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THE INHERITANCE OF SEVERAL CHARACTERISTICS
IN CAULIFLOWER AND PEPPER

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Major professor

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THE INHERITANCE OF SEVERAL CHARACTERISTICS IN CAULIFLOWER AND PEPPER

By

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ABSTRACT

THE INHERITANCE OF SEVERAL CHARACTERISTICS IN CAULIFLOWER AND PEPPER

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Studies were carried out on cauliflower to develop a measurement and sampling technique for the determination of leaf geometry, and to investigate the inheritance of this character.

A measurement technique was developed which suggested that a valid measure of a plant's leaf geometry was obtained by using the mean of the first, fifth, and ninth leaves subtending the curd. Data from two field plantings showed that upright leaf geometry was partially dominant, with both additive and dominance gene action involved in trait expression. Evidence was obtained to suggest that epistasis was involved in the expression of leaf geometry. Narrow-sense heritability estimates of 67 percent and 65 percent were obtained for the two field plantings. Expected gain from selection estimates of 31.5 percent and 27.8 percent were also calculated.

Genetic analysis suggested that 3 major loci (A, B, C) controlled the expression of leaf geometry in cauliflower. A (9:7)(3:1) factorial of the 3 loci best explained the observed ratios. The presence of both A and B dominant genes were essential for upright leaf expression, i.e., A and B were complementary to each other. C was epistatic to the expression of aa and bb, the presence of dominant C in combination with either A- or B- conditioning upright expression. Thus, upright expression can occur by the presence of the C gene in combination with genes A or B or by the presence of A and B in the absence of C.

Studies on peppers were conducted to determine the mode of inheritance of pedicel width and fruit-calyx detachment force, and to determine the relationship of these characters with fruit length, width, and weight.

Data from 6 x 6 diallel analysis and F_2 analysis showed that pedicel width was quantitatively inherited, with additive and dominance gene action both involved in the expression of this character. Epistatic gene action was also suggested. Estimates of the number of effective factors, k, indicated that approximately 12 loci were involved in controlling pedicel width. Narrow-sense heritability estimates of 84 percent and 67.5 percent were obtained in the diallel and F_2 experiments, respectively. An expected gain from selection of 21 percent was estimated. Correlation coefficients between pedicel width with fruit length, width, and weight were calculated from both the diallel and F_2 analysis. All correlations were significant at the 1% level in both experiments, but were of greater magnitude in the diallel analysis.

Fruit-calyx detachment force was shown to be controlled by additive gene action, with estimates of k ranging from 1.29 to 1.86. Correlation coefficients between detachment force and fruit length, width, and weight were calculated from F_2 data. All coefficients were positive and significant at the 1% level.

To my grandparents, Sylvia and Milton Bixler, for all they have given me,

and

To the memory of Mrs. Elsie Benedick, who taught me to appreciate the beauty of a flower.

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CHAPTER I

THE INHERITANCE OF LEAF GEOMETRY IN CAULIFLOWER (*BRASSICA OLERACEA* L. VAR. *BOTRYTIS*)

INTRODUCTION

Geometric configuration of leaves on a plant has important implications relative to the cultural and production practices utilized. The alteration of leaf geometry also offers a possible means of modifying photosynthetic efficiency, and therefore, total yield. Several workers (Pearce et al., 1967; Sakamoto and Shaw, 1967; Tanner et al., 1966) have suggested that leaf angle is related to crop efficiency. Variation exists among cauliflower (*Brassica oleracea* L. var. *botrytis*) germplasm in the geometric configuration of the leaves, thus presenting the plant breeder with the opportunity to utilize this variation in the development of new cultivars.

Most cauliflower produced in Michigan is hand-tied, a practice necessary to present curd discoloration caused by sunlight exposure. Discolored or yellow curds are commercially unacceptable. Manual tying of the leaves is estimated to be 70 percent of total labor costs. Migrant labor is also becoming increasingly difficult to obtain during the fall when most of the crop is harvested, and many Michigan growers are reluctant to grow cauliflower.

In an attempt to reverse this trend, efforts were initiated in the 1960's to develop cauliflower cultivars that did not require tying. These efforts were realized with the development of the cultivars 'Greenball' in 1971 and 'Self-Blanche' in 1973. 'Greenball' is chartreuse-green at maturity and does not require tying, while the 'Self-

Blanche' cultivar produces inner leaves that wrap around the curd, protecting the curd from sunlight. Although these cultivars are used commercially, there are certain disadvantages associated with them. Public acceptance of green cauliflower has been poor. For 'Self-Blanche', the wrapping character is manifested only when night temperatures are less than 10°C, therefore, during a warm growing season, manual tying of the leaves would be necessary. Problems with 'Self-Blanche' also arise if hot weather arrives after the leaves have wrapped around the curd. This causes a rise in the temperature around the curd due to insufficient aeration, and often results in riciness. Under conditions which favor heavy guttation, such as foggy conditions, guttated water released from the wrapper leaves onto the curd can cause brown spots, resulting from the salts present in the guttation water.

Although 'Self-Blanche' and 'Greenball' made a significant contribution to no-tie cauliflower production, the disadvantages associated with these cultivars made it necessary to search for germplasm with alternative means of natural curd protection. This effort has resulted in the development of strains with other types of leaf arrangement for curd protection. Currently, strains are being developed in which the leaves assume a more upright or erect position around the developing curd, in contrast to a more horizontal position. The upright leaves form a 'stovepipe' arrangement around the curd, therefore, protecting it from sunlight. Besides providing natural sun protection to the curd, the upright leaf habit allows for sufficient aeration, preventing the problems associated with high temperatures.

Information regarding the genetic control of leaf geometry would be helpful in designing an efficient breeding scheme for the development of superior genotypes. The objectives of the following study were:

1. To develop a technique for measuring leaf geometry.
2. To develop a sampling technique appropriate for a genetic study.
3. To investigate the inheritance of leaf geometry.

REVIEW OF LITERATURE

Variation in leaf geometry exists in many agriculturally important plant species. The majority of the literature focuses on the effect of leaf geometry on plant growth and yield.

Donald (1968b) suggested that erect leaves are more efficient in light utilization within a plant community than horizontal leaves. He bases this on the fact that erect leaves allow better light penetration into the crop canopy, allowing for adequate illumination of a greater leaf area, as compared with horizontal of drooping leaves, in which the upper leaves would be overlit and the lower leaves harmfully shaded. However, Anderson (1966) reported that upright leaves do not necessarily result in a uniform light distribution into a crop canopy, since light distribution is also a function of angle of the sun, cloud cover, crop density, wind, and other factors. A number of studies have demonstrated the value of erect leaves on crop growth rate and yield. Chang and Tagumpay (1970), in studying the association between grain yield and 6 agronomic traits in rice, found that high grain yield was significantly correlated with erect leaves. Tanner et al. (1966) characterized approximately 300 strains of barley, wheat, and oats, and found that erect leaves were associated with high yield in all cases but two. Similar conclusions have been reached by other workers (Gardener et al., 1964; Pearce et al., 1967; Pendleton et al., 1968; Rutger and Crowder, 1967).

In contrast, various studies have failed to detect any significant beneficial effect of leaf angle on yield. Yap and Harvey (1972) found that erect leaves in corn were not associated with high yield. However, these authors used a low planting density, and cautioned that the value of erect leaves is probably related to crop canopy parameters and growing conditions. Studies by Hicks and Stucker (1972), Russell (1972), Ariyanayagam et al. (1974), and Frölich et al. (1977) also failed to consistently support the beneficial effect of upright leaves on yield.

The interrelationship of leaf angle and crop density to yield was investigated by Winter and Ohlrogge (1973), who found that at a high leaf area index (high crop density), upright leaves tended to increase grain yield in corn, whereas at a low leaf area index (low crop density), upright leaves reduced yield. Whigham and Woolley (1974), and Hopper (1971), using corn, also determined that upright-leaved types were superior in yield only when grown in narrow rows and/or at high population densities. Duncan's (1971) computer simulation model, which predicts that at a high leaf area index, more erect leaves should give greater production. In contrast, model computations done by Kuroiwa (1970) showed that with canopies at optimal leaf area indices, the most efficient utilization of light will occur when the uppermost foliage is erect, the lowest foliage horizontal, and the transitional foliage angles at intermediate levels.

Although studies evaluating the role of leaf angle on crop productivity have resulted in conflicting results, Mock and Pearce (1975), and Donald (1968a) still maintain that erect leaves are an important component in the development of ideotypes of corn and wheat, respectively.

Gardener et al. (1966) discussed the relationship of crop leaf angle to weed growth. They observed that at locations where weeds were chemically controlled, upright-leaved wheat strains were highest yielding. However, at locations with no herbicidal treatments, upright types yielded lowest. They observed that weed growth between the rows of the upright-leaved types was more profuse as compared with the horizontal-leaved types. The horizontal leaves apparently established a canopy over the rows and suppressed weed growth. These observations tend to support the findings of Sinclair (1972), and Allen (1973), who showed that in an erect-leaved wide-row maize canopy, more irradiation reached the soil surface than in a normal-leaved canopy.

Literature on measurement of leaf geometry is limited. In crop plants, investigators have used direct measurement between the base of the leaf and the main axis of the plant using either a protractor (Ariyanayagam et al., 1974; Yap and Harvey, 1972) or a clinometer (Whigham and Woolley, 1974; Mason and Zuber, 1976).

Genetic studies on leaf geometry are also limited. Seetharaman and Srivastava (1971) reported that erect flag leaf in rice was controlled by a single recessive gene. Yap and Harvey (1972) investigated the inheritance of flag leaf angle in barley using a 7 x 7 diallel over 2 years, and found highly significant additive gene effects. In corn, combining ability estimates for leaf angle expression were equally influences by additive and non-additive gene effects (Mason and Zuber, 1976). Nigam and Srivastava (1976) investigated the inheritance of leaf angle in wheat and concluded that additive gene action controlled trait expression.

Swarup and Chatterjee (1972) described the leaf geometry characteristics of the major European cauliflower types. These same authors (Swarup and Chatterjee, 1974) classified the leaf geometric type of 290 inbred lines derived from inbreeding 200 heterozygous Indian cauliflower cultivars. However, no genetic investigation was undertaken.

MATERIALS AND METHODS

Development of Sampling Technique

This investigation was undertaken to obtain a technique for measuring the leaf geometry of the cauliflower plant. Two inbred (6 generations) cauliflower lines, MSU 831, a horizontal-leaved line, and MSU 839, an upright, were utilized (Figure 1). In cauliflower, the mature plant consists of a single axis, terminating in a curd which is subtended by leaves arranged in a whorl at various stages of development (Figure 2). Due to the whorled leaf arrangement and the absence of a clearly defined angle between the base of the leaf and the main stem (Figure 3), measurement with a protractor or clinometer was not feasible. Alternatively, a relative measure of geometry for an individual leaf was determined in the following manner (Figure 4): A point 35 cm from the base of the leaf petiole (B), measured along the midrib of the leaf, was marked. A metal rod was inserted in the vertical axis of the plant (dotted line) and the distance from the vertical axis (A) to the B point was determined (ab). An upright leaf will show a smaller value than a horizontal leaf.

Fifteen plants of each line were field grown from July to September, 1977. The first, third, fifth, seventh, and ninth fully-expanded leaves subtending the curd were measured when the curd was 4-6 cm in diameter. These leaves were samples since these leaves contributed to curd protection. The first fully-expanded leaf was the leaf closest to the curd, and was equal to or longer than 35 cm.

Figure 1. Leaf geometry of the two parental types. Left, MSU 839 (P_2), upright; right, MSU 831 (P_1), horizontal.

Figure 2. Longitudinal view of cauliflower plant, showing arrangement of leaves.

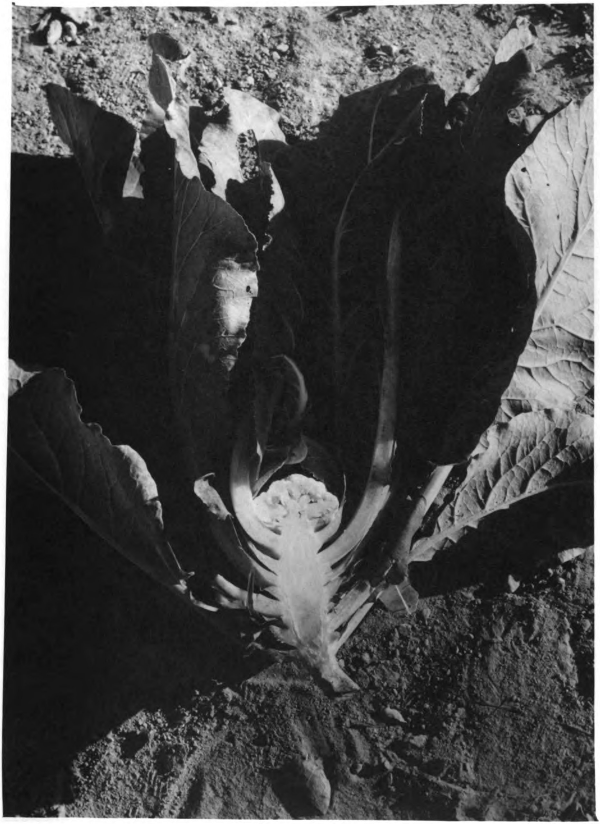


Figure 3. Schematic representation of the various leaf types encountered in cauliflower plants, showing absence of clearly defined angle between leaf base and main axis.

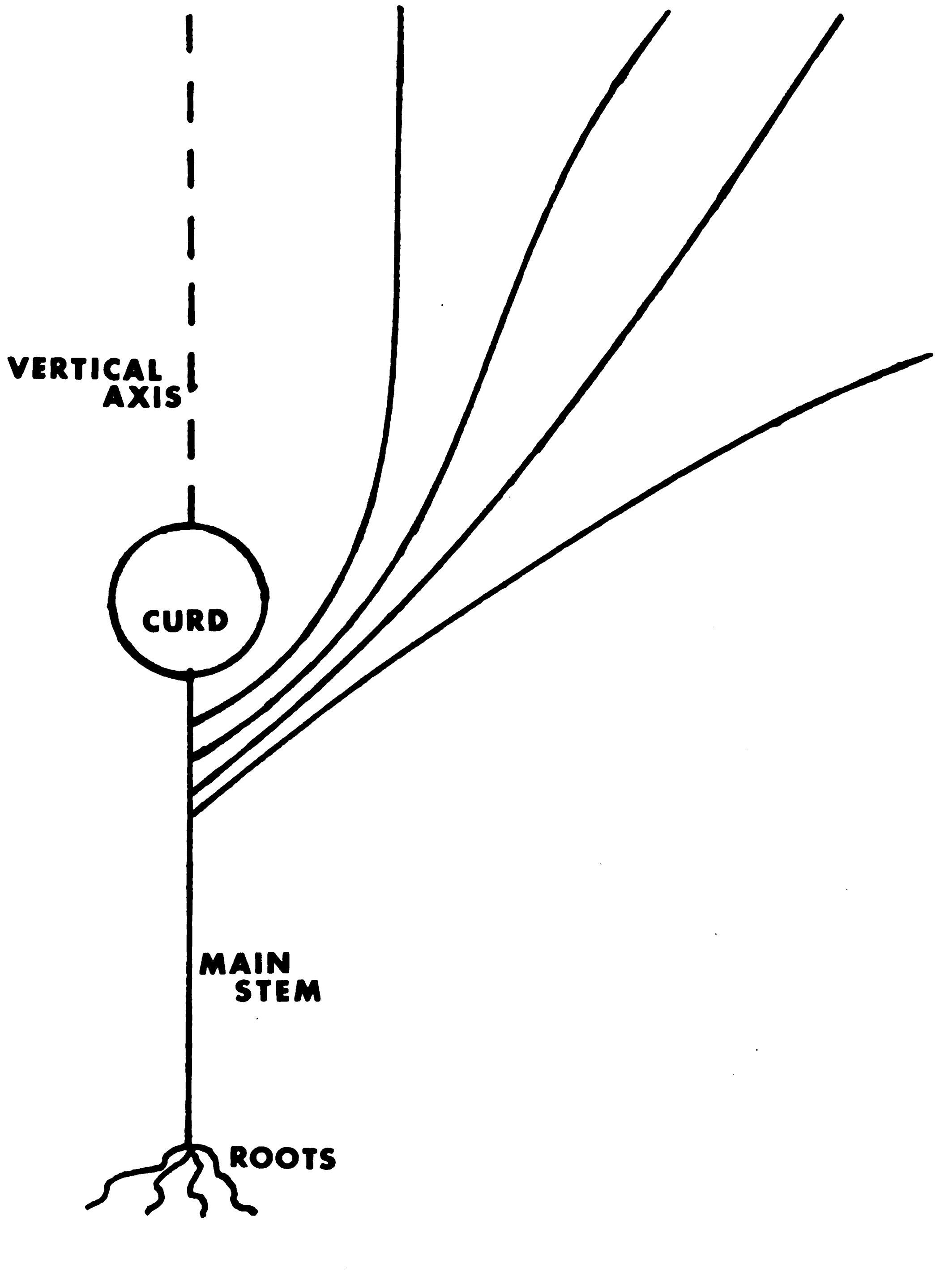

VERTICAL AXIS
CURD
MAIN STEM
ROOTS

Figure 4. Diagram of technique used in measuring leaf geometry in cauliflower.

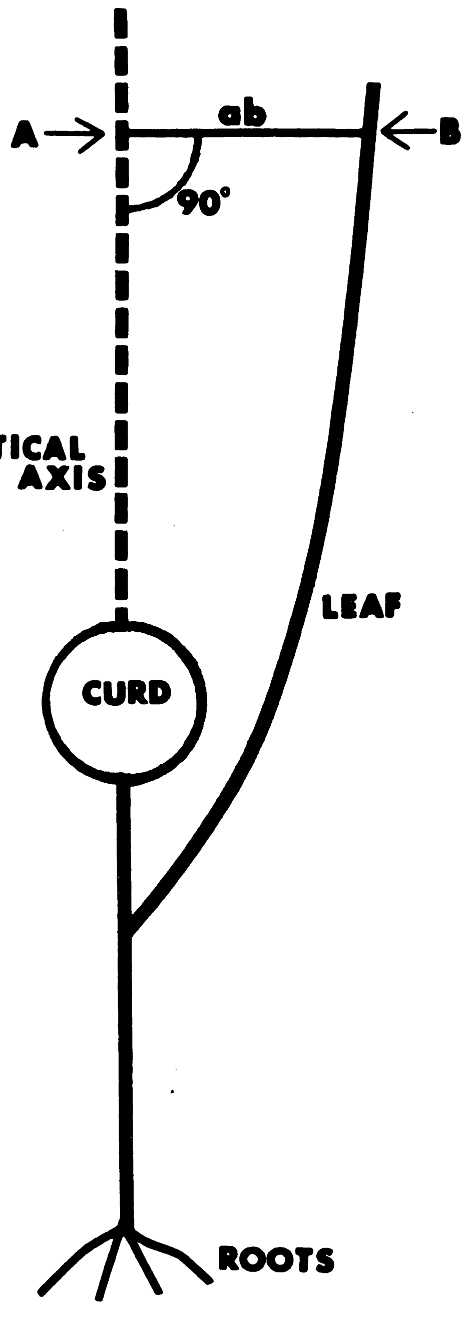
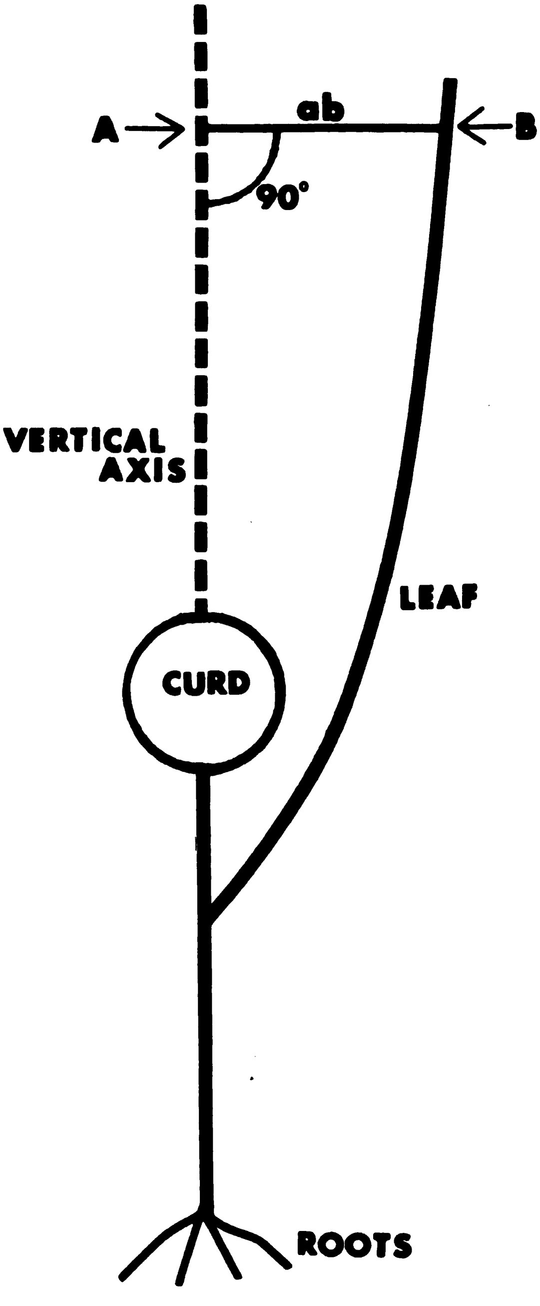

A
ab
B
90°
VERTICAL AXIS
LEAF
CURD
ROOTS

Figure 4. Diagram of technique used in measuring leaf geometry in cauliflower.


A
ab
B
90°
VERTICAL AXIS
LEAF
CURD
ROOTS

Data from individual plants were entered on IBM cards. Means, variances, and standard deviations were obtained for each population from individual plant data and calculated by the use of the Control Data Corporation 6500 computer. Population means were statistically compared by the use of the 2-tailed t-test (Steel and Torrie, 1960).

Field Studies

Two field experiments, a summer and a fall crop, were conducted during the 1978 growing season. Two inbred parents (6 generations), MSU 831 (P_1), and MSU 839 (P_2), were used to produce the various populations for the study. Both parents were selections from the cross (Pua Kea x Snowball M) x 'Self-Blanche'. None of these cultivars exhibit upright leaf geometry. Families P_1, P_2, F_1, F_2, BC_1, and BC_2 were produced by hand pollination in a greenhouse. In both experiments, parents and progenies were grown using a randomized complete-block design with 3 replications. Each replicate contained 15 plants of each parental, backcross, and F_1 family and 120 F_2 individuals. The plants were grown in rows spaced 1.07 m apart, with plants spaced at intervals of 0.60 m in the row. Cultural practices were those recommended for commercial production in Michigan. The first experiment (summer crop) was sown April 14 in a cold frame and transplanted in the field June 2. Plants were measured for leaf geometry in July. The second experiment (fall crop) was sown June 14, and transplanted in the field July 7. Plants were measured for leaf geometry in September. Individual plant data were recorded based on the sampling technique developed.

Data from individual plants were entered on IBM cards. Means, variances, and standard deviations were obtained for each population from individual plant data and calculated by the use of the Control Data Corporation 6500 computer. Population means were statistically compared by the use of the 2-tailed t-test (Steel and Torrie, 1960).

The distribution of the segregating generations was continuous, exhibiting no clear-cut modes which suggested division into phenotypic classes. Consequently, data were analyzed biometrically using the methods outlined by Mather and Jinks (1971).

Mather's ABC saclling test (Mather and Jinks, 1971) with $A = 2\overline{BC_1} - \overline{F_1} - \overline{P_1}$, $B = 2\overline{BC_2} - \overline{F_1} - \overline{P_2}$, and $C = 4\overline{F_2} - 2\overline{F_1} - \overline{P_1} - \overline{P_2}$, was applied to the generation means to determine if the data fulfilled the assumptions of the additive-dominance model. Cavalli's scaling test (Mather and Jinks, 1971) was also conducted. This test utilizes data from all generations to provide estimates of the mean, additive, and dominance effects, derived by the procedure of weighted least squares, using as weights the inverses of the variances of generation means. This joint scaling test also evaluates the goodness of fit of the data to the three-parameter model (mean, additive, and dominance effects), by assuming that the sum of squared deviations weighted with the appropriate coefficients are distributed as a X^2 distribution with 3 df. Lack of fit suggests the existence of non-additive gene effects other than dominance.

Generation means were also analyzed using the method of Jinks and Jones (1958) to fit a six-parameter model. The symbols used in the six-parameter test and in Cavalli's joint scaling test are those utilized by Gamble (1962). Those parameters are the mean effect, $\underline{m}$; the pooled additive effects, $\underline{a}$; the pooled dominance effects, $\underline{d}$; the pooled additive x additive epistatic effects, $\underline{aa}$; the pooled additive x dominance epistatic effects, $\underline{ad}$; and the pooled dominance x dominance epistatic effects, <u>dd</u>. The equations giving the estimates of gene effects in terms of the generation means are:

$$m = \overline{F_2}$$

$$a = \overline{BC_1} - \overline{BC_2}$$

$$d = -0.5\overline{P_1} - 0.5\overline{P_2} + \overline{F_1} - 4\overline{F_2} + 2\overline{BC_1} + 2\overline{BC_2}$$

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

$$ad = -0.5\overline{P_1} + 0.5\overline{P_2} + \overline{BC_1} - \overline{BC_2}$$

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

Significance of the various gene effects for this model were determined by computing standard errors of the corresponding population means.

Heritability in the narrow sense, h^2ns, was estimated using Warner's procedure (1952) as:

$$h^2ns = [2VF_2 - (VBC_1 + VBC_2)] / VF_2$$

where VF_2, VBC_1, and VBC_2 are the variances of the F_2, BC_1, and BC_2 generations, respectively. A standard error for h^2ns was derived as the square root of the following:

$$V(h^2ns) = 2\{[(VBC_1 + VBC_2)^2/df\ F_2] + (VBC_1{}^2/df\ BC_1) + (VBC_2{}^2/df\ BC_2)\}/ VF_2{}^2.$$

Expected gain from selection (G.S.), was calculated following Allard (1960) as G.S. = $k\ \sigma p\ h^2ns$, where <u>k</u> is the selection differential, σp is the phenotypic standard deviation of the F_2, and h^2ns is defined as above.

The minimum number of loci differentiating the parents was computed using the methods reported by Castle (1921) and Burton (1951).

To determine if the data from the 2 different experiments could be pooled prior to genetic analysis, an analysis of variance was made using data from both planting times to test time x generation effects.

Furthermore, segregating generations from both locations were individually compared using Bartlett's Test of Homogeneity of Variance (Steel and Torrie, 1960).

RESULTS AND DISCUSSION

Development of Sampling Technique

Mean leaf geometry values for the parents MSU 831 and MSU 839 were obtained by measuring leaves 1, 3, 5, 7, and 9. MSU 831, the open line, with a mean value of 22.37 cm, differed by 9.81 cm from MSU 839, the upright line, which had a mean value of 12.56 cm. Since the sampling of five leaves per plant was time consuming, it was necessary to determine the minimum number of leaf measurements per plant necessary to obtain a valid measure of the plant's leaf geometry. Table 1 shows the means and standard deviations obtained for each leaf and for the various leaf combinations for MSU 839. The 't' and the probability values were obtained by comparing the populations from the various individual leaf measurements or combinations of leaf measurements with the mean of the five leaf measurement (leaves 1, 3, 5, 7, and 9). The means of individual leaf measurements 1, 3, 7, and 9 were each significantly different (5% level) from the mean of the five leaf measurement. The mean of leaf 5 did not significantly differ from the five leaf measurement, but had a higher standard deviation. The leaf combination 1 and 5 and 1, 5, and 9 means were not significantly different from the mean of the five leaf measurement. For the MSU 839 parent, the data suggest that sampling leaf numbers 1 and 9 or 1, 5, and 9 would provide a valid estimate of the plant's leaf geometry.

Table 1. Geometric values (cm) for individual leaf and various leaf combinations for MSU 839.

Leaf or Leaves	Mean (cm)	S.D.	T Value	Prob.
1	6.79	3.58	-6.27	.000
3	9.91	3.24	-4.45	.001
5	12.96	4.30	0.52	.612
7	14.84	4.20	2.99	.010
9	18.11	2.80	8.86	.000
1,9	12.54	2.35	0.03	.975
1,5,9	12.68	2.26	-0.48	.641
1,3,5,7,9	12.56	2.30	--	--

Table 2 shows the results obtained with MSU 831, the horizontal leaf line. As noted in MSU 839, the sampling means of individual leaves 1, 3, 7, and 9 were significantly different (5% level) from the mean of the five leaf measurement. The mean of leaf 5 was not significantly different from the five leaf measurement but had a higher standard deviation. The mean of leaves 1 and 9 was not significantly different from the five leaf mean. The mean of leaves 1, 5, and 9 was not significantly different from the five leaf mean and had a similar standard deviation, and was judged to be the appropriate sample in this line.

On the basis of this study, the mean of leaves 1, 5, and 9 was used to determine leaf geometry.

Field Studies - Pooled Analysis

The analysis of variance for leaf geometry for the two plantings is presented in Table 3. There was no significance (5% level) for either time or time x generation interaction effects. Table 4 shows the results obtained using Bartlett's test individually comparing the F_2, BC_1, and BC_2 variances between the two planting dates. No significant difference (5% level) was noted for either backcross generation. However, a significant difference (1% level) was noted for the F_2 population. Therefore, data were not pooled, and the results of the two experiments are presented separately.

Field Study (Summer)

There were no differences (5% level) between the generation means of the reciprocal F_1's or between reciprocal F_2's, and therefore, the data were pooled. The frequency distributions for leaf geometry and

Table 2. Geometric values (cm) for individual leaf and various leaf combinations for MSU 831.

Leaf or Leaves	Mean (cm)	S.D.	T Value	Prob.
1	17.91	2.82	-6.30	.000
3	20.08	4.40	-2.25	.041
5	20.64	4.24	-1.79	.095
7	24.42	4.12	2.39	.032
9	28.81	1.48	12.81	.000
1,9	23.36	1.91	-1.86	.084
1,5,9	22.45	1.64	-0.24	.812
1,3,5,7,9	22.37	1.59	--	--

Table 3. Analysis of variance for leaf geometry for summer and fall crop.

Source	df	Mean Square	F	Prob.
Generations	5	89.35	182.69	.00001
Time	1	.10	0.19	.66
Generations x Time	5	.81	1.65	.18
Error	24	.49		

Table 4. Bartlett's test for homogeneity of variance on F_2, BC_1, and BC_2 generations individually compared between two planting times.

Generation	X^2	P
BC_1	1.02	.250
BC_2	1.28	.100
F_2	14.96	.001**

**Significant at 1% level.

graphic frequency distributions are presented in Table 5 and Figure 5, respectively.

The F_1 and F_2 frequency distributions were slightly skewed toward the upright parent (P_2). Sixty-eight and one-half percent of the F_2 plants had geometric values lower than the midparent value (16.12 cm). The high frequency of P_2 phenotypes in the F_2 population suggests that leaf geometry was controlled by a small number of loci in this cross. Of the total F_2 individuals, 3 percent lay above the mean of P_1, while 8.9 percent lay below the mean of P_2.

The means of the different populations (Table 5) substantiate the dominance patterns. The F_1 mean was lower than the midparent value (F_1 - midparent = -1.46 cm), and was significantly different (5% level) from the midparent value. The F_2 showed a similar relationship. The mean of the BC to P_2 fell between the F_1 and P_2 mean, and was closer to the mean of P_2 than was the mean of the BC to P_1, which lay between the F_1 and P_1 means. The parental range was 11.47 cm.

The results of Mather's A, B, C and Cavalli's joint scaling tests are shown in Table 6. Factor C was significant in the A, B, C scaling test (1% level), and the joint scaling test was significant (1% level). Significance in either test suggests the possibility of epistasis in the expression of leaf geometry.

The suggestion that there may be epistatic gene action made it necessary to abandon the three-parameter model and use Jinks and Jones' six-parameter model to help explain gene action. The $\underline{aa}$, $\underline{ad}$, and $\underline{dd}$ components of the six-parameter model provide true estimates of the epistatic effects. However, the $\underline{m}$, $\underline{a}$, and $\underline{d}$ effects are confounded by epistasis and do not provide valid estimates of the type and magnitude

Table 5. Frequency distributions of leaf geometry values (cm) in the cross MSU 831 x MSU 839. Summer crop.

Pedigree	Generation	Class Centers									Mean	s	No. of Plants
		9	11	13	15	17	19	21	23	25			
MSU 831	P_1					1	5	13	24	2	21.85	1.69	45
MSU 839	P_2	17	16	4							10.38	1.23	37
MSU 831 x MSU 839	F_1		2	18	45	9	0	1			14.65	1.43	75
F_1 self	F_2	19	49	72	65	50	30	8	5	4	14.65	3.34	302
F_1 x P_1	BC_1		2	2	4	14	5	8	3		17.74	3.01	36
F_1 x P_2	BC_2	3	16	8	3	3	1				12.40	2.41	34

Figure 5. Frequency distributions for leaf geometry (cm) in cauliflower from the cross MSU 831 x MSU 839. Summer.

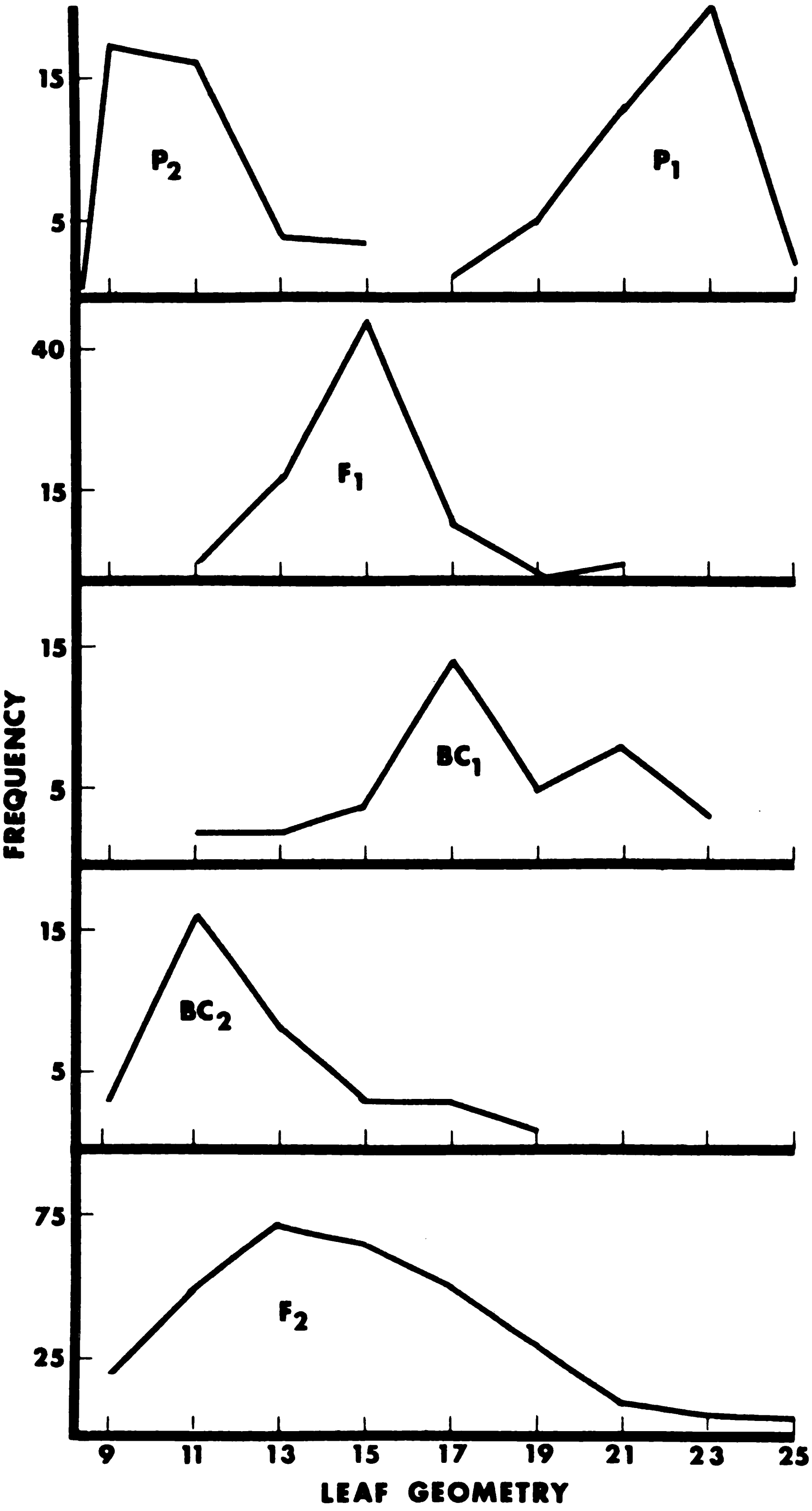

15
5
P2
P1
40
15
F1
15
5
BC1
15
5
BC2
75
25
F2
FREQUENCY
9
11
13
15
17
19
21
23
25
LEAF GEOMETRY

Table 6. Significance of the A, B, C and joint scaling tests for leaf geometry in a MSU 831 x MSU 839 cross. Summer crop.

Test			
A	B	C	Joint
ns	ns	**	**

**Significant at 1% level.

ns, non-significant at 5% level.

of gene action independent of epistasis (Ketata et al., 1976). Hayman (1958) proposed that the best approximation to epistasis-free estimates of $\underline{m}$, $\underline{a}$, and $\underline{d}$ would be the estimates obtained from the three-parameter model. Following this suggestion, it appears that additive effects played a major role in the expression of leaf geometry, although dominance gene action was significant (Table 7).

The six-parameter model estimates (Table 7) did not show significant epistatic effects ($\underline{aa}$, $\underline{ad}$, and $\underline{dd}$). It is possible that the epistatic effects were not of sufficient magnitude to be detected from this test. There is also the possibility that significance was not detected due to a cancelling out of positive and negative gene effects. The $\underline{ad}$ epistatic estimate is particularly sensitive to this possible problem (Ketata et al., 1976).

Narrow-sense heritability, which reflects the effectiveness of selection for leaf geometry, was estimated at 67 ± 26 percent. This estimate may have its limitations, since epistatic effects can inflate the narrow-sense heritability estimate as measured by Warner's method (Ketata et al., 1976). In the scaling test, factor C was significant. However, non-significance of epistatic estimates obtained in the six-parameter model suggests that this narrow-sense heritability estimate is reasonably valid. This estimate, however, should be interpreted as a theoretical maximum, and should be judged as moderate to moderately high.

The estimate of genetic advance under selection (G.S.), which evaluates the expected rate of genetic gain under directional selection, was 31.5 percent. This suggests that a 31.5 percent increase in the F_3 mean above the F_2 mean can be expected if the best 5 percent of the F_2 plants are selected.

Table 7. Gene effects estimated using three and six-parameter models on generation means in a MSU 831 x MSU 839 cross. Summer crop.

Model and Effect	Estimates
<u>Three-parameter</u>	
m	15.92** ± .15
a	5.67** ± .16
d	- 1.43** ± .23
X^2	11.71
P	.01
<u>Six-parameter</u>	
m	14.65** ± 0.03
a	5.34** ± 0.42
d	0.19 ± 2.15
aa	1.66 ± 2.12
ad	- 0.40 ± 0.45
dd	- 0.38 ± 7.34

**Significantly different from zero.

Two estimates of k, the minimum number of effective factors controlling leaf geometry, were computed. Estimates of 1.00 and 1.08 were arrived at using Castle's and Burton's method, respectively. Similar to the narrow-sense heritability estimate, these estimates suggest that a low number of loci are involved in the expression of this trait.

The F_2 and backcross populations were partitioned into upright and horizontal geometric types based on the arithmetic mean of the two parents (16.12 cm) (Table 8). The following genetic model is proposed: Three major loci (designated A, B, and C) make up the parents MSU 831 (P_1) and MSU 839 (P_2). The proposed genotype of MSU 839 is AABBCC (upright), and that of MSU 831 is aabbcc (horizontal). The F_1, with a genotype of AaBbCc, is upright. The observed F_2 and backcross ratios suggest a (9:7)(3:1) factorial gene model. A-B- conditions upright expression regardless of the state of the C locus. Recessive homozygosity at either the A or the B locus in combination with cc (aaB-cc or A-bbcc) conditions horizontal leaf expression. C- is epistatic to the expression of aa and bb, and conditions upright expression when combined with either gene A or gene B. The dominance of genes A, B, and C is incomplete, allowing for intermediate levels of leaf geometry. The F_2 and backcross generation genotypes A-B-C-, A-B-cc, aaB-C-, and A-bbC- are upright types, while aaB-cc, aabbC-, A-bbcc, and aabbcc are horizontal types (Table 9). The ratios expected (upright:horizontal) from the (9:7)(3:1) factorial gene model are 54:10, 1:1, and 1:0 in the F_2, BC_1, and BC_2 generations, respectively. A poor fit (P = <.005) was obtained in both the F_2 and BC_1 generations (Table 8). The aberrant ratio obtained in these generations suggest the presence of modifier genes or an incorrect model.

Table 8. Chi-square test for 3-gene model for leaf geometry in the F_1, BC_1, and BC_2 in the cross MSU 831 x MSU 839. Summer crop.

Generation	Observed		Observed		X^2	P
	Upright	Open	Upright	Open		
F_2	207	95	254	47	>10.00	<.005
BC_1	9	27	18	18	9.00	<.005
BC_2	31	3	34	0		

Table 9. Proposed genotypes and phenotypes of F_2 and backcross generation individuals.

Genotype	Phenotype
A-B-C-	Upright
A-B-cc	Upright
aaB-C-	Upright
A-bbC-	Upright
aabbC-	Horizontal
aaB-cc	Horizontal
A-bbcc	Horizontal
aabbcc	Horizontal

The BC_2 generation ratio is not testable using X^2, since 0 is the expected frequency in one of the classes. However, based on the assumptions of the model, the observed ratio of 31 upright:3 horizontal suggests agreement with the expectation of the model.

Field Study (Fall)

There were no differences (5% level) between the generation means of the reciprocal F_1's or between reciprocal F_2's, and therefore, the data were pooled. The frequency distributions for leaf geometry and graphic frequency distributions are presented in Table 10 and Figure 6, respectively.

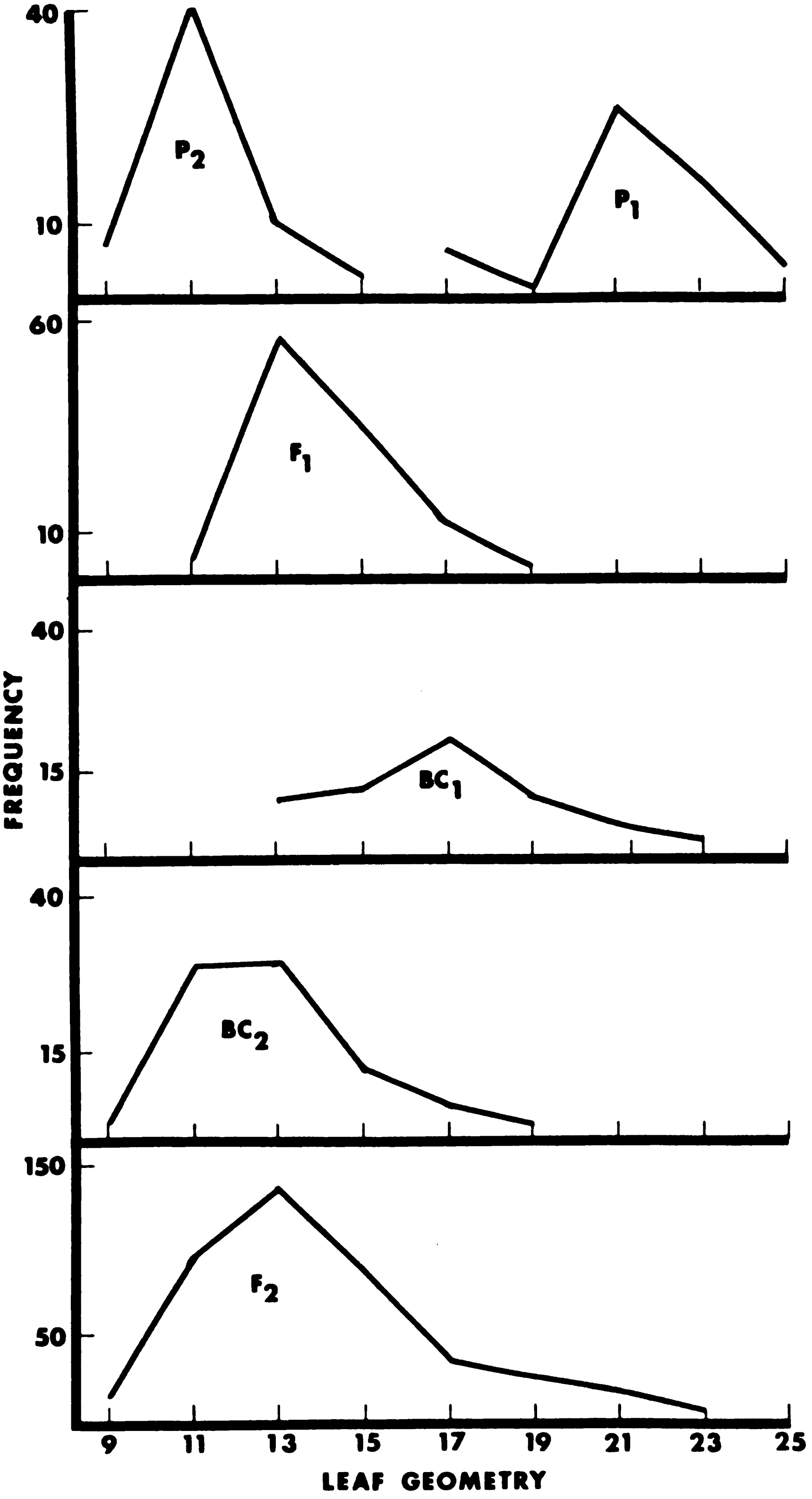
The F_1 and F_2 frequency distributions were slightly skewed toward the upright parent (P_2). Approximately 82 percent (81.9) of the F_2 plants showed geometric values lower than the midparent value (16.44 cm). The high frequency of P_2 phenotypes recovered in the F_2 population suggests that leaf geometry was controlled by a small number of loci in this cross. Of the total F_2 individuals, 2.0 percent lay above the mean of P_1, while 7.4 percent lay below the mean of P_2.

The means of the different populations (Table 10) substantiate the dominance patterns. The F_1 mean was lower than the midparent value (F_1 - midparent = -2.20 cm), and was significantly different (5% level) from the midparent value. The F_2 showed a similar relationship. The mean of the BC to P_2 lay between the F_1 and P_2 mean, and was closer to the mean of P_2 than was the mean of the BC to P_1, which lay between the F_1 and P_1 means. The parental range was 10.06 cm.

Table 10. Frequency distributions of leaf geometry values (cm) in the cross MSU 831 x MSU 839. Fall crop.

Pedigree	Generation	Class Centers									Mean	s	No. of Plants
		9	11	13	15	17	19	21	23	25			
MSU 831	P_1					6	1	26	16	2	21.46	1.75	51
MSU 839	P_2	7	40	10	3						11.41	1.30	60
MSU 831 x MSU 839	F_1		3	55	45	12	2				14.23	1.30	117
F_1 self	F_2	12	95	133	84	34	25	16	4		13.95	2.89	403
F_1 x P_1	BC_1			9	12	21	11	6	3		17.06	2.66	62
F_1 x P_2	BC_2	4	29	31	11	6	1				12.84	2.05	82

Figure 6. Frequency distributions for leaf geometry (cm) in cauliflower from the cross MSU 831 x MSU 839. Fall.


40
10
P2
P1
60
10
F1
40
15
BC1
40
15
BC2
150
50
F2
FREQUENCY
9
11
13
15
17
19
21
23
25
LEAF GEOMETRY

The results of Mather's A, B, C and Cavalli's joint scaling tests are shown in Table 11. Factors A and C were significant in the A, B, C scaling test (1% level), and the joint scaling test was significant (1% level).

The results obtained from the three-parameter model suggest that both additive and dominance gene action play a major role in the expression of this trait, with additive effects being of larger magnitude (Table 12). Examining the estimates provided by the six-parameter model, the aa effects and the ad effects were significantly different from zero.

A narrow-sense heritability of 65 ± 20 percent was obtained, suggesting that selection for this trait should be effective. The limitations of this estimate should be considered, due to the presence of epistasis.

A genetic advance under selection (G.S.) of 27.8 percent was estimated.

Values of k using Castle's and Burton's method were estimated at 1.79 and 1.96, respectively, suggesting that a small number of loci are involved in trait expression. These estimates may also be biased by epistatic effects.

The F_2 and backcross generations were partitioned into upright and horizontal geometric types based on the arithmetic mean of the two parents (16.44 cm) (Table 13). Based on the ratios expected with the three loci model previously proposed, a good fit was obtained for the F_2 (P = .10-.25) and BC_1 (P = .25-.50) generations. The BC_2 ratio of 76 upright:6 horizontal suggests agreement with the expectation of the model. Compared to the results of the summer crop, a better fit was obtained for the BC_1, and

Table 11. Significance of the A, B, C and joint scaling tests for leaf geometry in a MSU 831 x MSU 839 cross. Fall crop.

Test			
A	B	C	Joint
**	ns	**	**

**Significant at 1% level.

ns, non-significant at 5% level.

Table 12. Gene effects estimated using three and six-parameter models on generation means in a MSU 831 x MSU 839 cross. Fall crop.

Model and Effect	Estimates
Three-parameter	
m	17.08** ± .14
a	5.16** ± .14
d	- 3.41** ± .20
X^2	64.46
P	<.001
Six-parameter	
m	13.95** ± 0.02
a	4.21** ± 0.17
d	1.81 ± 1.01
aa	4.01** ± 1.00
ad	- 0.81** ± 0.19
dd	- 2.50 ± 3.13

**Significantly different from zero.

Table 13. Chi-square test for 3-gene model for leaf geometry in the F_1, BC_1, and BC_2 in the cross MSU 831 x MSU 839. Fall crop.

	Observed		Observed			
Generation	Upright	Open	Upright	Open	X^2	P
F_1	330	73	340	63	1.88	.10-.25
BC_1	28	34	31	31	.58	.25-.50
BC_2	76	6	82	0		

this may be explained by the differential expression of major genes and/or modifier genes under the environmental conditions of each experiment.

SUMMARY AND CONCLUSIONS

A technique for determining leaf geometry in cauliflower was developed. Sampling technique revealed that a valid measure of a plant's leaf geometry was obtained by sampling the first, fifth, and ninth fully-expanded leaves subtending the curd.

The progenies of reciprocal crosses between MSU 831 and MSU 839 were evaluated in two field studies (a summer and a fall crop) to determine the mode of inheritance of leaf geometry. In both plantings, partial dominance of the upright parent was noted. Both additive and dominance gene action played a role in trait expression, with additive action being of larger magnitude. Analysis of generation means suggested that epistatic gene action played a role in the expression of leaf geometry, with epistasis more pronounced in the fall crop than in the summer crop.

Hayman (1958) suggested that the lack of evidence for epistasis in a particular environment may be due to a rise in the error variance rather than to a change in the action of the genes. Analysis of variance of leaf geometry in the summer crop (Table 14) and in the fall crop (Table 15) revealed that the error mean square was higher in the summer crop (12.30) than in the fall crop (3.01). This difference is reflected in the standard errors of the epistatic estimates (Tables 7 and 11), the standard errors being larger in the summer crop than in the fall crop. However, further examination revealed that the magnitude of the epistatic estimates was lower in the summer crop than in the fall crop. Therefore,

Table 14. Analysis of variance of leaf geometry. Summer crop.

Source	df	Mean Square	F	Prob.
Generations	5	690.57	56.14	.00001
Replications	2	49.93	4.06	.051
Error	10	12.30		

Table 15. Analysis of variance of leaf geometry. Fall crop.

Source	df	Mean Square	F	Prob.
Generations	5	760.34	252.32	.00001
Replications	2	18.92	6.28	.017
Error	10	3.01		

it appears that the lack of evidence for epistasis in the summer crop as compared to the fall crop was due mainly to a change in gene action in the different environments rather than to a difference in error. Hayman (1958) also noted that the environment influenced the expression and magnitude of epistasis.

Mather and Jinks (1971) reported that the type of epistatic interaction (complementary or duplicate) can be inferred from the relative signs of $\underline{d}$ and $\underline{dd}$. Like signs of $\underline{d}$ and $\underline{dd}$ indicate complementary interaction, while opposite signs indicate duplicate interaction. In both experiments, $\underline{d}$ and $\underline{dd}$ exhibited opposite signs (Tables 7 and 11), suggesting duplicate interactions. However, neither the $\underline{d}$ or $\underline{dd}$ estimates are significantly different from zero, and the inference as to the type of interaction is probably not valid.

Narrow-sense heritability estimates of 67 percent and 65 percent were obtained for the summer and fall crops, respectively. Expected gain from selection estimates of 31.5 percent and 27.8 percent were also calculated.

Ratios obatined by partitioning the segregating generations into phenotypic classes based on the arithmetic mean of the parental lines suggested a three loci system (designated $\underline{A}$, $\underline{B}$, and $\underline{C}$) controlling leaf geometry. A (9:7)(3:1) factorial of the three loci best explained the observed ratios. Parental line MSU 839 (P_2) was designated $\underline{AABBCC}$ and MSU 831 (P_1) was designated $\underline{aabbcc}$. The data suggested the presence of modifier genes.

Differences in the segregation ratios and in the estimates of the various genetic parameters may be due to the differential expression of the major genes and/or the modifier genes in each of the plantings.

Both of the parents used in this study, MSU 831 (P_1) and MSU 839 (P_2), were derived from the cross (Pua Kea x Snowball M) x 'Self-Blanche'. None of these cultivars exhibit upright leaf geometry. The probable occurrence of uprights from this cross is based on the following observations.

(a) No upright progeny were recovered from segregating generations from the cross Pua Kea x Snowball M.

(b) Upright phenotypes were recovered in segregating generations derived from the cross (Pua Kea x Snowball M) x 'Self-Blanche'.

Based on the proposed genetic model, these observations suggest the presence of an activator loci (D) controlling the expression of leaf geometry. It is proposed that this locus is an activator of gene C. The following genotypes are proposed for the various cultivars:

(a) Pua Kea - aaBBccdd - horizontal leaf type

(b) Snowball M - aabbCCdd - horizontal leaf type

(c) Self-Blanche - AAbbccDD - horizontal leaf type

(d) Pua Kea x Snowball M - aaBbCcdd - horizontal leaf type

Crosses between Pua Kea and Snowball M will not yield upright progeny, due to the presence of dd and aa in both parents. In progeny derived from this cross, the epistatic expression of C over aa will not be manifested, since the activator locus D is present as dd. A cross of (Pua Kea x Snowball M) x 'Self-Blanche' will yield upright progeny, since 'Self-Blanche' carries both AA and DD. Both MSU 831 (P_1) and MSU 839 (P_2) were selected from this cross. The data suggest that both parents are homozygous DD.

Swarup and Chatterjee (1972) concluded that Indian cauliflower originated mainly but not exclusively from the Cornish cauliflower type of the United Kingdom. Cornish types are characterized by horizontal leaf geometry. Swarup and Chatterjee (1974) later characterized the leaf geometry of 290 inbred lines derived from selfing 200 Indian cauliflower cultivars. A high percentage of inbreds exhibiting upright leaf geometry were obtained. The recovery of a high percentage of upright inbreds that initially originated from horizontal-leaved parents tends to support the proposed epistatic gene model with an activator gene. Crosses between different Cornish types or between Cornish types and other cauliflower types with horizontal leaf geometry could result in recombination of the proposed genes and ultimately may have resulted in the upright phenotypes.

CHAPTER II

THE INHERITANCE OF PEDICEL WIDTH AND FRUIT DETACHMENT FORCE IN PEPPER (*CAPSICUM ANNUUM* L.)

INTRODUCTION

Increase in harvest cost and the unavailability of labor have necessitated the development of mechanical harvesters for many vegetable crops. Recently, research has been directed to the development of a mechanical harvester for the pepper. Consequently, the development of pepper cultivars adapted to mechanized harvest is of importance. Two problems associated with mechanical harvesting of peppers are fruit damage and low yield due to difficulty of fruit removal.

The percentage of unharvested and damaged fruit can be minimized by breeding cultivars with low fruit detachment forces. Strains of peppers exist which require little force to separate the calyx from the fruit. The incorporation of this trait into commercial pepper cultivars would be an important step in the development of strains suitable for mechanical harvest.

For the fresh market, fruit with pedicels are a definite necessity. The lowering of detachment force of the pedicel from the main stem or minimizing the force necessary to break the pedicel may be realized by developing strains with narrow pedicels.

Information regarding the genetic control of pedicel width and fruit detachment force would be helpful in designing an efficient breeding scheme for the development of desirable genotypes. The objectives of the present study were:

1. To determine the inheritance of fruit-calyx detachment force in mature fruit.

2. To determine the inheritance of pedicel width.

3. To establish relationships of the above characters with fruit length, fruit width, and fruit weight.

REVIEW OF LITERATURE

Literature on the genetics of pedicel characteristics in pepper is limited. Deshpande (1933) reported that pedicel length was inherited as a quantitative character, with short pedicel dominant over long. Pedicel length in the tomato has also been shown to be quantitatively inherited (Bouwkamp and Honma, 1970).

Smith (1951) reported that the 'deciduous' fruit character in pepper was controlled by a single dominant gene. This gene, expressed late in the fruit ripening process, conditions easy separation of the fruit from the calyx. This character was later designated 'soft-flesh', since detachment was principally a result of the breakdown of the fruit wall and placental tissue. This character has been of little importance in the development of cultivars adapted to mechanical harvesting.

Spasojevic and Webb (1971) reported on the inheritance of abscission of ripe pepper fruit from the calyx, controlled by an incompletely dominant gene. This gene differed from the soft flesh character in that detachment was not a result of fruit and placental breakdown.

Stall (1973), using an Ametek Model LG-5 strain gauge, determined that detachment characteristics in pepper were under genetic control and found that the pull force of the fruit at the calyx detachment site was significantly correlated to stem-scar diameter. No detailed description of the procedure used to measure detachment force was given. A correlation between detachment force and stem-scar diameter has also been observed in cucumber (Burnham and Peterson, 1970). Hield et al. (1967) found linear correlations between detachment force and both fruit and stem size in citrus fruits. Villalon and Bryan (1970) evaluated numerous tomato cultivars for ease of fruit-pedicel separation, and found large differences between cultivars for ease of separation. Interaction between fruit-pedicel separation force and maturity was significant. Separation force was found to be related to stem-scar diameter. The results obtained suggested that the same breeding stocks reacted differently with location and season.

Inheritance of fruit detachment has been reported in various crops. Barritt (1976) determined that additive gene action controlled calyx removal in strawberry, and obtained a heritability of 84 percent based on parent-offspring regression. Brown and Moore (1975), using a diallel analysis to investigate the inheritance of fruit detachment in strawberry, determined that both additive and dominance gene action controlled trait expression, and that environmental effects largely influenced detachment force. Bassett (1976) investigated the inheritance of pod detachment force in snap beans, and determined that two dominant genes controlled pod detachment force. Narrow-sense heritability was estimated to be 61 percent.

MATERIALS AND METHODS

Pedicel Width - Diallel Analysis

Six inbred lines, MSU 193, MSU 238, MSU 250, MSU 333, MSU 365, and MSU 393 were used in this study. These lines were selected on the basis of variation in pedicel width and exhibited contrasting fruit characteristics. Crosses were made in a greenhouse in all possible combinations including reciprocals to produce a 6 x 6 diallel. The F_1's and parents of these crosses were sown in April, 1977 in the greenhouse in peat pots and transplanted to the field in June. A randomized-complete block design with 3 replications was used. Each replicate consisted of one row of each F_1 and parent, with each row containing 10 plants. Each row was spaced 1.07 m apart, with plants spaced at intervals of 0.60 m in the row. During the growing season, the plants were irrigated and fertilized as necessary.

Data were taken in the following manner: Four mature fruits were removed from each plant. The length, width, weight, and pedicel width were recorded for each fruit. Pedicels were removed from the fruit prior to weighing. Fruit width was measured at the calyx end. Pedicel width was determined with a Helios caliper (VWR Scientific, Chicago, Illinois) by measuring the pedicel immediately below the pedicel-stem attachment zone. The mean of four observations from each plant was used for all calculations.

Data from individual plants were entered on IBM cards. Means were obtained for each population from individual plant data and calculated by the use of the Control Data Corporation 6500 computer.

The genetic analysis was based on the method developed by Jinks (1954) and Hayman (1954a, 1954b). This method allows for the estimation of parameters which provide information about the genetic system controlling a quantitative trait. According to this method, variance of the parental and F_1 lines can be partitioned into four parts:

a: variation in the mean effects of the parental lines

b: variation which is caused by mean dominance effects of the parents

c: average maternal effects of the parental lines

d: variation in reciprocal differences not ascribable to c

The variation b is further subdivided into: b_1, variance due to directional dominance effects; b_2, dominance deviation due to asymmetrical gene frequencies; and b_3, residual dominance effects.

Statistics and the genetic components of variation (D, H_1, H_2, and F) were calculated following Hayman's method (1954a, 1954b). The genetic components of variation measure:

D = additive effects of genes

H_1 = dominance effects of genes

H_2 = dominance indicating asymmetry of positive and negative gene effects

F = covariation of dominance and additive effects

Narrow-sense heritability was estimated using the formula proposed by Crumpacker and Allard (1962):

$$h^2ns = .25D / (.25D + .25H_1 - .25F + E)$$

where D, H_1, F, and E are the same as those defined by Hayman (1954b).

Pedicel Width - F_2 Analysis

Two inbred parents, MSU 333 (wide pedicel) and MSU 365 (narrow pedicel) were used to produce the various populations for the study. These parents also exhibited contrasting fruit characteristics (Table 16). Families P_1, P_2, F_1, F_2, BC_1, and BC_2 were produced by hand pollination in a greenhouse. Parents and progenies were sown April 13, 1978 in the greenhouse in peat pots and transplanted to the field June 18. A randomized-complete block design with 3 replications was used. Each replicate consisted of one row (15 plants) of each parental, F_1, and BC generation, and 8 rows (120 plants) of F_2 individuals. Each row was spaced 1.07 m apart, with plants spaced at intervals of 0.60 m in the row. During the growing season, the plants were fertilized and irrigated as necessary.

Data were recorded in the following manner: Three mature fruit were removed from each plant. The length, width, weight, and pedicel width were recorded for each fruit. Fruit width was measured at the calyx end. Pedicel width was determined with a Helios caliper (VWR Scientific, Chicago, Illinois) by measuring the pedicel immediately below the pedicel-stem attachment zone. Pedicels were removed from the fruit prior to weighing. The mean of three observations from each plant was used for all calculations.

Data from individual plants were entered on IBM cards. Means, variances, and standard deviations were obtained for each population from individual plant data and calculated by the use of Control Data Corporation 6500 computer. Population means were statistically compared by the use of the 2-tailed t-test (Steel and Torrie, 1960).

Table 16. Characteristics of the parental lines. Pedicel width investigation.

Parent	Pedicel Width (mm)	Fruit Length (cm)	Fruit Width (cm)	Fruit Weight (g)
MSU 333	9.33	9.39	6.27	116.94
MSU 365	2.93	6.35	1.94	6.67

The distribution of the segregating generations was continuous, exhibiting no clear-cut modes which suggested division into phenotypic classes. Consequently, data were analyzed biometrically using the methods outlined by Mather and Jinks (1971).

Mather's ABC scaling test (Mather and Jinks, 1971) with $A = 2\overline{BC_1} - \overline{F_1} - \overline{P_1}$, $B = 2\overline{BC_2} - \overline{F_1} - \overline{P_2}$, and $C = 2\overline{F_1} - \overline{P_1} - \overline{P_2}$, was applied to the generation means to determine if the data fulfilled the assumptions of the additive-dominance model. Cavalli's scaling test (Mather and Jinks, 1971) was also conducted. This test utilizes data from all generations to provide estimates of the mean, additive, and dominance effects, derived by the procedure of weighted least squares, using as weights the inverses of the variances of generation means. This joint scaling test also evaluates the goodness of fit of the data to the three-parameter model (mean, additive, and dominance effects), by assuming that the sum of squared deviations weighted with the appropriate coefficients are distributed as a X^2 distribution with 3 df. Failure of fit suggests the existence of non-additive gene effects other than dominance.

Generation means were also analyzed using the method of Jinks and Jones (1958) to fit a six-parameter model. The symbols used in the six-parameter test and in Cavalli's joint scaling test are those utilized by Gamble (1962). Those parameters are the mean effect, *m*; the pooled additive effects, *a*; the pooled dominance effects, *d*; the pooled additive x additive epistatic effects, *aa*; the pooled additive x dominance epistatic effects, *ad*; and the pooled dominance x dominance epistatic effects, *dd*. The equations giving the estimates of gene effects in terms of the generation means are:

$$m = \overline{F_2}$$

$$a = \overline{BC_1} - \overline{BC_2}$$

$$d = -0.5\overline{P_1} - 0.5\overline{P_2} + \overline{F_1} - 4\overline{F_2} + 2\overline{BC_1} + 2\overline{BC_2}$$

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

$$ad = -0.5\overline{P_1} + 0.5\overline{P_2} + \overline{BC_1} - \overline{BC_2}$$

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

Significance of the various gene effects for this model were determined by computing standard errors of the corresponding population means.

Heritability in the narrow sense, h^2ns, was estimated using Warner's procedure (1952) as:

$$h^2ns = [2VF_2 - (VBC_1 + VBC_2)] \,/\, VF_2$$

where VF_2, VBC_1, and VBC_2 are the variances of the F_2, BC_1, and BC_2 generations, respectively. A standard error for h^2ns was derived as the square root of the following:

$$V(h^2ns) = 2\ \{[(VBC_1+VBC_2)^2/df\ F_2] + (VBC_1{}^2/df\ BC_1) + (VBC_2{}^2/df\ BC_2)\}/ VF_2{}^2.$$

Expected gain from selection (G.S.), was calculated following Allard (1960) as G.S. = $k\ \sigma p\ h^2ns$, where $\underline{k}$ is the selection differential, σp is the phenotypic standard deviation of the F_2, and h^2ns is defined as above.

The minimum number of loci differentiating the parents was computed using the methods reported by Castle (1921) and Burton (1951).

Detachment Force

Two inbred parents, MSU 160 (high detachment force) and MSU 249 (low detachment force) were used to produce the various populations for the study (Table 17). Families P_1, P_2, F_1, and F_2 were produced in a greenhouse. Although the BC_1 and BC_2 families were produced, most of

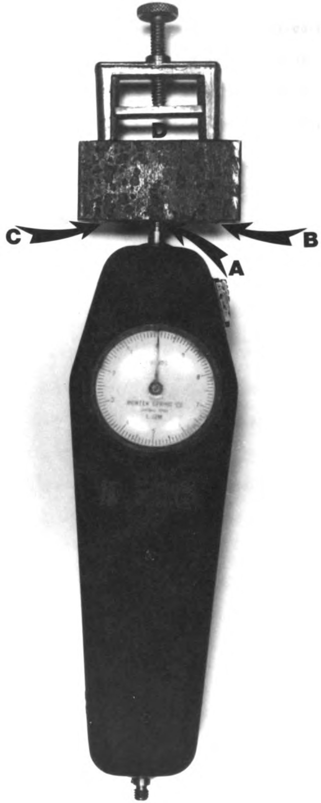
Table 17. Characteristics of the parental lines. Detachment force investigation.

Parent	Detach Force (kg)	Fruit Width (cm)	Fruit Length (cm)	Fruit Weight (g)
MSU 160	4.20	4.04	12.33	35.11
MSU 249	1.77	2.00	6.87	7.57

the plants perished in the field. Seeds of the parents and progenies were sown April 13, 1978 in the greenhouse in peat pots and transplanted to the field June 18. A randomized-complete block design with 3 replications was used. Each replicate consisted of 15 plants of each parental and F_1 generation, and 120 plants of F_2 individuals. Each row was spaced 1.07 m apart, with plants spaced at intervals of 0.60 m in the row. During the growing season, plants were irrigated and fertilized as necessary. Due to poor growing conditions, fruit set was not obtained on all plants.

Data were recorded in the following manner: Four mature fruits with the pedicel attached were removed from the plant. A modified Hunter L-10M spring gauge (Hunter Gauge Co., Lansdale, PA) was used to measure detachment force. The gauge was modified in the following manner (Figure 7): A 2.6 cm x 5.0 cm piece of 6 mm pressed steel sheeting was tapped at point A and attached to the threaded extension on the guage. Holes were drilled through the entire width of the steel bar at the end of the bar closest to the gauge, and extended through the bar and into the holes of a common laboratory clamp (Precision Scientific clamp #59-552). The pedicel was then firmly clamped directly above the calyx between the steel bar and the adjustable bar on the clamp (point D). Detachment force was determined by slowly pulling the pedicel perpendicular to the longitudinal axis of the fruit until the fruit and pedicel separated. Force was recorded in pounds and converted to kilograms prior to analysis. The length, width, and weight of each fruit were also measured. The mean of four observations from each plant was used for all calculations.

Figure 7. Instrumentation used to measure fruit detachment force.


D
C
B
A

Data from individual plants were entered on IBM cards. Means, variances, and standard deviations were obtained for each population from individual plant data and calculated by the use of the Control Data Corporation 6500 computer. Population means were statistically compared by the use of the 2-tailed t-test (Steel and Torrie, 1960).

RESULTS AND DISCUSSION

Pedicel Width - Diallel Analysis

Linear regression between the array variances (Vr) and the parent-offspring covariances (Wr), using replicate and reciprocal cross means (Table 18), was conducted to determine if the data fulfilled the assumptions of the additive-dominance model (Mather and Jinks, 1971). A coefficient of .57 was obtained. This coefficient was not significantly different from zero (P = .20-.30) or from one (P = .40). A regression coefficient of one is expected if non-additive genetic variation is present as dominance variation. A non-significant coefficient from zero suggests that epistasis may have played a role in the expression of this trait. Since the coefficient was not significantly different from one, it appears that an additive-dominance model may explain gene action for this character.

Mean square values from diallel analysis of variance are presented in Table 19. The six error variances (Replication (R) x $\underline{a}$, R x $\underline{b_1}$, R x $\underline{b_2}$, R x $\underline{b_3}$, R x $\underline{c}$, and R x $\underline{d}$) were pooled to give R x $\underline{t}$ as a common error variance. A highly significant value for $\underline{a}$ was obtained, suggesting the existence of substantial additive genetic variation controlling the expression of this trait. A highly significant $\underline{b}$ mean square was also obtained, which was mainly effected by the $\underline{b_3}$ parameter, suggesting the existence of dominance gene action expressed as specific combining

Table 18. Mean pedicel width (mm) for a set of diallel crosses between 6 inbred lines of pepper.

Inbred	MSU 193	MSU 238	MSU 250	MSU 333	MSU 365	MSU 393	Vr	Wr
MSU 193	3.41	4.13	4.19	4.68	3.21	5.45	0.68	2.84
MSU 238	4.13	5.59	5.60	6.47	7.70	7.82	1.99	2.58
MSU 250	4.19	5.60	5.62	6.82	4.15	9.14	3.50	6.63
MSU 333	4.68	6.47	6.82	7.50	4.52	9.99	4.07	7.06
MSU 365	3.21	7.70	4.15	4.52	3.10	8.01	4.81	5.75
MSU 393	5.45	7.82	9.14	9.99	8.01	12.82	6.09	8.06
Array Means	4.18	6.22	5.92	6.66	5.12	8.87		

Table 19. Analysis of variance of diallel table for pedicel width.

Source	df	Mean Square	F Ratio
a	6	89.73	287.04**
b	15	255.61	817.69**
b_1	1	3.22	10.30**
b_2	5	1.33	4.25**
b_3	9	424.91	1359.28**
c	5	0.14	0.45
d	10	0.37	1.18
Error	70	0.31	

**Significant at 1% level.

ability in certain hybrid combinations. Reciprocal effects were not detected, as evidenced by the small mean square values for c and d.

Since no reciprocal effects were detected, the mean values of each cross and its reciprocal (Table 19) were used for the estimation of genetic components of variation D, H_1, H_2, and F as defined by Hayman (1954b) (Table 20). Although no estimate of error of these components is available, a comparison of their relative magnitude provides some indication of their significance (Mather and Jinks, 1971).

The ratio (H_1/D) of 0.33 indicates that both dominant and additive genes contributed to pedicel width. A (H_1/D) value equal to one suggests complete dominance.

The ratio ($H_2/4H_1$) provides an estimate of the average frequency of negative (u) and positive (v) alleles (at loci exhibiting dominance) in the parents. An ($H_2/4H_1$) value of 0.25 would suggest that positive and negative alleles were equally distributed in the parental lines. A value of 0.21 was obtained, suggesting equal allele distribution.

The ratio of $[4(DH_1) + F/DH_1 - F]$ was used to estimate the total number of dominant (K_D) to recessive (K_R) alleles in the parents. A (K_D/K_R) ratio of 1.13 was obtained, suggesting that more dominant than recessive alleles were present in the parents.

Narrow-sense heritability was measured as the ratio of additive variance to total phenotypic variance (Crumpacker and Allard, 1962). An estimate of 84 percent was obatined, providing further evidence of additive gene action in trait expression.

Phenotypic correlation coefficients between pedicel width and fruit length, width, and weight for F_1's and parents were calculated (Table 21). All correlations were significant at the 1% level, suggesting that

Table 20. Components of variation for pedicel width.

D	H_1	H_2	F	$D - H_1$	H_1/D	$H_2/(4H_1)$
12.38	4.00	3.35	3.01	8.38	.32	.21

Table 21. Correlation coefficients of pedicel width with fruit width, length, and weight.

Fruit Width	Fruit Length	Fruit Weight
0.91	0.54	0.94

All correlations significant at 1% level with 1010 d.f.

breeding for plants with large fruits and narrow pedicels would be difficult. However, since these correlations were performed on F_1 and parental lines, each of which is genetically uniform, the values obtained are likely to be dependent on the characteristics of the parental material.

Pedicel Width - F_2 Analysis

There were no differences (1% level) between the generation means of reciprocal F_1's or reciprocal F_2's, and therefore, the data were pooled. The frequency distributions for pedicel width and graphic frequency distributions are presented in Table 22 and Figure , respectively.

The F_1 and F_2 frequency distributions were skewed toward the narrow pedicel parent (P_2) (Figure 8). Of the total F_2 individuals, 293 lay on the P_2 side of the midparent value (6.13 mm). The low frequency of P_1 or P_2 phenotypes recovered in the F_2 population suggests that pedicel width was controlled by a large number of genes in this cross. No plants of the P_1 phenotype were recovered in the F_2 population, while only one individual of the P_2 phenotypic class was recovered.

The means of the various populations are shown in Table 22. The F_1 mean fell on the P_2 side of the midparent value (F_1 - midparent = -1.22 mm), and was significantly different (5% level) from the mid-parent value. The F_2 showed a similar relationship. The mean of the BC to P_2 fell between the F_1 and P_2 mean, and was closer to the mean of P_2 than was the mean of the BC to P_1, which fell between the F_1 and P_1 means. The range of difference between the parents was 6.40 mm. The results of Mather's A, B, C and Cavalli's joint scaling test are shown in Table 23. All factors were significant at the 1% level in the A, B, C tests, and the

Table 22. Frequency distributions of pedicel width values (mm) in the cross MSU 333 x MSU 365.

Pedigree	Generation	Class Centers								Mean	s	No. of Plants
		2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5			
MSU 333	P_1							6	14	9.33	0.42	20
MSU 365	P_2	32	10							2.93	0.11	42
MSU 333 x MSU 365	F_1		1	45	27					4.91	0.29	73
F_1 self	F_2	1	40	179	70	13	2			4.70	0.71	305
F_1 x P_1	BC_1			2	20	13	5			6.16	0.69	40
F_1 x P_2	BC_1	2	31	9						3.66	0.45	42

Figure 8. Frequency distributions for pedicel width (mm) in pepper from the cross MSU 333 x MSU 365.

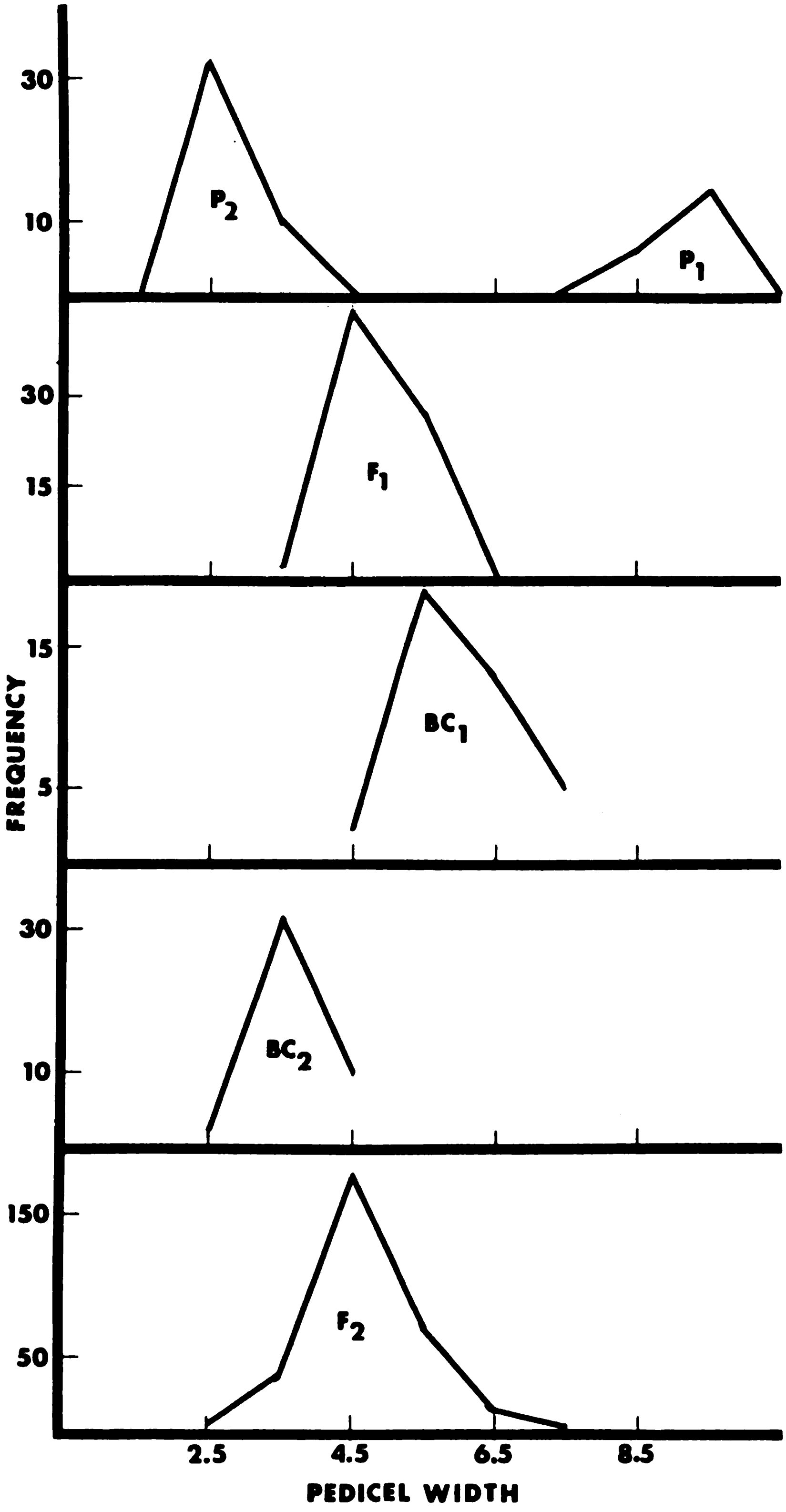

30
10
P2
P1
30
15
F1
15
5
BC1
FREQUENCY
30
10
BC2
150
50
F2
2.5
4.5
6.5
8.5
PEDICEL WIDTH

Table 23. Significance of the A, B, C and joint scaling tests for pedicel width in a MSU 333 x MSU 365 cross.

Test			
A	B	C	Joint
**	**	**	**

**Significant at 1% level.

joint scaling test was significant (1% level). Significance in either test suggests the possibility of epistasis in the expression of pedicel width. To further understand the possible gene action, Jinks and Jones' six-parameter model was investigated. The aa, ad, and dd components of the six-parameter model provide true estimates of the epistatic effects. However, the m, a, and d effects are confounded by epistasis and do not provide valid estimates of the type and magnitude of gene action independent of epistasis (Ketata et al., 1976). Hayman (1958) proposed that the best approximation to epistasis-free estimates of m, a, and d would be the estimates obtained from the three-parameter model. Therefore, it appears that additive and dominance gene action affected the expression of pedicel width, with additive effects being of larger magnitude (Table 24). Significant (1% level) estimates were obatined using the six-parameter model. Unlike signs of d and dd suggests the existence of duplicate gene interactions (Mather and Jinks, 1971).

A narrow-sense heritability of 67.5 ± 26 percent was obtained, suggesting that selection for this trait should be effective. This estimate must be used with caution, since the additive-dominance model did not adequately explain gene action for this character, and epistatic effects can inflate the narrow-sense heritability estimate as measured by Warner's method (Ketata et al., 1976). This estimate should be interpreted as a theoretical maximum, and can be judged as moderate to moderately high.

The estimate of genetic advance under selection (G.S.), which evaluates the expected rate of genetic gain under directional selection, was 21.1 percent. A 21.1 percent increase in the F_3 mean above the F_2 mean can be expected if the best 5 percent of the F_2 plants are selected.

Table 24. Gene effects estimated using three and six-parameter models on generation means in a MSU 333 x MSU 365 cross.

Model and Effect	Estimates
Three-parameter	
m	6.23** ± .04
a	3.06** ± .04
d	-1.11** ± .06
X^2	P = <.005
Six-parameter	
m	4.70** ± .002
a	2.50** ± .017
d	-2.85** ± .098
aa	0.82** ± .092
ad	-1.95** ± .013
dd	1.63** ± .305

**Significantly different from zero.

Two estimates of k, the minimum number of effective factors controlling pedicel width, were computed. Estimates of 12.05 and 12.93 were obtained using Castle's and Burton's method, respectively. These estimates may also be biased by epistatic effects.

The correlation coefficients between pedicel width with fruit length, width, and weight were calculated from F_2 generation data (Table 25). All correlation coefficients were significant at the 0.01 level, suggesting that selection for plants with large fruit and narrow pedicels may be difficult. The coefficients of determination (r^2) corresponding to these correlation coefficient values are 0.11, 0.13, and 0.29, respectively (Table 25). The (r^2) statistic is equal to the proportion of total variability of the dependent variable that may be ascribed to the effect of the independent variable. Thus, 11 percent of the variation in fruit width, 13 percent of the variation in fruit length, and 29 percent of the variation in fruit weight can be ascribed to the effect of pedicel width. The positive correlation coefficients suggest that, in most cases, selection for fruit with a narrower pedicel will also result in a slight reduction of fruit size. However, the relatively low coefficients of determination suggest that the breeding of individuals with larger fruit and narrower pedicels is, within limits, a feasible objective.

Detachment Force

There were no differences (5% level) between the generation means of the reciprocal F_1's or reciprocal F_2's, and therefore, the data were pooled. The frequency distributions for detachment force and graphic frequency distributions are presented in Table 26 and Figure 9, respectively.

Table 25. Correlation coefficients (r) and coefficients of determination (r^2) of pedicel width with fruit width, length, and weight in a F_2 generation of the cross MSU 333 x MSU 365.

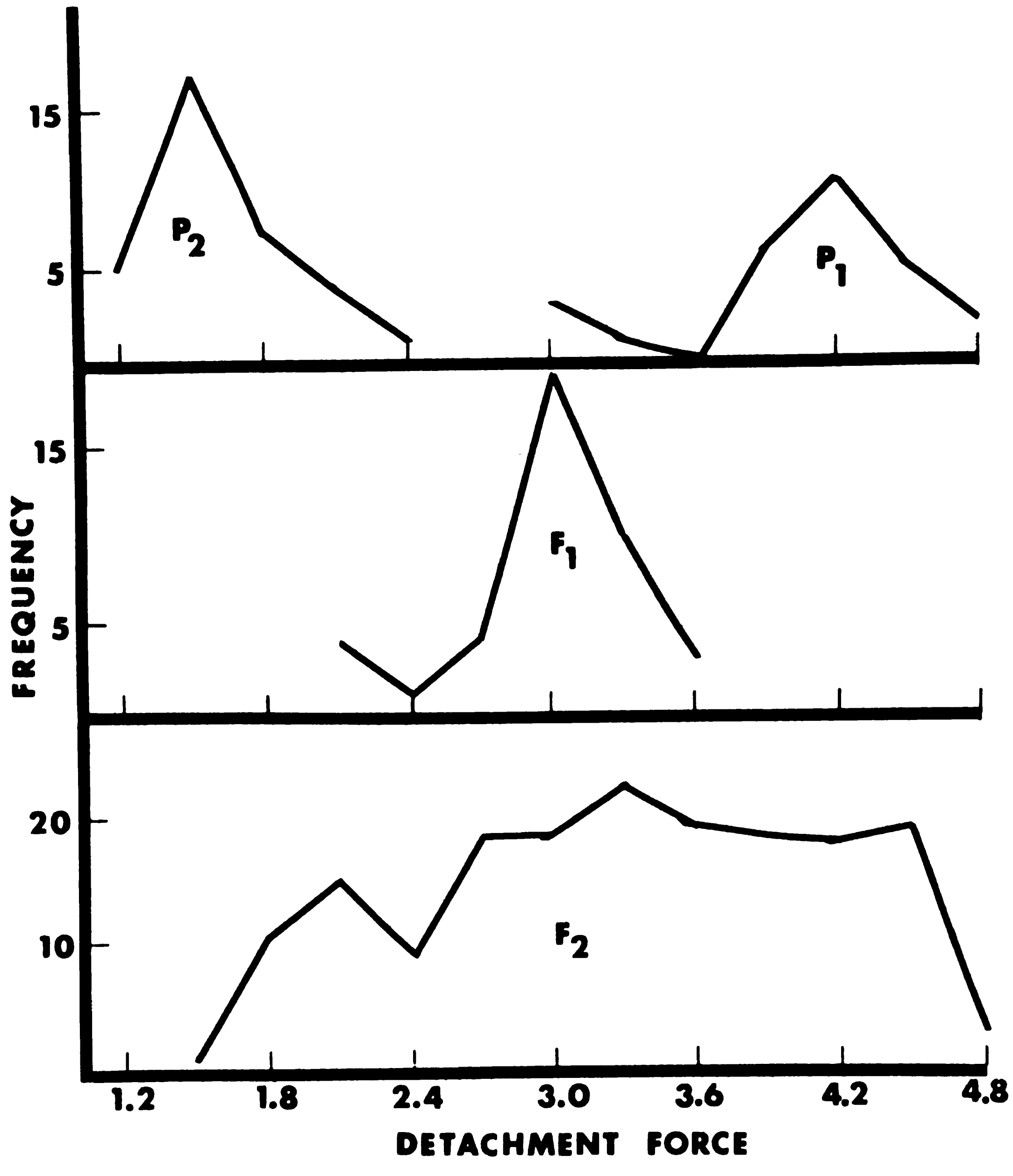
Statistic	Fruit Width	Fruit Length	Fruit Weight
r	0.33	0.36	0.54
r^2	0.11	0.13	0.29

All correlations (r) significant at 1% level with 304 d.f.

Table 26. Frequency distributions of detachment force values (kg) in the cross MSU 160 x MSU 249.

		Class Centers															No. of
Pedigree	Generation	1.2	1.5	1.8	2.1	2.4	2.7	3.0	3.3	3.6	3.9	4.2	4.5	4.8	Mean	s	Plants
MSU 160	P_1							3	1	0	6	10	5	2	4.20	0.51	27
MSU 249	P_2	5	17	7	4	1									1.77	0.27	34
MSU 160 x MSU 249	F_1				4	1	4	22	10	3					3.14	0.36	44
F_1 self	F_2		1	11	15	9	18	18	23	19	18	17	19	4	3.45	0.86	172

Figure 9. Frequency distributions for detachment force (kg) in pepper from the cross MSU 160 x MSU 249.


15
5
15
5
20
10
FREQUENCY
P2
P1
F1
F2
1.2
1.8
2.4
3.0
3.6
4.2
4.8
DETACHMENT FORCE

The F_1 and F_2 frequency distributions were skewed slightly toward the high detachment force parent (P_1). Of the total F_2 individuals, 118 lay on the P_1 side of the midparent value (2.98 kg). The F_1 mean (Table 26) lay on the P_1 side of the midparent (F_1 - midparent = -0.16 kg), but was not significantly different (5% level) from the midparent value. The F_2 mean was significantly different (1% level) from the F_1 mean and the midparent value. The difference between the parents was 2.42 kg.

Two estimates of k, the minimum number of effective factors controlling detachment force, were computed. Estimates of 1.29 and 1.86 were obatined using Castle's (1921) and Burton's (1951) method, respectively.

Due to the lack of BC generation data, no narrow-sense heritability estimate was made. However, the close proximity of the F_1 and F_2 means to the midparent value suggests a high degree of additive gene action controlling trait expression. This fact, together with the estimate of k indicating a small number of genes controlling this trait, suggests that selection for individuals requiring low detachment force would be possible.

Correlation coefficients between detachment force and fruit length, width, and weight were calculated from F_2 data. These coefficients are shown in Table 27. All coefficients were significant at the 1% level. The coefficients of determination (r^2) corresponding to these correlation coefficient values are 0.44, 0.16, and 0.62, respectively (Table 27). Thus, 44 percent of the variation in fruit width, 16 percent of the variation in fruit length, and 62 percent of the variation in fruit weight can be ascribed to the effect of detachment force.

These positive correlation coefficients suggest that, in most cases, selection for fruit with lower detachment force can also result in a slight reduction of fruit size. However, the relatively low to intermediate coefficients of determination suggest that the breeding of individuals with larger fruit and lower detachment forces is, within limits, a feasible objective.

Table 27. Correlation coefficients (r) and coefficients of determination (r^2) of detachment force with fruit width, length, and weight in the F_2 generation of the cross MSU 160 x MSU 249.

Statistic	Fruit Width	Fruit Length	Fruit Weight
r	0.66	0.40	0.79
r^2	0.44	0.16	0.62

All correlations (r) significant at 1% level with 171 d.f.

SUMMARY

The progenies from 2 mating schemes, diallel analysis and F_2 analysis, were evaluated to determine the mode of inheritance of pedicel width, and to determine the relationship of pedicel width with fruit length, width, and weight.

Pedicel width was determined to be quantitatively inherited, controlled by approximately 12 loci. Both additive and dominance gene action were involved in the expression of pedicel width. Epistatic gene action was also detected. Reciprocal effects were negligible. Narrow-sense heritability estimates of 84 percent and 67.5 percent were obtained from the diallel analysis and F_2 analysis, respectively, suggesting that selection for this trait should be effective. Expected gain from selection was estimated at 21.1 percent. In both experiments, correlation coefficients between pedicel width and fruit length, width, and weight were determined. All correlations were positive and significant at the 1% level, and were of greater magnitude in the diallel analysis. These coefficients suggested that, in most cases, selection for fruit with a narrower pedicel will result in a slight reduction of fruit size. However, the low coefficients of determination suggest that the breeding of individuals with larger fruit and narrower pedicels is possible.

Fruit-calyx detachment force was found to be controlled by a low number of loci, approximately 1 to 2. The expression of fruit-calyx

detachment force was controlled mainly by additive gene action. Correlation coefficients between detachment force and fruit length, width, and weight were calculated from F_2 data. All coefficients were positive and significant at the 1% level. These coefficients suggested that, in most cases, selection for fruit with lower detachment force will result in a slight reduction in fruit size. However, the relatively low to intermediate coefficients of determination suggest that the breeding of individuals with larger fruit and lower detachment force is possible.

The results from this study show that pedicel width and fruit detachment force are heritable traits. The information obtained on the genetics of these traits and on their relationship to fruit characteristics is important in the development of cultivars adapted to mechanical harvest. Other plant characteristics, such as branching habit, fruit bearing habit, fruit location, and fruit maturation are factors that are also involved in mechanical harvesting suitability. An understanding of the genetics of these and other components and of their interrelationship to each other will be necessary for the design of optimal breeding schemes for the recovery of desirable genotypes.

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