus increasing the bacterial and fungal content of the processed product.

Puncture damage can be eliminated by breeding varieties that are free of pedicels when the fruits are harvested. The separation of the pedicel from the fruit at harvest can be effected when one of the jointless genes is present in the variety. The jointless characters in existent stocks are often associated with undesirable characters such as reduced yield and poor quality. Another more serious problem is that the fruit is often very difficult to separate from the pedicel.

Short pedicel length may help solve the fruit puncture problem. If the pedicels were short (i.e., below the shoulders of the fruit), they would avoid puncturing other fruits. The fruit would also separate easily from the

plants. For the fresh market, the calyx and short pedicel would add to the attractiveness of the harvested fruit. In the Cleveland, Ohio and Grand Rapids, Michigan area, the greenhouse growers are clipping the pedicel and using the calyx as a "trademark" for greenhouse grown tomatoes.

The objectives of this study were:

1. To identify the factors controlling the inheritance of pedicel length, sepal length, sepal shape, and fruit shape.
2. To establish linkage relationships between the above characters and with factors conditioning beaked fruit.

REVIEW OF LITERATURE

Genetically, the tomato is more widely studied than any other horticultural species. In spite of this wealth of information, there are few genetic studies of sepal shape or length. Young and MacArthur (77) described a gene affecting sepals which they designated macrocalyx, mc. The recessive allele expresses itself as very large sepals, almost the size of leaflets. Young (75) described a character called fleshy calyx, fl, which expresses itself in the recessive condition as fleshy calyx bases. Rick and Robinson (44) reported that Cl-l (cleistogamous flowers) or a closely linked allele affected sepal length; homozygous Cl-l produces longer sepals than homozygous cl-l or the heterozygote.

Reynard (39) noted differences between tomato lines for pedicel length. He reported tomato lines with pedicel lengths ranging from 9 to 22 millimeters. Although no genetic studies were reported, he suggested the symbol lp to designate long pedicel. Culp (11) found pedicel length was controlled by a single gene in castor beans, Ricinus communis L.

Several investigators have attempted to determine the mode of inheritance of fruit shape in tomato. Yeager (74) reported the gene Lc for locule number, which affected fruit shape. Few (two or three) locules was dominant to many and in the presence of O produced round fruit. Lc and o together produced oval fruit and O and lc produced oblate or flat fruit. Yeager postulated that the o and lc combination should produce round fruit; however, he did not observe plants of this genotype in his investigations. Young and MacArthur (77) reported the combination of o and lc produced a giant plum-shaped phenotype.

Dennett and Larson (14) concluded from their data that fruit shape was determined by a single gene pair designated as Ol. Non-ovate fruit was dominant over ovate fruit. The allele, ol, or a very closely linked gene also caused a marked increase in locule number. In their studies a non-ovate, few loculed or an ovate, many loculed plant was not observed.

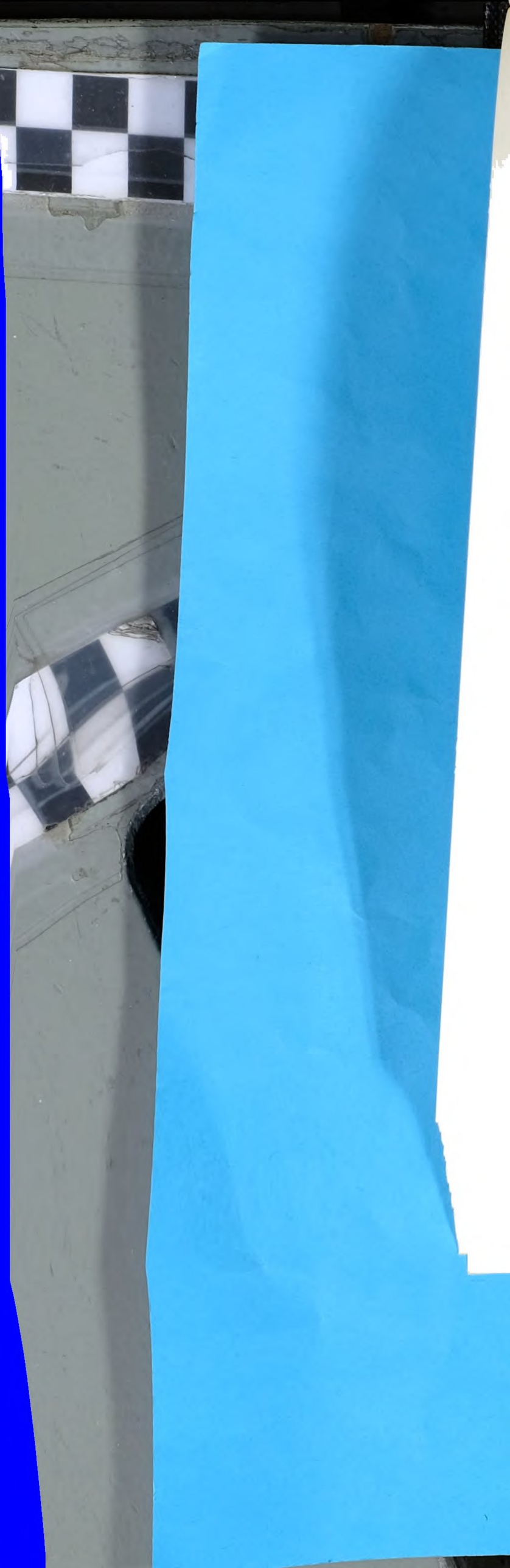
Warren (68) investigated fruit shape in tomatoes and found that two complementary genes were responsible for the expression of round vs. oblate fruit shape. He concluded that A_B_ gave a deep fruited phenotype while A_bb, aaB_, and aabb all produced shallow fruited phenotypes.

Currence (12) showed o and s (compound inflorescence) were linked with a cross-over value of 20.0%.

Yeager (74) reported lc to be located 20.5 cross-over units from the s locus on the opposite end of the chromosome from the o locus.

Young and MacArthur (77) reported a recessive gene, bk, which expresses itself as a sharp beak on the blossom end of the fruit. Boswell (4) discovered a gene with similar effect, n, for nipple-tip fruit. This gene is inherited as a simple recessive to normal fruit.

There are many instances of recessive and dominant mimics in the literature of tomato genetics. Rick (41) reported a dominant gene, f^D, which causes fasciated fruit to be allelic to f which causes fasciation in the recessive condition. The gene, V-3, which causes virescence, is inherited as a dominant character (27), while v-2 causes virescence in the recessive condition (25). Crn-1 and crn-2, crimson 1 and 2, have similar effects on fruit color but are not inherited in the same way (6).



MATERIALS AND METHODS

Plants with short and long pedicels and sepals and contrasting sepal shapes and fruit characteristics were derived from a cross between VF13-L, VF145-B, and a MSU jointless (j-1) line. The parents were selfed and the resulting plants were grown to establish uniformity. Plants from uniform lines were selfed again prior to using them for hybridization in the greenhouse.

Seeds of both parents, the F_1, and F_2 were planted in vermiculite. When the cotyledons had fully expanded, the seedlings were transplanted into flats. The treatment contained 70 plants of both parents and the F_1 and 280 plants of the F_2. When the plants reached an appropriate size, they were transplanted to the field. During the growing season, the plants were fertilized and irrigated as necessary.

Data were taken in the following manner: Two fruit clusters were removed from each plant; at least one fruit and, whenever possible, two mature green fruits were sampled from each cluster; the length, equatorial diameter (to be called breadth for the remainder of this thesis), pedicel length, and fruit characteristic (beaked

or non-beaked) were recorded for each fruit. The means of two to four observations from each plant were used for all calculations.

A calyx, considered to be typical of the plant, was pressed in an herbarium press. When the calyx had dried, the samples were measured and scored for acuminate or ensiform sepal shape. The mean of two sepal measurements was used to describe sepal length. All data were punched on IBM cards for statistical analysis. Observed frequencies were compared to theoretical frequencies by means of the Chi-square test.

RESULTS AND DISCUSSION

Fruit Shape

Parental and F_1 fruit shapes are illustrated in Figure 11. The P_1 parent mean length:breadth ratio was 2.08 ± 0.253 while the P_2 parent mean ratio was 0.99 ± 0.039. The F_1 mean ratio was 1.52 ± 0.007 and the F_2 mean ratio was 1.52 ± 0.358. The frequency distributions for these populations may be seen in Figure 12.

Hypotheses on the inheritance of fruit shape were based on the following observations:

1. The F_1 mean was approximately midway between the parental means (1.54 calculated, 1.52 observed).
2. The distribution of the F_1 slightly overlaps the distribution of the long-fruited parent (P_1).
3. Fruit shapes occurred in the F_2 which were not present in the P_1, P_2, or the F_1 populations.

The F_2 population was divided into classes according to the distributions of the P_1, P_2, and F_1. All plants with length:breadth ratios of 0.90 to 1.05 were considered class 1 or the P_2 phenotype. Plants whose

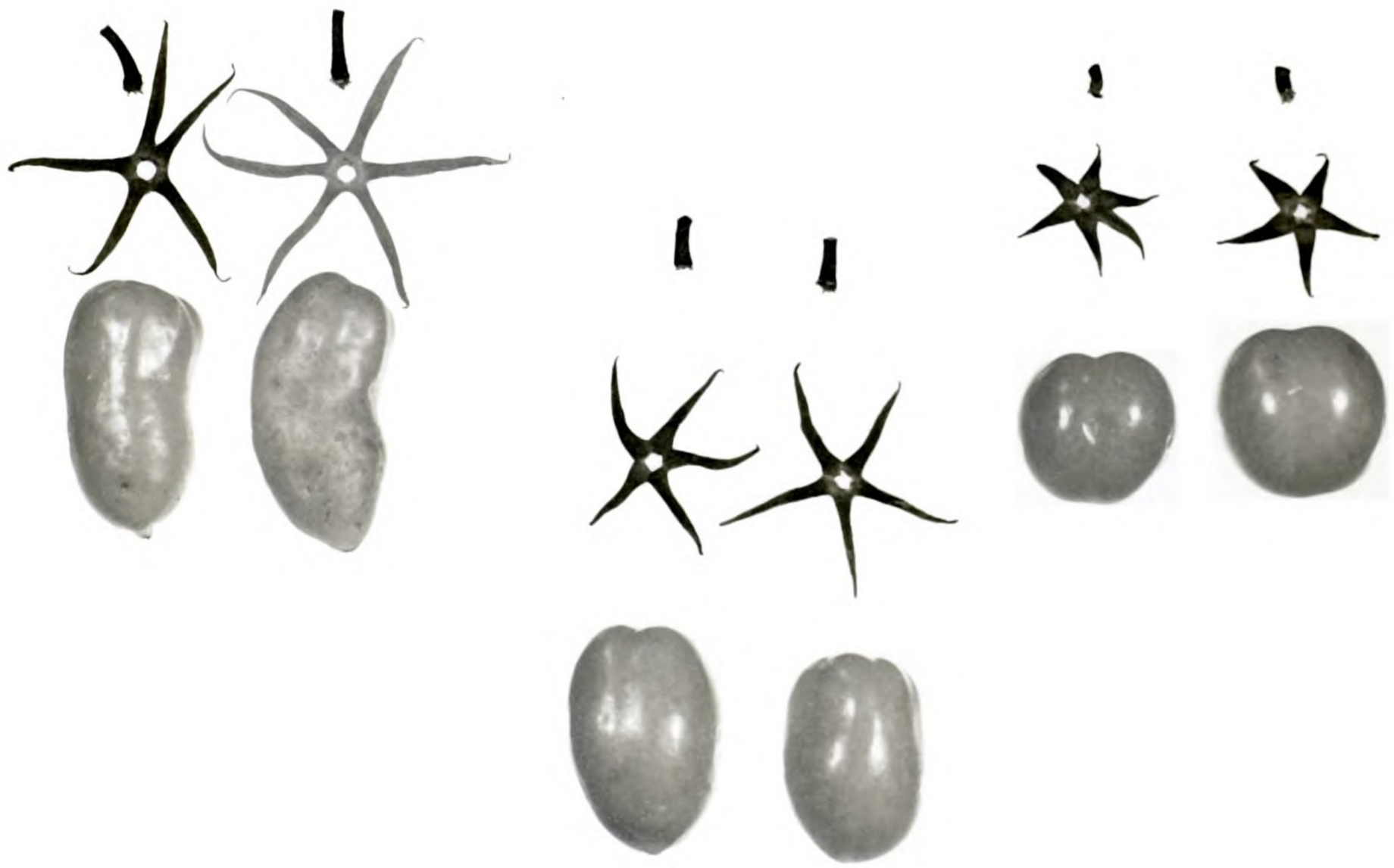


Figure 11.--Parental and F_1 fruits, calyxes, and pedicels upper left P_1, upper right P_2, and lower center F_1 (see text for fruit length: breadth ratios).

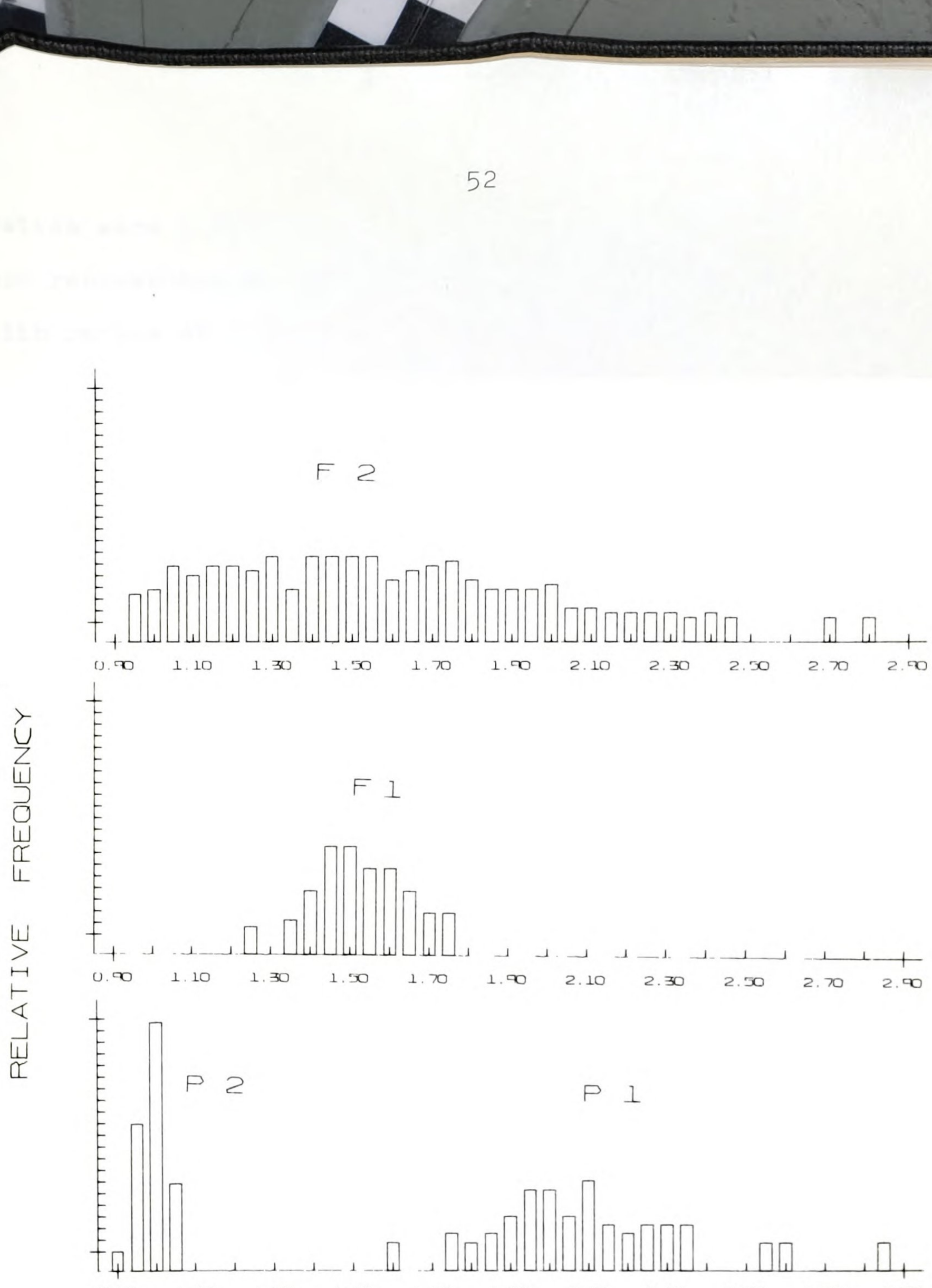


Figure 12.--Relative frequency of fruit shape ratios for parental, F_1, and F_2 populations.

ratios were 1.10 to 1.35 are classified class 2, a class not represented by the P_1, P_2, or F_1 populations. Plants with ratios of 1.40 to 1.75 are classed in class 3 or the F_1 phenotype. Plants with ratios greater than 1.80 were placed in class 4, the P_1 phenotype.

In the F_2, the mean length:breadth ratio of 1.01 ± 0.042 for class 1 did not differ significantly from the value of 0.99 ± 0.039 for the P_2 population (t = 2.09). The length:breadth ratios 1.21 ± 0.074 for class 2 and 1.53 ± 0.108 for class 3 did not differ significantly from the F_1 ratio of 1.52 ± 0.007 (t = 0.538). The ratio of 1.97 ± 0.227 for class 4 did not differ significantly from the P_1 ratio of 2.08 ± 0.253 (t = 2.50).

It appears that two genes are responsible in determining fruit shape and that the P_1 parent carries the recessive alleles at both loci, while the P_2 parent is dominant at both loci. The fruit shape genes are designated as $\underline{o}^{rf}$ and $\underline{Lc}^{rf}$. Postulated genotypes and phenotypes are listed below:

$\underline{o}^{rf}\underline{o}^{rf}\underline{Lc}^{rf}\underline{Lc}^{rf}$ round fruit, P_2 phenotype, class 1

$\underline{o}\ \underline{o}\ \underline{lc}\ \underline{lc}$ long fruit, P_1 phenotype, class 4

$\underline{o}^{rf}\underline{o}\ \underline{Lc}^{rf}\underline{lc}$ intermediate fruit shape, F_1 phenotype, class 3

This leaves two genotypic classes; those with one dominant allele and those with three dominant alleles.

Based on the intermediate length:breadth ratios of the F_1, it is postulated that the genes operate additively

and show no dominance when zero, one, or two dominant alleles are present. Since the distribution of the F_1 slightly overlaps the P_1 parent distribution, it is postulated that three and four dominant alleles behave phenotypically alike and make up class 4.

Table 8 shows a poor fit to a two gene additive model for fruit shape and suggests the presence of linkage. Since the two postulated genes are indistinguishable phenotypically, the standard method for determining linkage was not used. Linkage was determined in the following manner.

The genotypes of the two parents were $\underline{o}\ \underline{lc}\ /\underline{o}\ \underline{lc}$ (long fruit) and $\underline{o}^{rf}\underline{Lc}^{rf}/\underline{o}^{rf}\underline{Lc}^{rf}$ (round fruit). The F_1 genotype $\underline{o}\ \underline{lc}\ /\underline{o}^{rf}\underline{Lc}^{rf}$, at meiosis produces four types of gametes. The frequency of each of the gametes when linkage is present is influenced by the strength of the linkage. These frequencies are $1/4\ (1 + L)$, where L is a term denoting the strength of linkage, for the parental type gametes. The recombinant type gametes have a frequency of $1/4\ (1 - L)$. The F_2 phenotypic classes, postulated genotypes, and the zygotic frequency of each phenotype in terms of L may be seen in Table 9. Combining the zygotic frequencies for each phenotypic class, the expected frequency for each class (illustrated in Table 10) is obtained. Equating the expected frequencies to the

TABLE 8.--Chi-square test for goodness of fit to a two gene additive model for fruit shape assuming independence.

Class	Frequency	Observed	Expected	Chi-square
1	1/16	25	15.6	5.664
2	4/16	59	62.5	.196
3	6/16	95	90.8	.194
4	5/16	71	78.1	.644
				6.698

$0.10 < p < 0.08$

TABLE 9.--F_1 gametic frequency and F_2 genotypes, phenotypes, and zygotic frequency for fruit shape.

F_1 Gametes	Gametic Frequency
o lc	1/4(1 + L)
$o^{rf}lc$	1/4(1 - L)
o Lc^{rf}	1/4(1 - L)
$o^{rf}Lc^{rf}$	1/4(1 + L)

Phenotypic Class	Genotype	Zygotic Frequency
4	o lc /o lc	$[1/4(1 + L)]^2$
3	o lc /$o^{rf}Lc^{rf}$	$[1/4(1 + L)]^2$
4	o lc /o Lc^{rf}	1/4(1 + L)1/4(1 - L)
4	o lc /$o^{rf}lc$	1/4(1 + L)1/4(1 - L)
3	$o^{rf}Lc^{rf}$/o lc	$[1/4(1 + L)]^2$
1	$o^{rf}Lc^{rf}/o^{rf}Lc^{rf}$	$[1/4(1 + L)]^2$
2	$o^{rf}Lc^{rf}/o^{rf}lc$	1/4(1 + L)1/4(1 - L)
2	$o^{rf}Lc^{rf}$/o Lc^{rf}	1/4(1 + L)1/4(L - L)
4	$o^{rf}lc$ /o lc	1/4(1 + L)1/4(1 - L)
2	$o^{rf}lc$ /$o^{rf}Lc^{rf}$	1/4(1 + L)1/4(1 - L)
3	$o^{rf}lc$ /$o^{rf}lc$	$[1/4(1 - L)]^2$
3	$o^{rf}lc$ /o Lc^{rf}	$[1/4(1 - L)]^2$
4	o Lc^{rf}/o lc	1/4(1 + L)1/4(1 - L)
2	o $Lc^{rf}/o^{rf}Lc^{rf}$	1/4(1 + L)1/4(1 - L)
3	o $Lc^{rf}/o^{rf}lc$	$[1/4(1 - L)]^2$
3	o Lc^{rf}/o Lc^{rf}	$[1/4(1 - L)]^2$

TABLE 10.--Observed and expected frequencies of fruit shape phenotypes when linkage is considered.

Class	Expected Frequency		Observed Frequency
1	$1/16(1 + 2L + L^2)$	=	.100
2	$1/16(4 - 4L^2)$	=	.236
3	$1/16(6 - 4L + 6L^2)$	=	.380
4	$1/16(5 + 2L - 3L^2)$	=	.284

observed frequencies yields the equation $1/16(1 + 2L + L^2) = 0.100$.

The equations can be solved by use of the formula for solving quadratic equations: $x = [-b \pm (b^2 - 4ac)^{1/2}]/2a$. Since there are four equations, four estimates of L are obtained. They are: for class 1, L = 0.265; class 2, L = 0.237; class 3, L = 0.020; and class 4, L = 0.180.

The mean of these four estimates (0.176) was used as a starting point in calculating the expected frequency for each class and the Chi-square value was calculated. The value of L was increased or decreased and a new Chi-square value was calculated. The value of L was adjusted until a value of L was obtained at which the Chi-square would be lower than the Chi-square for any other value of L. This value was considered the best estimate of L.

The best estimate of L for the fruit shape genes was 0.2, which gives the expected values as shown in Table 11. The Chi-square value has two degrees of freedom since one is attributed to linkage.

The relationship between L and r, the recombination percentage, can be determined by comparing gametic frequencies. Bailey (1) gives the gametic frequencies of $1/2 (1 - r)$ for the parental type gametes and $1/2\ r$ for the recombinant gametes. Therefore, $1/4 (1 + L)$ equals $1/2 (1 - r)$ and $1/4 (1 - L)$ equals $1/2\ r$. Thus, the relation $L = 1 - 2r$ between L and r is obtained. Substituting

TABLE 11.--Chi-square test for goodness of fit to a two gene additive model for fruit shape assuming a linkage intensity value of 0.2.

Class	Observed	Expected	Chi-square
1	25	22.5	0.278
2	59	60	0.017
3	95	85	1.176
4	71	82.5	1.603
			3.074

$0.3 < p < 0.2$

0.2 for L, a value of r = 0.40 is obtained which is approximately the reported distance between o and lc.

Beaked Fruit

Young and MacArthur (77) reported beaked fruit to be conditioned by a recessive gene designated bk. This character appears as a sharp point or beak on the blossom end of the fruit. The data in this study suggest that beaked is controlled by a single dominant gene which is designated Bk-2.

Attempts were made to locate Bk-2 on the chromosome map with o^{rf} and Lc^{rf}. Since o^{rf} and Lc^{rf} are phenotypically indistinguishable, the standard methods could not be applied. The analysis was accomplished using the model on Table 12. The parental genotypes are $o^{rf}Lc^{rf}bk\text{-}2/o^{rf}Lc^{rf}bk\text{-}2$ and o lc Bk-2/o lc Bk-2. The F_1 genotype is $o^{rf}Lc^{rf}bk\text{-}2/o$ lc Bk-2 and produces eight types of gametes with the frequencies illustrated in Table 12. L_1 is designated as the linkage between o and lc and L_2 the linkage between Bk-2 and the position midway between the loci of o and lc. The linkage between beaked and o and beaked and lc is difficult to determine since the individual effects of o and lc cannot be measured.

Substituting 0.2 for L_1, the gametic frequencies as shown in the right column of Table 12 are obtained. The eight gametes recombine to produce 64 possible zygotes and eight phenotypic classes (each of the four fruit shape

TABLE 12.--Gametic types and their frequencies for fruit shape and beaked fruit.

Gametes	Frequencies	Frequencies
o Lc Bk-2	$1/8(1 + L_1 + L_2)$	$1/8(1.2 + L_2)$
o Lc^{rf} Bk-2	$1/8(1 - L_1 - L_2)$	$1/8(.8 - L_2)$
o^{rf} Lc Bk-2	$1/8(1 - L_1 + L_2)$	$1/8(.8 + L_2)$
$o^{rf}Lc^{rf}$ Bk-2	$1/8(1 + L_1 - L_2)$	$1/8(1.2 - L_2)$
o Lc bk-2	$1/8(1 + L_1 - L_2)$	$1/8(1.2 - L_2)$
o Lc^{rf} bk-2	$1/8(1 - L_1 + L_2)$	$1/8(.8 + L_2)$
o^{rf} Lc bk-2	$1/8(1 - L_1 - L_2)$	$1/8(.8 - L_2)$
$o^{rf}Lc^{rf}$ bk-2	$1/8(1 + L_1 + L_2)$	$1/8(1.2 + L_2)$

classes is divided into beaked and non-beaked fruit). Summing the frequencies of each class and solving for L_2 as in "Fruit Shape" gives an estimate for linkage between Bk-2 and the position midway between the loci of o^{rf} and Lc^{rf}. Table 13 shows the eight phenotypic classes, the observed and expected frequencies, and Chi-square test. A linkage value of 1.0 suggests that Bk-2 is linked to the position midway between the loci of o^{rf} and Lc^{rf}, or 20 recombination units from o^{rf} on one side and Lc^{rf} on the other. This corresponds closely to the position of bk from o and lc, as shown on the tomato chromosome map (9). This information suggests that bk may be allelic to Bk-2, o may be allelic to o^{rf}, and lc may be allelic to Lc^{rf}.

The effect of Lc^{rf} and lc genes on locule number was not studied in the F_2, although the $Lc^{rf}Lc^{rf}$ parent (P_2) had few locules (2-3) and the lc lc parent (P_1) had many (4 or more).

Sepal Length

The frequency distributions for sepal length of the parents, F_1, and F_2 generations are shown in Figure 13. The distribution of the sepal length of the F_1 was intermediate to the two parents. The F_2 was divided into three classes of 16 - 20, 21 - 27, and 28 - 40 mm corresponding to P_2, F_1, and P_1 phenotypes, respectively. A 61:124:65 ratio of short:intermediate:long sepals was obtained which

TABLE 13.--Chi-square test of goodness of fit to a three gene model for fruit shape and beaked fruit with a linkage intensity value of 1.0.

Fruit shape Class	Beaked	Observed	Expected	Chi-square
1	+	4	3.6	0.044
1	-	21	18.9	0.233
2	+	27	32.5	0.931
2	-	32	27.5	0.736
3	+	81	71.6	1.241
3	-	14	13.4	0.025
4	+	68	79.85	1.759
4	-	3	2.65	0.046
				5.015

$0.6 < p < 0.5$

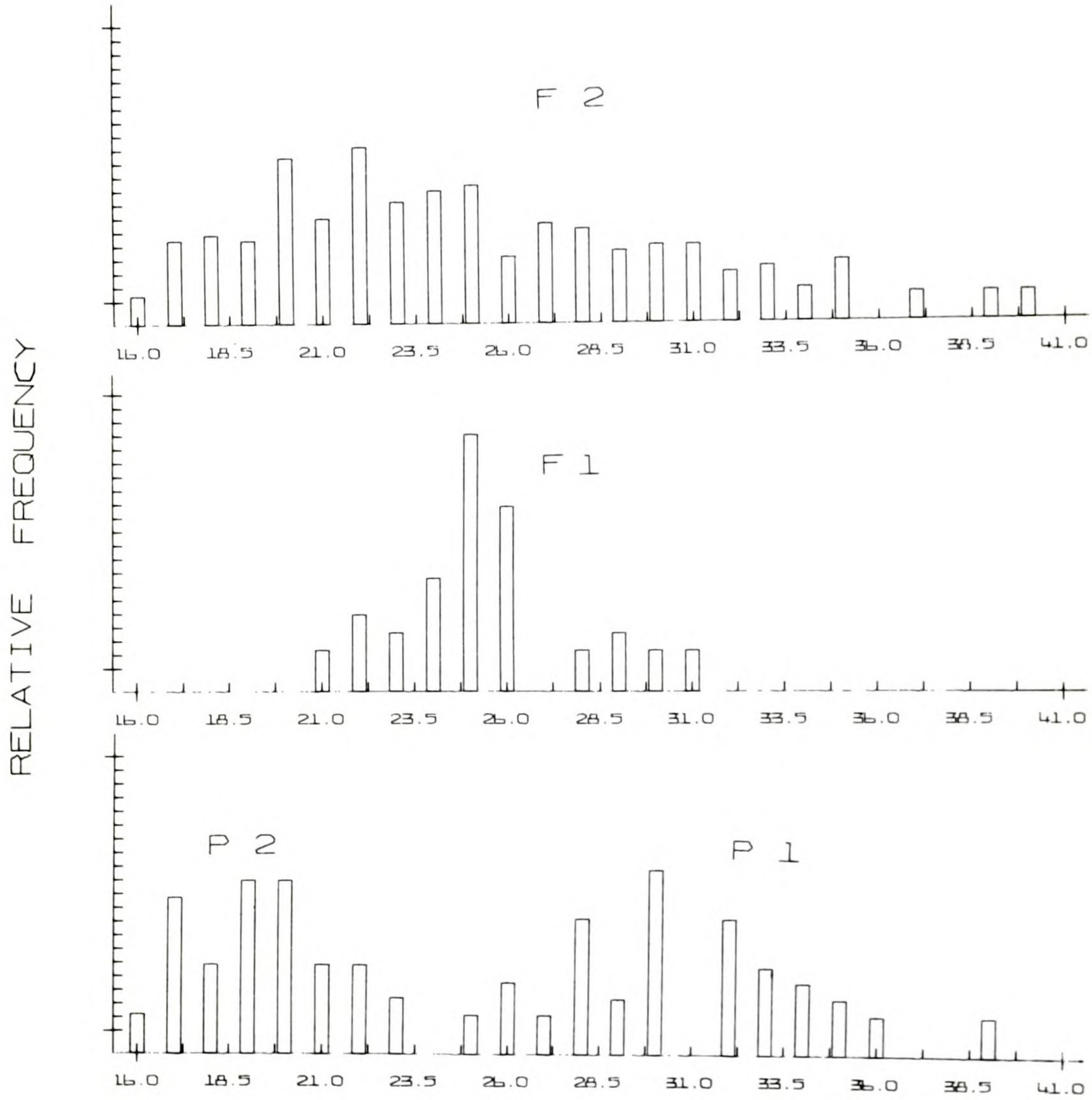


Figure 13.--Relative frequency of sepal lengths (in mm) of parental, F_1, and F_2 populations.

gave a Chi-square value of 0.144 and a P value of 0.95 - 0.90. The ratio obtained suggests that a single gene pair with incomplete dominance was responsible for sepal length. This gene is designated Sx for sepal extender. The genotype Sx Sx produces long sepals; sx sx produces short sepals; and Sx sx produces intermediate sepals.

The Chi-square test of an independent gene model for beaked fruit and sepal length gave a Chi-square value of 10.882 with a P value of 0.05 - 0.03. The low probability suggested linkage. Linkage intensity was determined by the method as outlined under "Fruit Shape." The best estimate of L was 0.212, which was used to calculate the expected frequencies illustrated in Table 14. This linkage intensity value corresponds to a recombination value of 39.4%.

The linkage intensity between sepal length and round fruit was determined similarly to "Beaked Fruit" except that the linkage was estimated from Sx to the nearest fruit shape gene. Table 15 shows the Chi-square test for a one gene additive model for fruit shape with a linkage factor of 0.52. This linkage intensity value corresponds to a recombination value of 24%.

Sepal Shape

The sepal shapes of the parents and F_1 may be seen in Figure 14. The top row depicts the recessive condition, called ensiform or sword-like, designated as en. The

TABLE 14.--Chi-square test for goodness of fit to a 3:6:3 1:2:1 ratio of sepal length and beaked fruit with a linkage intensity value of 0.212.

Sepal Length	Beaked Fruit	Observed	Expected	Chi-square
Short	+	35	39.55	0.523
Intermediate	+	93	95.15	0.049
Long	+	52	52.80	0.012
Short	-	26	22.95	0.405
Intermediate	-	31	29.85	0.044
Long	-	13	9.70	1.123
				2.156

$0.8 < p < 0.7$

TABLE 15.--Chi-square test of goodness of fit to a 1:2:1:4:8:4:6:12:6:5:10:5 ratio for sepal length and fruit shape assuming a linkage intensity value of 0.52.

Fruit shape Class	Sepal Length	Observed	Expected	Chi-square
1	Short	13	11.55	0.182
1	Intermediate	10	9.125	0.084
1	Long	2	1.80	0.022
2	Short	16	18.25	0.277
2	Intermediate	35	30.00	0.833
2	Long	8	11.75	1.197
3	Short	23	19.125	0.785
3	Intermediate	48	46.75	0.033
3	Long	24	19.125	1.243
4	Short	9	10.275	0.158
4	Intermediate	31	39.125	1.687
4	Long	31	33.05	0.127
				6.628

$0.8 < p < 0.7$

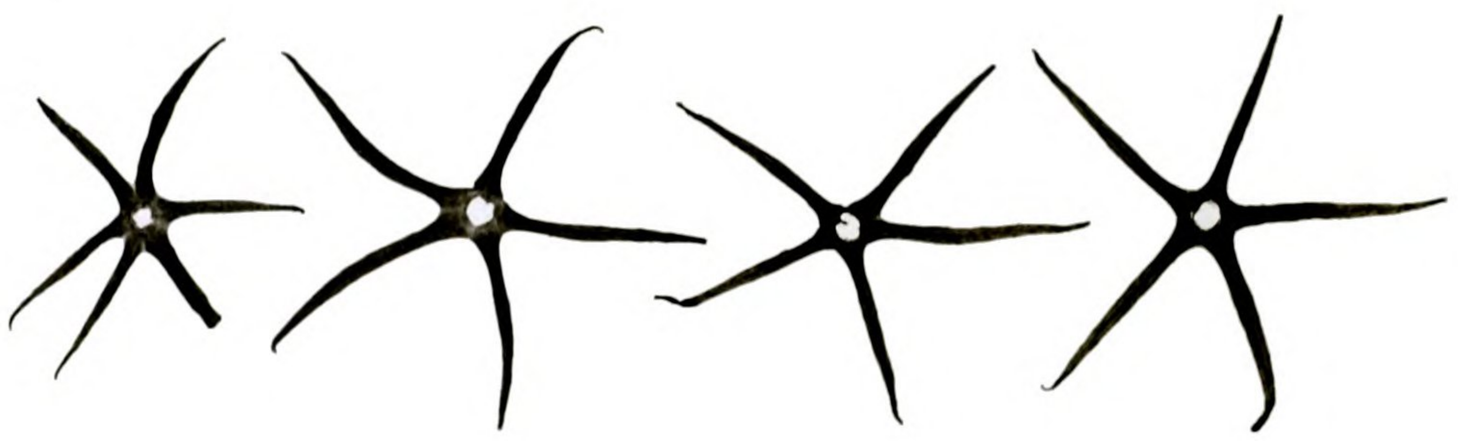


Figure 14.--Sepal shapes. Top row, recessive en showing ensiform sepals of P_1; second row, heterozygous with acuminate sepals of F_1; bottom row, homozygous En with acuminate sepals of P_2.

bottom row shows the dominant homozygote En, acuminate sepals. The center row illustrates the heterozygous condition for sepal shape. The taper of the sepal in the En parent and the F_1 begins at the base, while the taper of the recessive begins from the middle of the sepal. The ratio of En:en was 184:66 which fits a 3:1 ratio giving a Chi-square value of 0.261 with a P value of 0.7 - 0.6.

The poor fit of an independent gene model for sepal shape and beaked fruit (Chi-square = 11.461; P value 0.01 - 0.005) suggests linkage between the two genes. The linkage intensity value, L, was determined using the method as described under "Fruit Shape." Table 16 illustrates the observed and expected frequencies and the Chi-square test calculated from an estimated L value of 0.32 or a recombination value of 34 per cent. The recombination value using Immer's product method (23) was 35 per cent suggesting close agreement between the two methods.

The segregation ratios of sepal shape and sepal length may be seen in Table 17. The expected values were calculated by using the estimated L value of 0.60 or a recombination value of 20 per cent. The Chi-square test shows a good fit to the proposed ratio of 3:6:3:1:2:1 with an L value of 0.60.

The linkage intensity between sepal shape and the nearest fruit shape gene was estimated as in "Beaked Fruit." The Chi-square test of a two gene model for fruit shape

TABLE 16.--Chi-square test of goodness of fit to a 9:3:3:1 ratio for sepal shape and beaked fruit assuming a linkage intensity value of 0.32.

Sepal shape	Beaked Fruit	Observed	Expected	Chi-square
En	+	123	132.225	0.644
en	+	57	55.275	0.054
En	-	61	55.275	0.593
en	-	9	7.225	0.436
				1.727

$0.7 < p < 0.6$

TABLE 17.--Chi-square test of goodness of fit to a 3:6:3 1:2:1 ratio for sepal length and sepal shape assuming a linkage intensity value of 0.60.

Sepal Length	Sepal Shape	Observed	Expected	Chi-square
Short	En	59	60	0.017
Intermediate	En	102	105	0.086
Long	En	23	22.5	0.011
Short	en	2	2.5	0.100
Intermediate	en	22	20	0.200
Long	en	42	40	0.100
				0.514

$0.95 < p < 0.90$

and a one gene model for sepal shape with an estimated L value of 0.68 is illustrated in Table 18. This L value corresponds to a recombination value of 16 per cent.

Double cross-overs for the genes sx, en, and Bk-2 were calculated as follows. Twelve phenotypic combinations of sepal length, sepal shape, and beaked fruit resulted from the recombination of eight possible gametic genotypes as shown in Table 19. The theoretical frequency of double cross-overs for each of the phenotypes were computed. For example, the phenotype short, ensiform sepals and non-beaked fruit is the result of the following gametic combinations: sx * en Bk-2 with itself, sx * en * bk-2 with sx * en Bk-2 and its reciprocal. Of the six gametes which make up these three individuals, two of the gametes are of the double recombinant type. Thus, one-third of all individuals with the phenotype short, ensiform sepals, and beaked fruit would be double recombinants.

Since the probability of a complex event occurring is equal to the product of its several single events, it is possible to calculate the percentage of double cross-overs. The probability of an individual carrying a double recombinant gamete is 1/3 in the example above. Thus the

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*Denotes cross-over at this position.

TABLE 18.--Chi-square test of goodness of fit to a 3:1: 12:4:18:6:15:5 ratio for fruit shape and sepal shape assuming a linkage intensity value of 0.68.

Fruit shape Class	Sepal shape	Observed	Expected	Chi-square
1	En	24	21.45	0.286
1	en	1	1.05	0.002
2	En	54	53.5	0.005
2	en	5	6.5	0.346
3	En	69	67.375	0.038
3	en	26	17.625	3.980
4	En	37	45.2	1.488
4	em	34	37.3	0.291
				6.437

$0.40 < p < 0.35$

TABLE 19.--Possible types of F_1 gametes bearing the genes sx, en, and Bk-2.

Types of F_1 gametes		
Sx	en	Bk-2
Sx	en *	bk-2
Sx *	En *	Bk-2
Sx *	En	bk-2
sx *	en	Bk-2
sx *	en *	bk-2
sx	En *	Bk-2
sx	En	bk-2

*Denotes cross-over at this position.

probability of obtaining a double cross-over individual is 1/3 times the probability of a double cross-over occurring. The probability of double cross-overs is the product of two times the probability of each single cross-over. For the genes sx, en, and Bk-2, the single cross-over probability is 20 units from sx to en and 34 units from en to Bk-2. The product of two times the single cross-overs is 0.272. Therefore 1/3 x 0.272 multiplied by the number of individuals in that phenotypic class will give the probable number of individuals with double cross-overs (Table 20). The sum of the probable number of double cross-over individuals divided by the number of individuals in the population gives the frequency of double cross-overs, which was 5.73%. This figure must be doubled since each double cross-over cancels two single cross-overs, thus giving 11.5 per cent double cross-overs. 11.5 added to 39.4 gives 50.9 as the distance between sx and Bk-2.

One postulated map for the 5 genes is shown in Table 21. Another possible map could be constructed interchanging the position of o^{rf} and Lc^{rf}. All distances would remain the same.

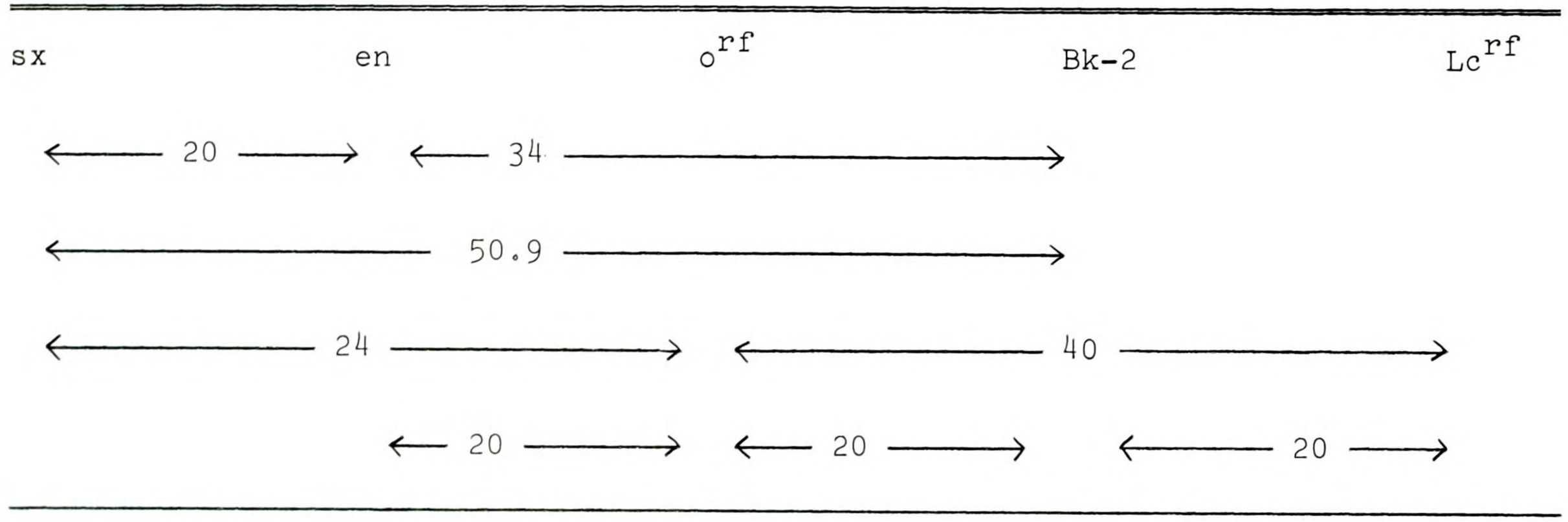
Pedicel Length

The relative frequency distributions for pedicel length of the parent, F_1, and F_2 generations may be seen in Figure 15. The inheritance of pedicel length appears

TABLE 20.--Phenotypes in the F_2, observed individuals in the phenotypic classes, and calculated cross-over individuals for sepal length and shape and beaked fruit.

Sepal Length	Sepal Shape	Beaked Fruit	Observed	Calculated cross-over individuals
Short	En	+		
Short	En	-	24	2.177
Short	en	+	1	0.091
Short	en	-	1	1.000
Intermediate	En	+	74	6.712
Intermediate	En	-	28	1.268
Intermediate	en	+	19	0.861
Intermediate	en	-	13	0.408
Long	En	+	15	1.814
Long	En	-		
Long	en	+		
Long	en	-		

TABLE 21.--One postulated order and distance between the genes o^{rf}, Lc^{rf}, Bk-2, en, and sx



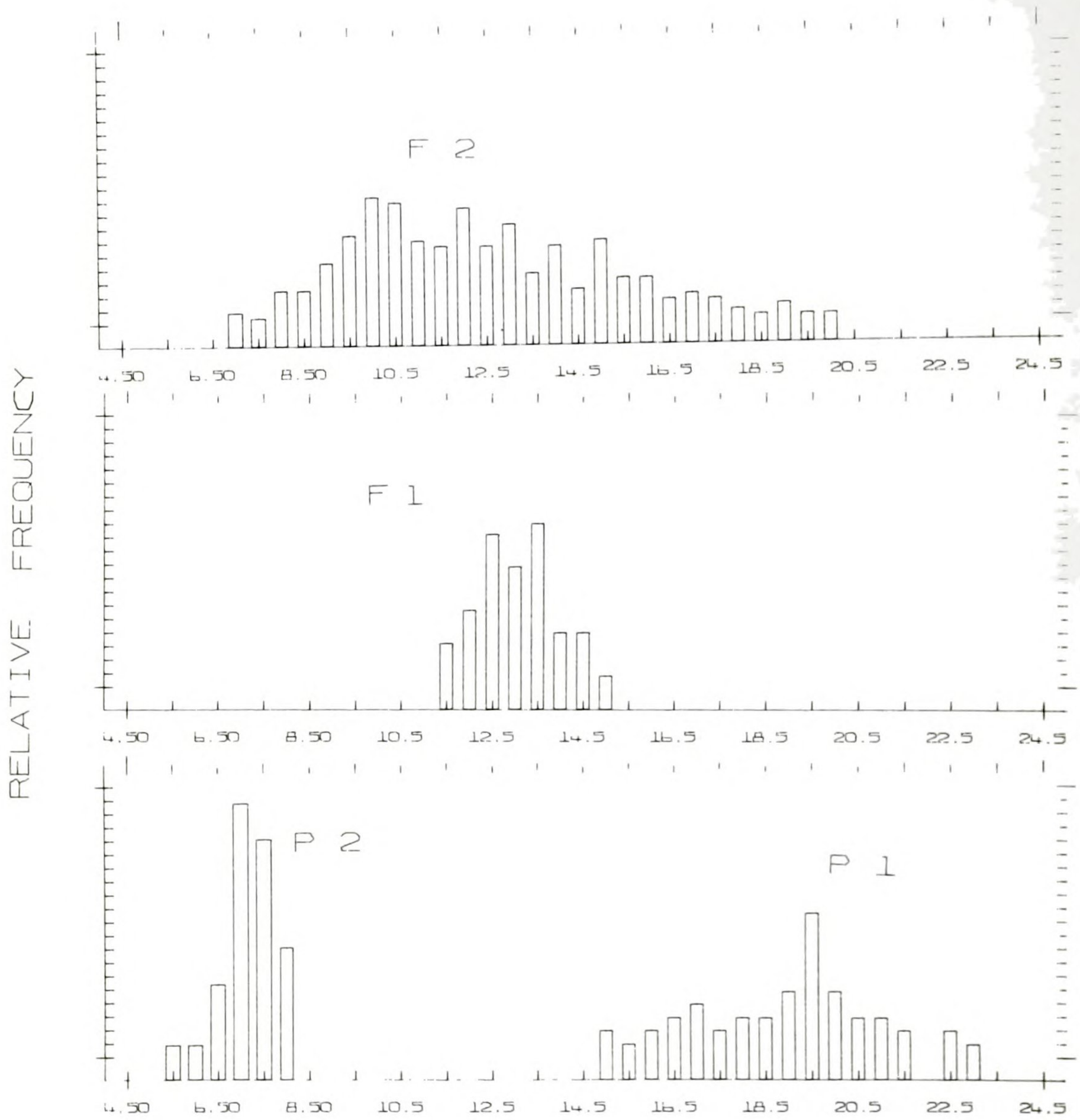


Figure 15.--Relative frequency distributions of pedicel length for parental, F_1, and F_2 populations.

to be polygenic. The mean length of the F_1 is 12.99 ± 0.810 which is approximately midway between the parental means of 7.20 ± 0.525 and 19.7 ± 2.205. The mean pedicel length of the F_2 is 12.28 ± 2.809 and does not differ significantly from the mean of the F_1 ($t = 1.952$).

The correlation coefficients between pedicel length and the characters described above were calculated to determine if pedicel length was associated with any of the characters. These coefficients are illustrated in Table 22. All correlation coefficients are significant at the 0.005 level. It may be noted that the magnitude of the correlation coefficients is in the following order: Sepal length, sx; sepal shape, en; fruit shape and beaked fruit, Bk-2. This is the order postulated from the recombination data.

TABLE 22.--Correlation coefficients between pedicel length, sepal length, sepal shape, fruit shape, and beaked fruit.

	Fruit Shape	Sepal Shape	Sepal Length	Pedicel Length
Beaked fruit	0.548	-0.192	0.181	0.266
Fruit shape		-0.360	0.370	0.408
Sepal shape			-0.562	-0.438
Sepal length				0.545

All coefficients significant at 0.005 level.

SUMMARY

1. The progenies of two genetic lines MSU A7 and MSU B12 together with the parents were evaluated to determine the mode of inheritance of fruit shape, beaked fruit, sepal length, sepal shape, and pedicel length.

2. The character fruit shape was conditioned by two genes, designated $\underline{o}^{rf}$ and $\underline{Lc}^{rf}$, which may be allelic to $\underline{o}$ and $\underline{lc}$, respectively. These genes behaved in the following way:

$\underline{o}^{rf}\underline{o}^{rf}\underline{Lc}^{rf}\underline{Lc}^{rf}$ produces round fruit (length:breadth ratio = 1.01 ± 0.042).

$\underline{o}^{rf}\underline{o}^{rf}\underline{Lc}^{rf}\underline{lc}$ and $\underline{o}\ \underline{o}^{rf}\underline{Lc}^{rf}\underline{Lc}^{rf}$ produces slightly oval fruit (length:breadth ratio = 1.21 ± 0.074).

$\underline{o}^{rf}\underline{o}\ \underline{Lc}^{rf}\underline{lc}$, $\underline{o}^{rf}\underline{o}^{rf}\underline{lc}\ \underline{lc}$, and $\underline{o}\ \underline{o}\ \underline{Lc}^{rf}\underline{Lc}^{rf}$ produces an oval fruit (length:breadth ratio = 1.53 ± 0.108).

$\underline{o}^{rf}\underline{o}\ \underline{lc}\ \underline{lc}$, $\underline{o}\ \underline{o}\ \underline{lc}\ \underline{Lc}^{rf}$, and $\underline{o}\ \underline{o}\ \underline{lc}\ \underline{lc}$ produce a long fruit (length:breadth ratio = 1.97 ± 0.227).

The two fruit shape genes were linked with a recombination value of 40%.

3. The character beaked fruit was conditioned by a single dominant gene, designated Bk-2, and may be allelic to bk. Bk-2 is postulated to be located approximately midway between the loci of o^{rf} and Lc^{rf}.

4. Sepal length was controlled by a single gene pair with no dominance. Sx, for sepal extender, when homozygous, effects a long sepal (30.60 ± 3.075 mm); sx, when homozygous, effects short sepals (19.36 ± 1.808 mm); and Sx sx effects an intermediate sepal length (25.24 ± 2.112 mm). This character was linked to Bk-2 with a recombination value of 39.4% and to the nearest fruit shape gene with a recombination value of 24%.

5. Sepal shape was determined by a single gene pair with acuminate sepal shape being dominant to ensiform or sword-shaped sepal. This character was designated en. En was linked to the nearest fruit shape gene with a recombination value of 20%, with beaked fruit Bk-2 (recombination value 34%) and with sx (recombination value 20%).

6. The character pedicel length was inherited polygenically. Correlation values suggest some of the genes for this character might be linked to the genes above.

CONCLUSIONS

Several important characters were shown to be heritable. Knowing the inheritance of bolting would be helpful in a breeding program since bolting resistance in celery is an important horticultural character.

Leaf shape, pinnae number, and petiole color in celery are not associated with bolting.

Fruit shape and pedicel length in tomato are important horticultural characters, and knowledge of their inheritance and linkage relationships is useful in a breeding program. Presently sepal size and shape are not economically important characters. If short pediceled varieties are introduced, the shape and size of the calyx would become more important and knowledge of their inheritance and linkage relationships would be useful.

In addition to the practical importance of the information in this thesis there is also a contribution to the knowledge about the species.

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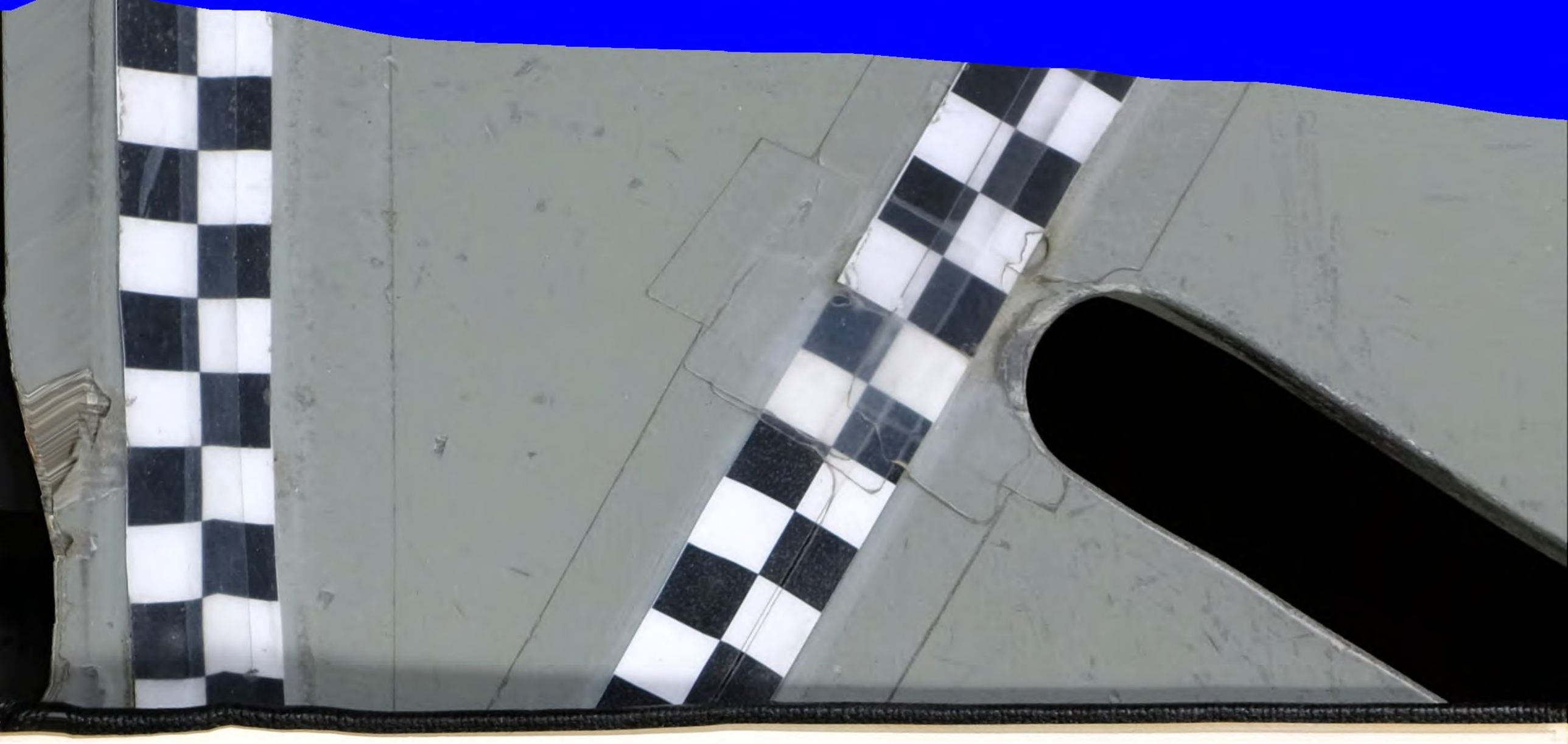

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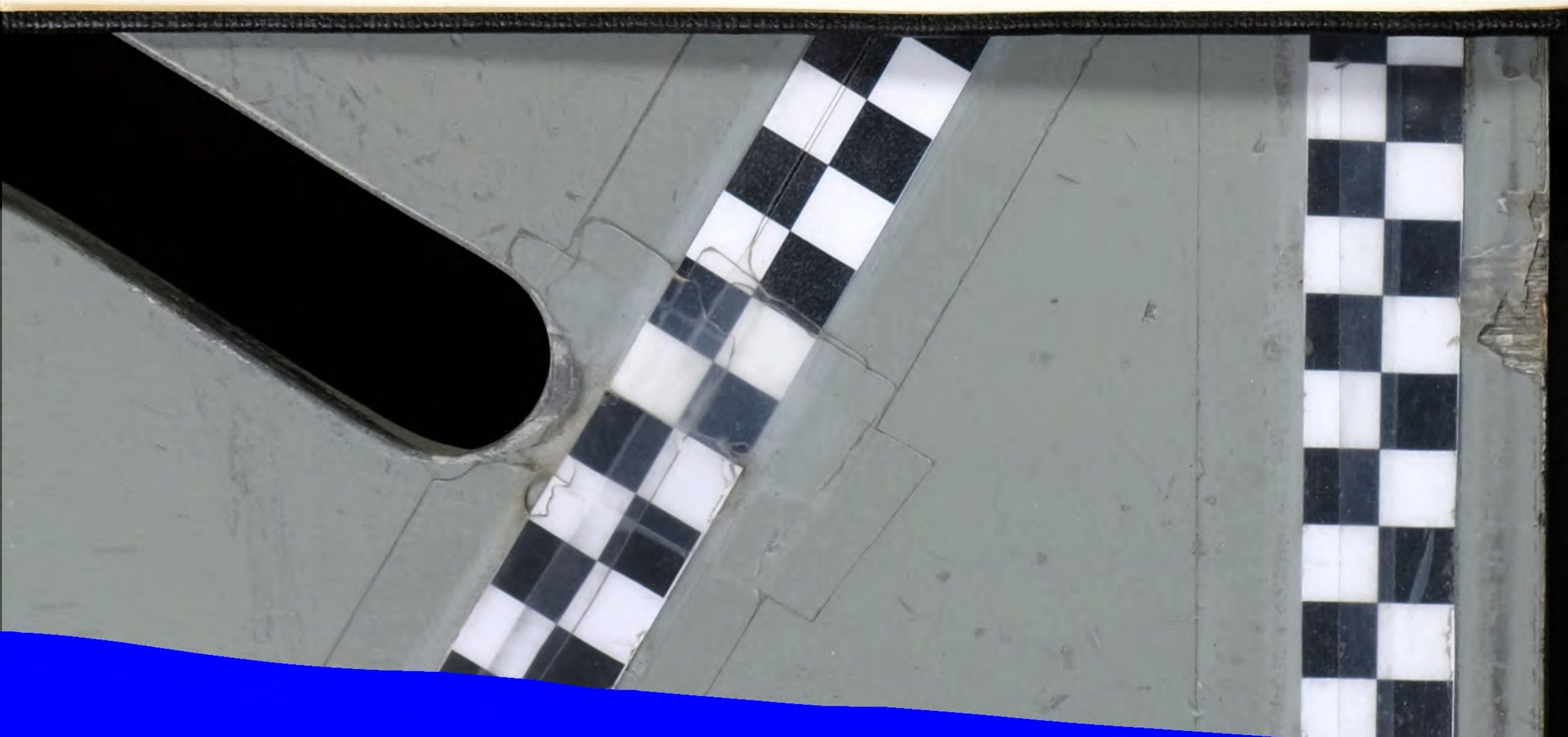

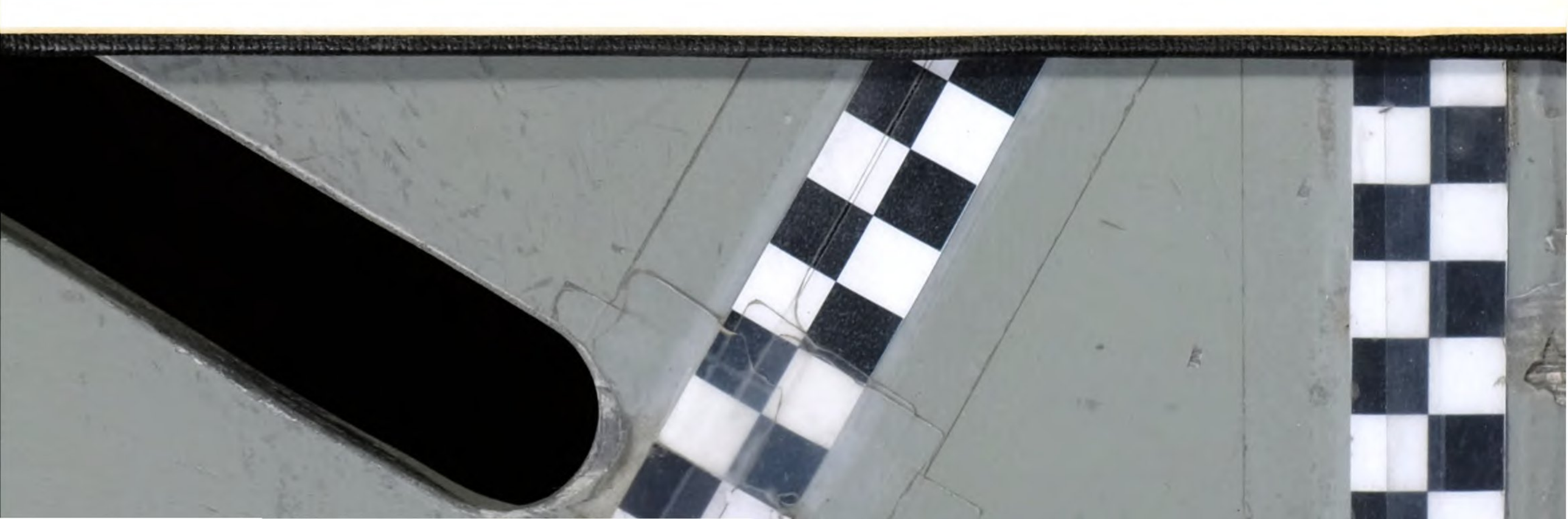

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