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THE INHERITANCE OF SEVERAL CHARACTERS

IN PAK-CHOI AND PEPPER

presented by

Kenneth R. McCammon

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THE INHERITANCE OF SEVERAL CHARACTERS IN PAK-CHOI AND PEPPER

By

Kenneth R. McCammon

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ABSTRACT

THE INHERITANCE OF SEVERAL CHARACTERS IN PAK-CHOI AND PEPPER

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Studies were conducted on Pak-choi (Brassica rapa L., Chinensis group), to develop a sampling technique for the determination of petiole width, thickness and angle of adaxial curvature, and to investigate the inheritance of these characters. A technique was developed, using the means of the fifth, seventh and ninth petioles, measured at a distance 9 cm from the base of each petiole. Inheritance studies were conducted in the field over two seasons.

Petiole width was determined to be simply inherited, with narrow petioles being dominant over wide. Petiole thickness was found to be controlled by two major genes, with thick petioles partially dominant over thin petioles. Dominance gene effects appeared most important, although additive gene effects were also significant. A 9:7 recessive suppressor model best explained the observed ratios.

Adaxial curvature was also determined to be controlled by two major loci, with curved petioles partially dominant over flat petioles. Both dominance and additive gene effects were involved in the expression of this trait. In addition, significant additive X additive, additive X dominance and dominance X dominance epistatic gene effects were noted. A 9:7 recessive suppressor model best explained the observed ratios.

Studies on pepper were conducted to determine the inheritance of the "umbrella" branching habit, a unique habit with possible use in mechanical harvesting. F_2 data from crosses between dwarf, indeterminate and umbrella lines showed a recessive inheritance of the dwarf and umbrella phenotypes. Four genes were involved in the expression of the phenotypes studied.

The dwarf habit was found to be controlled by two linked recessive genes, dt, a gene conditioning determinate growth, and fa, a gene controlling the clustered bearing habit. The umbrella habit was controlled by three recessive genes, dt, fa and ct. The gene ct controls the number of axillary branches produced by the plant. Dt and Ct condition indeterminate growth. In the homozygous or heterozygous conditions, Ct is epistatic to the expression of dt, while Dt is epistatic to the expression of ct. A fourth gene, Su, is a dominant suppressor which acts to suppress the epistatic action of the _Ct_ gene.

This dissertation is dedicated to my wife, Marlise, and daughter, Mollie...

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CHAPTER I

THE INHERITANCE OF PETIOLE CHARACTERS IN PAK-CHOI

INTRODUCTION

Pak-Choi (Brassica rapa L., Chinensis group) is a member of the mustard family, closely related to Chinese cabbage, though it differs greatly in appearance. It is actually two vegetables in one and is used in a variety of oriental dishes, the leaves prepared like spinach, the petioles like asparagus. The influx of large numbers of Asians into the United States over the past 20 to 25 years, coupled with a greater popularity of ethnic foods by the general public, has led to an increase in the use of and demand for Pak-choi.

Commercial production of Pak-Choi has been limited mainly to California, Hawaii and New Jersey, with shipment to other regions of the country for distribution and sale. Reports on total production of Pak-choi are limited. In California in 1971, about 30 acres were produced in the Carmel and Salinas Valleys south of San Francisco. Hawaii produced approximately 196,000 pounds of Pak-Choi in the same year (Yamaguchi, 1973). There has been a steady increase over the years in the number of acres in Hawaii devoted to the production of Pak-Choi, increasing from 84 acres in 1975, to 120 acres in 1979, for a total value in 1979 of approximately $360,000 (Statistics of Hawaiian Agriculture, 1979).

In view of the large oriental population in the Chicago area, with its close proximity to Michigan, and the high value of the crop, commercial production of Pak-Choi by Michigan farmers could become a very profitable enterprise. However, early attempts at Pak-Choi culture in Michigan often resulted in loss of the crop due to bolting.

While Pak-Choi is often sold with small flowers in China and Japan, this trait is undesirable in terms of consumer preference in the United States. The major seed sources for Pak-Choi are seed houses located in Japan and Taiwan. Unfortunately, cultivars produced by these companies are not well adapted to Michigan or to the needs of U.S. consumers. Acceptance of flowering Pak-Choi in other countries has severely limited interest in selecting for bolt resistant lines. The concern instead lies in the production of cultivars with wide, thick and succulent petioles.

While the major emphasis of the MSU Pak-Choi breeding program has been the development of bolt resistant cultivars, selection has also been directed towards cultivars with wide, thick petioles. As selection pressure for bolt resistance increased, there was a decrease in the number of plants within the population exhibiting these characters.

Elucidation of the factors controlling petiole characters such as shape, width and thickness would facilitate efficient breeding for the development of cultivars exhibiting the desired petiole characteristics.

The objectives of the present study were:

1. To develop a technique for measuring petiole shape, width and thickness.
2. To develop a sampling technique appropriate for genetic study.
3. To investigate the inheritance of petiole shape, width and thickness.

REVIEW OF LITERATURE

There are two main groups of Chinese cabbage, the heading group called Pe-Tsai (Brassica rapa L., Pekinensis group), and the non-heading group called Pak-Choi (Brassica rapa L., Chinensis group). Both Pe-Tsai and Pak-Choi mean "white vegetable", Pe-Tsai is the Peking dialect while Pak=Choi is the Cantonese dialect (Lee, 1982).

Pak-Choi (also referred to as Bok Choy and Bok Tsoi in the literature) is a vegetable of ancient origin, believed to have originated in Japan and Eastern China (Vavilov, 1949/1950) or China (Lee, 1982). Early literature from the 5th century A.D. indicates that Pak-Choi was a relatively unimportant crop in China at that time. However, it is now the most common and extensively used leafy vegetable in China (Li, 1969).

There is little mention in the literature of the use of Pak-Choi in the U.S. Bailey, in 1894, described Pak-Choi as, "leaf stalks are light colored, sometimes almost ivory white and celery-like," adding that the plant had little use in the U.S. (Bailey, 1922). Discussion of its use as a vegetable crop increased in the 1940's (Smith, 1945;

Whallon, 1948), but no work has been reported on the breeding of the crop since then. To the author's knowledge, no work has been reported concerning the petiole morphology of Pak-Choi. A comprehensive search of the literature on other petiole crops such as celery and rhubarb also failed to expose previous research of this type. Frazier, et al, (1960) conducted correlation studies between immature and mature rhubarb, in which they studied seedling petiole color, vigor and habit. In a subsequent study on the forcing of rhubarb, Martin (1962) found high correlations between parental and progeny petiole types, but failed to report any criteria upon which petiole type was defined.

MATERIALS AND METHODS

Sampling Technique

Greenhouse Study

This investigation was undertaken to develop a rapid and reliable sampling method for measuring the petiole morphology of the Pak-Choi plant. Two Pak-Choi lines inbred for seven generations, MSU 78-7A, a narrow, thick petiole line, and MSU 78-9A, a wide, thin petiole line were utilized. The lines were derived from the cross, Taisai X Jiang-Mein. In Pak-Choi, the mature plant consists of a single axis, with a whorled leaf arrangement.

Seventy-five plants of each of the parents were grown in the greenhouse bed in a completely randomized design with five replicates of fifteen plants each, from February to April, 1980. The petioles of the third, fifth, seventh, ninth and eleventh fully-expanded leaves above the cotyledon were measured when the plants were mature. (Plants were considered mature when they reached marketable size.) Measurements of petiole width and thickness were made with a caliper, at 3, 6, 9 and 12 cm from the base of the petiole, in order to determine the best distance from the base for measuring these characters. Means, variances and standard deviations were calculated from individual plants. Population means were statistically compared by use of the two-tailed t-test (Steel and Torrie, 1960).

Field Study

Due to the laborious and time consuming problem of measuring each petiole with a caliper, a more rapid data collecting technique was investigated. A second study was made by stamping a cross-section of each petiole on paper. Seventy-five plants of each line were field grown in a completely randomized design with five replicates of fifteen plants each, from June to July, 1980, in an effort to further refine the procedure by reducing the number of petioles sampled. The petioles of the third, fifth, seventh, ninth and eleventh fully-expanded leaves were measured. Based on the results of the previous study, cross sections were made 9 cm from the base of the petiole, using a single-edge razor blade. The stamp pad was then used to produce an ink impression of the petiole on a data sheet, providing a rapid and permanent recording of the petiole shape for subsequent measurement.

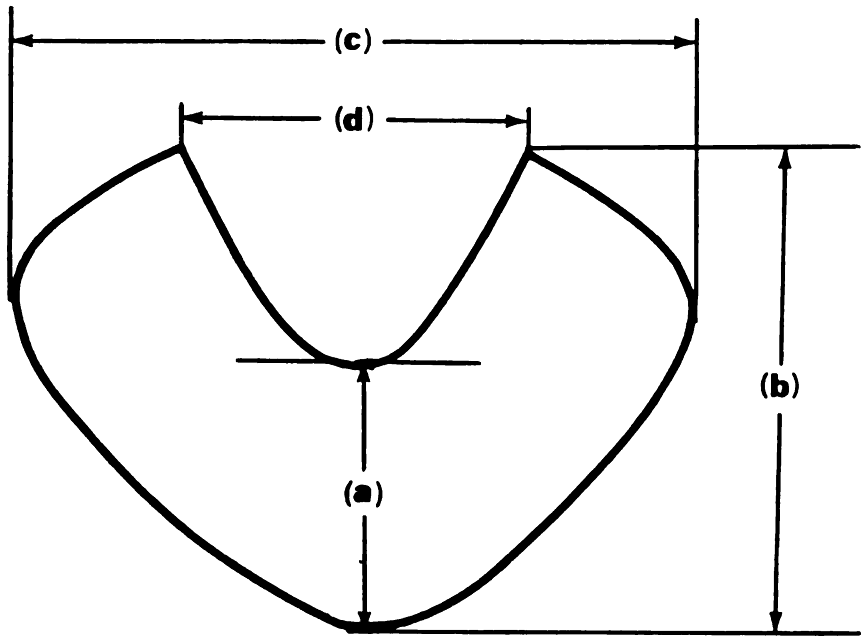
Data was obtained for petiole width, thickness and angle of adaxial curvature for each of the five petioles sampled from each plant. A millimeter ruler was used for measuring the thickness and width, while a modified protractor was used to measure the angle. Statistical treatment of the data was similar to the greenhouse grown plants. Data from the two studies were utilized to determine the relationship between measurements taken in the greenhouse and field under different environmental conditions.

Inheritance Studies - 1981

Two inbred parents, MSU 78-7A (P_1) and MSU 78-9A (P_2), were used to produce the various populations for the study. Both parents were derived from the cross, Taisai X Jiang-Mein. Reciprocal populations of F_1, F_2, BC_1 and BC_2 were produced by hand pollination in the greenhouse. Seeds of parents and progenies were planted in a greenhouse in No. 96 PVC growing trays containing VSP artificial soil mix on May 3, 1981, and transplanted to the field on June 2, 1981, using a randomized complete block design with three replications. Each replicate contained 12 plants of each parental line, 24 plants of each F_1 family, 36 plants of each backcross population, and 108 of each F_2 population.

Plants were grown in rows 61 cm apart and spaced at intervals of 30 cm in the row. Cultural practices were those recommended for commercial production in Michigan. Imprints of the fifth, seventh and ninth petioles, 9 cm from the base, were made in July. Each imprint was measured for thickness (a),

FIGURE 1 SCHEMATIC REPRESENTATION OF A PAK-CHOI PETIOLE CROSS-SECTION


(c)
(d)
(b)
(a)

height (b), and outer (c) and inner (d) width (Figure 1). Since the measuring of the adaxial curvature angle was difficult, a curvature index (CI) was determined, using the formula:

$$\mathrm{CI} = \frac{\text{height (b) - thickness (a)}}{\text{inner width (d)}}$$

The numerator of the above formula expresses the height of the curvature which, when divided by the denominator (inner width), produces a ratio or relative degree of curvature; 0 representing no curvature, with a greater degree of curvature as the value increases (Table 1).

TABLE 1 TABLE OF CALCULATED CURVATURE INDEX VALUES WITH APPROXIMATE CORRESPONDING ANGLES

Curvature Index (CI)	Angle (degrees)
0.0	180
0.1	160
0.2	145
0.3	125
0.4	110
0.5	90
0.6	75
0.7	65
0.8	55
0.9	50
1.0	40

Data from the three petioles were pooled to obtain a plant mean prior to analysis. Statistical treatment of the data was similar to the previous experiment. Data was also obtained for bolting stage using the following rating system: (1) vegetative, (2) flower primordia visible, (3) bolted, seedstalk elongation of 2" or greater. Determination of bolting stage was made by visual observation of the apical meristem.

Inheritance Studies - 1982

Identical genetic material as used in 1981 and two F_3 families were grown in 1982. Due to shortage of seed, some population sizes were limited. Seeds of the parents and progenies were planted in a greenhouse in vermiculite on May 6, 1982, transplanted to PVC growing trays one week later, and transplanted to the field on June 8, 1982. A randomized complete block design with three replications was utilized. Each replicate contained 12 plants of each parental line and F_1 family, 18 plants of each F_3 family, 36 plants of each backcross family, and 72 plants of each F_2 family. Cultural practices were similar to the 1981 experiment. Petiole imprints were made in July. Measurements and data analysis were similar to the 1981 experiment.

Analysis of variance was conducted on the data for each character (Little and Hills, 1975). The means of reciprocal populations were tested for homogeneity prior to analysis of the data. The distributions of the segregating generations were continuous, with no apparent division into phenotypic classes. Thus, the data were analyzed biometrically.

For each character, Mathers' 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 $C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$, was applied to the generation means to determine the adequacy of the additive-dominance model. When significant results were obtained from Mathers' scaling test, a generation means analysis was conducted using the method outlined by Mather and Jinks (1971), and notations used by Gamble (1962) to fit a six parameter model. The parameters tested are the mean effect (m), the pooled additive effect (a), the pooled dominance effect (d), the pooled additive X additive effect (aa), the pooled additive X dominance effect (ad), and the pooled dominance X dominance effect (dd). The equations used for estimating these parameters in terms of generation means are:

$$m = \overline{F}_2$$

$$a = \overline{BC}_1 - \overline{BC}_2$$

$$d = 0.5\overline{P}_1 - 0.5\overline{P}_2 + \overline{F}_1 - 4\overline{F}_2 + 2\overline{BC}_1 + 2\overline{BC}_2$$

$$aa = 2\overline{BC}_1 + 2\overline{BC}_2 - 4\overline{F}_2$$

$$ad = -0.5\overline{P}_1 + 0.5\overline{P}_2 + \overline{BC}_1 - \overline{BC}_2$$

$$dd = \overline{P}_1 + \overline{P}_2 + 2\overline{F}_1 + 4\overline{F}_2 - 4\overline{BC}_1 - 4\overline{BC}_2$$

Standard errors of the corresponding generation means were used to test the significance of the various gene effects. Narrow sense heritability, h^2ns, was estimated by Warners' 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. Standard errors for each h^2ns estimate were derived by the square root of the formula:

$$\begin{aligned} V(h^2ns) \;=\; & 2\{[(VBC_1 + VBC_2)\;^2/df] \\ & + (VBC_1\;^2/dfBC_1) \\ & + (VBC_2\;^2/dfBC_2)\} \;/VF_2{}^2. \end{aligned}$$

Expected gain from selection (G. S.) was calculated using Allards' formula (1960) as G.S. = k ph^2ns, where k is the selection differential, p is the phenotypic standard deviation of the F_2, and h^2ns is heritability in the narrow sense.

Theoretical F_2 means were calculated, based on the number of gene pairs assumed to be differentiating the parents, after the formulas proposed by Powers, et al (1950). Theoretical means were tested for significance from the observed means by the use of a one-tailed t-test (Steel and Torrie, 1960). The minimum number of gene pairs differentiating the parents were computed using the methods of Castle (1921) and Burton (1951). To determine if the data from the two years could be pooled prior to genetic analysis, an analysis of variance was conducted using data from both years to test year X generation effects. Pearson's correlation coefficients were obtained for the three characters in relation to bolting stage.

RESULTS AND DISCUSSION

Sampling Technique

Greenhouse Study

Mean petiole thickness and width data for the parents MSU 78-7A and MSU 78-9A were obtained by measuring the third, fifth, seventh, ninth and eleventh petioles at distances 3, 6, 9 and 12 cm from the base of each petiole. MSU 78-7A, the narrow, thick petiole line, had means of 16.2 mm wide and 7.7 mm thick. MSU 78-9A exhibited wide, thin petioles with means of 19.0 mm wide and 5.5 mm thick. Since sampling of four distances along the petiole was time consuming, it was necessary to determine the proper distance from the base to obtain a valid sample measurement.

For petiole width of MSU 78-7A and MSU 78-9A, the means of 3 cm and 12 cm were both significantly different (1% level) from the mean of all four distances (Table 2). The 6 cm and 9 cm means were not significantly different from the mean of all four distances. The data suggest that sampling at 6 cm or 9 cm from the base of the petiole in the MSU 78-7A and MSU 78-9A parents would provide a valid estimate of petiole width. The 't' and probability values were obtained by comparing the mean of each individual distance measurement with the mean of all distances combined (3, 6, 9 and 12 cm).

TABLE 2 MEANS AND STANDARD DEVIATIONS FOR PETIOLE WIDTH AT INDIVIDUAL VS. ALL DISTANCES MSU 78-7A AND MSU 78-9A

	Distance (cm)	Mean (mm)	S.D.	T Value	Probability
MSU 78-7A					
	3	21.8	5.11	7.68	.000
	6	16.6	3.37	0.78	.458
	9	15.8	2.99	-0.85	.400
	12	11.0	2.58	-13.29	.000
	3,6,9,12	16.2	3.64	-	-
MSU 78-9A					
	3	26.8	3.76	14.41	.000
	6	19.7	3.90	1.33	.192
	9	18.4	3.23	-1.35	.186
	12	12.6	2.21	-17.61	.000
	3,6,9,12	19.0	3.40	-	-

TABLE 3 MEANS AND STANDARD DEVIATIONS FOR PETIOLE THICKNESS AT INDIVIDUAL VS. ALL DISTANCES MSU 78-7A AND MSU 78-9A

	Distance (cm)	Mean (mm)	S.D.	T Value	Probability
MSU 78-7A					
	3	7.9	1.51	0.78	.458
	6	7.8	1.41	0.44	.662
	9	7.8	1.37	0.15	.881
	12	7.4	1.49	-1.34	.190
	3,6,9,12	7.7	1.44	-	-
MSU 78-9A					
	3	6.3	1.19	4.89	.000
	6	5.7	1.19	1.39	.177
	9	5.4	1.18	-0.35	.728
	12	4.6	0.99	-5.53	.000
	3,6,9,12	5.5	1.15	-	-

For petiole thickness of MSU 78-7A, none of the four distances from the base of the petiole differed significantly from the mean for all four distances. For MSU 78-9A, the 3 cm and 12 cm distances were significantly different (1% level) from the mean of all four distances. The 6 cm and 9 cm distances were not significantly different and had approximately equal standard deviations. However, the 9 cm distance from the base of the petiole exhibited the mean closest to the total mean, and was thus selected as the proper distance for obtaining a valid estimate of petiole thickness. Based on the results of this study, the 9 cm distance from the base of the petiole was used for sampling petiole width, thickness and the angle of adaxial curvature.

Field Study - 1980

For petiole width of MSU 78-7A, means of each individual petiole per plant were significantly different (1% level) from the mean of all five petioles (Table 4). The mean of petioles 3, 7 and 11 and the mean of petioles 5, 7 and 9 were not significantly different from the five petiole mean. The 5, 7, 9 combination exhibited the lowest standard deviation of the two petiole combinations. For MSU 78-9A, the mean of the third petiole was significantly different (1% level) from the mean of all five petioles.. The mean of the seventh petiole was significantly different (5% level) from the five petiole mean. The mean of petiole numbers 3, 7, and 11 was not significantly different from the five petiole mean. The mean of petioles numbers 5, 7, and 9 was not significantly different from the five petiole mean and had a similar standard deviation.

TABLE 4 WIDTH OF INDIVIDUAL PETIOLES AND VARIOUS PETIOLE COMBINATIONS FOR MSU 78-7A AND MSU 78-9A

Petioles	Mean (mm)	S.D.	T Value	Probability
MSU 78-7A				
3	15.0	2.80	2.78	.009
5	15.5	2.44	5.21	.000
7	15.1	2.70	3.34	.002
9	12.3	2.42	-6.20	.000
11	10.5	1.56	-17.14	.000
3,7,11	13.8	3.21	-1.17	.245
5,7,9	14.3	3.06	1.22	.225
3,5,7,9,11	14.1	2.47	-	-
MSU 78-9A				
3	19.8	4.18	-2.79	.008
5	20.4	4.67	-1.56	.128
7	22.9	5.47	2.52	.015
9	21.7	5.71	0.55	.585
11	21.5	6.15	0.32	.750
3,7,11	21.5	5.68	0.48	.632
5,7,9	21.6	5.39	0.97	.334
3,5,7,9,11	21.3	5.33	-	-

For petiole thickness of MSU 78-7A, individual means of petioles 5, 7, 9, and 11 were significantly different (1% level) from the five petiole mean (Table 5). The mean of petiole 3 was significantly different (5% level) from the five petiole mean. The mean of petioles 3, 7, and 11 and the mean of petioles 5, 7, and 9 were not significantly different from the five petiole mean. The 5, 7, 9 combination exhibited the lowest standard deviation of the two petiole combinations. For MSU 78-9A, the mean of the third petiole was significantly different (1% level) from the five petiole mean. None of the other individual petiole means were significantly different from the five petiole mean, and had similar standard deviations. Based on data obtained from this study, sampling petioles 3, 7, and 11 or 5, 7, and 9 would provide a reliable estimate of petiole thickness.

Table 5
THICKNESS OF INDIVIDUAL PETIOLES AND VARIOUS PETIOLE COMBINATIONS FOR MSU 78-7A AND MSU 78-9A

Petioles	Mean (mm)	S.D.	T Value	Probability
MSU 78-7A				
3	9.3	1.56	2.22	.038
5	9.5	1.18	4.30	.000
7	9.4	1.29	3.08	.005
9	8.2	1.47	-3.90	.001
11	7.2	1.20	-10.56	.000
3,7,11	8.7	1.68	1.29	.205
5,7,9	9.0	1.49	1.24	.217
3,5,7,9,11	8.9	1.36	-	-
MSU 78-9A				
3	5.9	1.48	-3.63	.000
5	6.3	1.75	-1.63	.109
7	7.0	1.75	1.83	.050
9	6.9	1.72	1.35	.185
11	6.9	1.54	1.28	.206
3,7,11	6.5	1.79	-0.64	.523
5,7,9	6.7	1.75	0.85	.399
3,5,7,9,11	6.6	1.66	-	-

For angle of adaxial curvature, none of the individual petiole means differed significantly from the mean of all petioles for either parent (Table 6). The 5, 7, 9 petiole combination exhibited a lower standard deviation than the 3, 7, 11 combination.

Table 6
ANGLE OF ADAXIAL CURVATURE OF INDIVIDUAL PETIOLES AND VARIOUS PETIOLE COMBINATIONS FOR MSU 78-7A AND MSU 78-9A

Petioles	Mean (degrees)	S.D.	T Value	Probability
MSU 78-7A				
3	119.9	16.87	0.05	.980
5	118.6	16.45	0.71	.495
7	117.2	15.45	-1.56	.125
9	120.5	17.69	0.28	.777
11	125.0	21.98	1.69	.095
3,7,11	120.2	18.46	0.22	.825
5,7,9	119.3	16.73	-0.59	.551
3,5,7,9,11	120.0	17.57	-	-
MSU 78-9A				
3	145.8	17.33	1.91	.062
5	142.6	19.96	0.51	.612
7	142.5	22.51	0.40	.693
9	140.4	22.88	-0.38	.701
11	138.0	20.94	-1.54	.133
3,7,11	141.8	20.94	0.08	.993
5,7,9	141.9	20.75	0.11	.991
3,5,7,9,11	141.7	20.96	-	-

Correlation coefficients between data taken from the 9 cm distance in greenhouse and field experiments were .73 for width, .82 for thickness, and .58 for angle of adaxial curvature. All were significant at the .001 level. Based on the results of the two studies on sampling methods, the combination of petioles 5, 7, and 9, measured at a distance 9 cm from the base of each petiole, was used to sample the populations for the various characters under investigation.

Inheritance Studies - Pooled Analysis

The analyses of variance for all three characters for both seasons showed significant generation, year, and generation X year effects (Table 7). Therefore, the data were not

TABLE 7 ANALYSES OF VARIANCE FOR PETIOLE WIDTH, THICKNESS AND ANGLE OF ADAXIAL CURVATURE FOR YEARS 1981 AND 1982

WIDTH

Source	df	MS	F
Total	1756		
Generation	5	3704.82	126.72**
Year	1	1429.16	48.88**
Generation X Year	5	84.56	2.89*
Error	1745	29.24	

THICKNESS

Source	df	MS	F
Total	1756		
Generation	5	63.23	17.65**
Year	1	432.39	120.68**
Generation X Year	5	12.04	3.36**
Error	1745	3.58	

ADAXIAL CURVATURE

Source	df	MS	F
Total	1756		
Generation	5	4.409	65.07**
Year	1	7.178	105.94**
Generation X Year	5	.308	4.55**
Error	1745	.068	

**significant at .01 level
*significant at .05 level

pooled, and the results of the two experiments are presented separately. Within each year, however, there were no significant differences between reciprocal population for all traits, and the data were pooled prior to analysis.

Petiole Width - 1981

The F_1 and F_2 frequency distributions were skewed towards the narrow parent, P_1, (Figure 2). Seventy-four percent of the F_2 population had widths lower than the mid= parent mean, 23.5 mm, (Appendix Table 28) suggesting a partial dominance of the narrow parent over the wide parent. The F_1 mean, 20.4 mm, was lower than the midparent mean, 23.5 mm, but was not significant. The F_2 mean showed a similar trend. The mean of the BC to P_1 fell between the P_1 and F_1 means, and was significantly different (5% level) from both means. The BC to P_2 mean fell closer to the P_2 mean, and was significantly different (5% level) from the P_2 and F_1 means. The parental difference was 14.5 mm.

The results of Mather's A, B, C scaling test were non-significant (Table 8). Significance for any of these estimates suggests the presence of epistasis.

Two estimates of k, the minimum number of loci controlling petiole width were computed. Estimates of 1.06 and 1.14 genes were obtained using the methods of Castle and Burton, respectively. Using the formula proposed by Powers,

FIGURE 2 FREQUENCY DISTRIBUTION FOR PETIOLE WIDTHS (mm)
FROM THE CROSS MSU 78-7A X MSU 78-9A, 1981

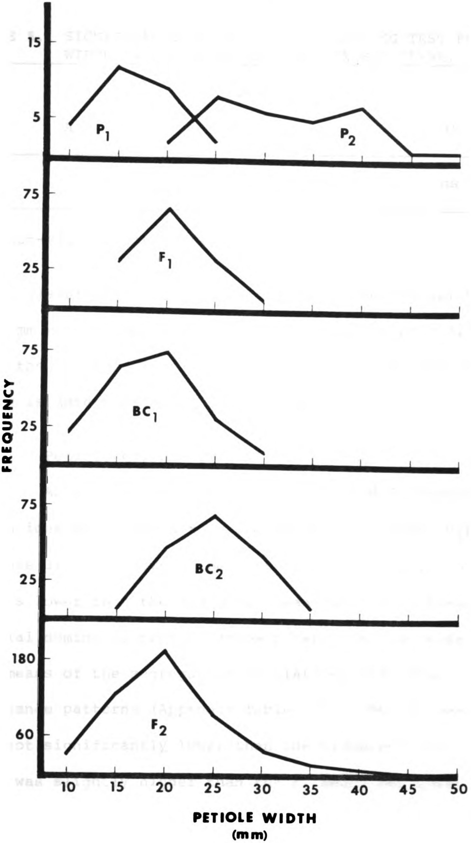

15
5
P1
P2
75
25
F1
75
25
BC1
75
25
BC2
180
60
F2
FREQUENCY
10
15
20
25
30
35
40
45
50
PETIOLE WIDTH
(mm)

TABLE 8. SIGNIFICANCE OF THE A, B, C SCALING TEST FOR PETIOLE WIDTH IN THE CROSS MSU 78-7A X MSU 78-9A, 1981

Test		
A	B	C
ns	ns	ns

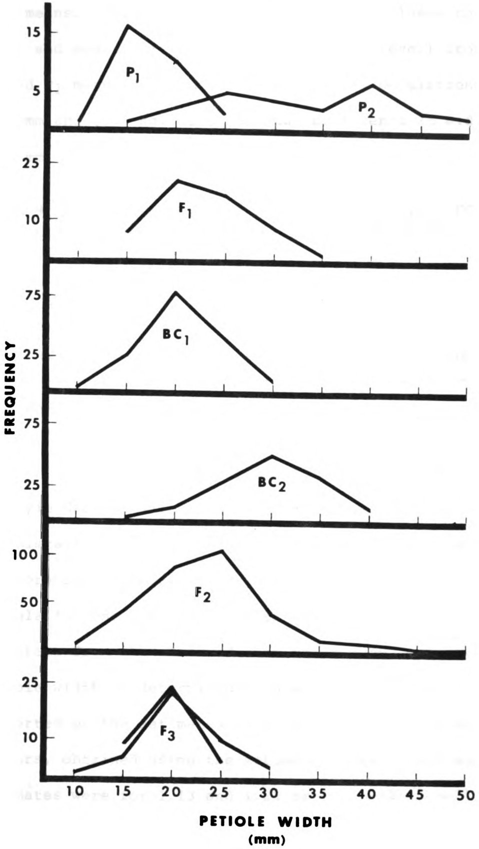
ns, non-significant at 5% level

et al (1950), $3/4(\bar{P}_1) + 1/4(\bar{P}_2) = F_2$, a theoretical F_2 mean of 19.8 mm was obtained, which was not significantly different from the observed mean (20.5 mm) and suggested that petiole width is determined by a single major gene.

Petiole Width - 1982

As in the previous year, the F_1 and F_2 frequency distributions were skewed towards the narrow parent (P_1) (Figure 3). Seventy-one percent of the F_2 population had values lower than the midparent mean (25.4 mm), suggesting a partial dominance of the narrow parent over the wide parent. The means of the segregating populations also show similar dominance patterns (Appendix Table 29). The F_1 mean (23.0 mm) was not significantly lower than the midparent mean. The F_2 mean was slightly higher than the F_1 mean, but lower than the midparent mean. The mean of the BC to P_1 fell between the F_1 and P_1 means, and was significantly different (5% level) from

FIGURE 3 FREQUENCY DISTRIBUTION FOR PETIOLE WIDTHS (mm) FROM THE CROSS MSU 78-7A X MSU 78-9A, 1982


15
5
P_1
P_2
25
10
F_1
75
25
BC_1
75
25
BC_2
100
50
F_2
25
10
F_3
FREQUENCY
10
15
20
25
30
35
40
45
50
PETIOLE WIDTH
(mm)

both means. The mean of the BC to P_2 fell closer to the P_2 mean, and was significantly different (5% level) from the P_2 and F_1 means. The means of the two F_3 populations were 20.8 mm and 19.5 mm. The parental difference in width was 17.1 mm.

TABLE 9 SIGNIFICANCE OF THE A, B, C SCALING TEST FOR PETIOLE WIDTH IN THE CROSS MSU 78-7A X MSU 78-9A, 1982

	Test	
A	B	C
ns	ns	ns

ns, non-significant at 5% level

As in the previous year, Mather's A, B, C scaling test yielded non-significant estimates, suggesting an absence of epistasis in the expression of petiole width (Table 9). A theoretical F_2 mean of 21.1 mm was obtained, using Powers' formula for one gene pair, which was not significantly different from the observed mean of 23.7 mm, suggesting that petiole width is determined by a single major gene. This is supported by the estimates of k, the number of effective factors, obtained using the methods of Castle and Burton. Estimates were for 1.13 and 1.23 genes, respectively

The F_2 and backcross generations from 1981 were partitioned into narrow and wide types based on the arithmetic mean of the two parents (23.5 mm), using the chi-square test to test for goodness of fit to a one gene model (Table 10).

TABLE 10 CHI-SQUARE TEST FOR GOODNESS OF FIT FOR POOLED POPULATIONS FROM THE CROSS MSU 78-7A X MSU 78-9A, BASED ON A ONE GENE HYPOTHESIS FOR PETIOLE WIDTH, 1981

Generation	Observed ratio	Theoretical ratio	Chi-sq.	P
Pooled F_1	12 :11	1:0	-	-
Pooled F_2	372:131	3:1	.247	.90-.50
Pooled BC to P_1	179:16	1:0	-	-
Pooled BC to P_2	61:102	1:1	9.44	.01-.004

Based on the ratios expected with a one major gene model, a good fit was obtained for the F_2 in 1981 (P = .90 - .50). The BC_2 ratio, however, was skewed towards the wide parent, suggesting the presence of modifiers in P_2 affecting the expression of this trait. The BC_1 ratio of 179:16 suggests agreement with the expectation of the model.

In 1982, the F_2 population showed an acceptable fit to the 3:1 expected ratio (P = .10 - .09), while the BC_2 fit was poor (P = < .001, Table 11). This may be explained by the differential expression of modifier genes in relation to different environmental conditions in the two experiments.

TABLE 11 CHI-SQUARE TEST FOR GOODNESS OF FIT FOR POOLED POPULATIONS FROM THE CROSS MUS 78-7A X MSU 78-9A, BASED ON A ONE GENE HYPOTHESIS FOR PETIOLE WIDTH, 1982

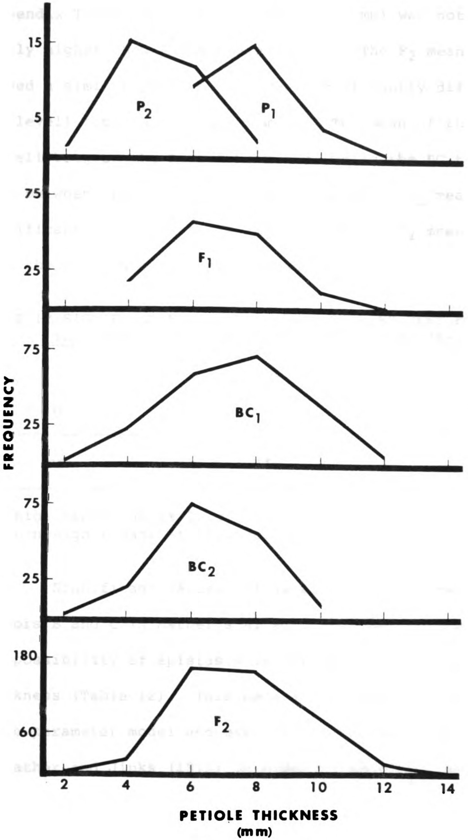
Generation	Observed ratio	Theoretical ratio	Chi-Sq.	P
Pooled F_1	50:4	1:0	-	-
Pooled F_2	214:88	3:1	2.76	.10-.09
Pooled BC to P_1	151:1	1:0	-	-
Pooled BC to P_2	26:115	1:1	56.176	<.001

The data indicate that there is dominance for narrow petioles, while wide, thick petiole phenotypes are desired. Therefore, selection of recessive genotypes (exhibiting wide petioles) would be necessary for improving petiole width in Pak-Choi.

Petiole Thickness - 1981

The F_1 and F_2 frequency distributions were skewed towards the thick parent (P_1) (Figure 4). Approximately fifty-nine percent of the F_2 population had mean thickness higher than the midparent mean (6.6 mm), suggesting a partial dominance of thick over thin petioles. The means of the various populations support the dominance pattern

FIGURE 4 FREQUENCY DISTRIBUTIONS FOR PETIOLE THICKNESS (mm) FROM THE CROSS MSU 78-A X MSU 78-9A, 1981


15
5
P$_2$
P$_1$
75
F$_1$
25
75
BC$_1$
25
75
BC$_2$
25
180
F$_2$
60
FREQUENCY
2
4
6
8
10
12
14
PETIOLE THICKNESS
(mm)

(Appendix Table 30). The F_1 mean (7.1 mm) was not significantly higher than the midparent mean. The F_2 mean (7.4 mm) showed a similar pattern, but was significantly different (5% level) from the midparent mean. The mean of the BC to P_1 fell between the F_1 and P_1 means, while the BC to P_2 mean fell between the F_1 and P_2 means. The BC to P_2 mean was significantly different (5% level) from the P_2 mean, but not from the F_1 mean or midparent mean.

TABLE 12 SIGNIFICANCE OF THE A, B, C SCALING TEST FOR PETIOLE THICKNESS IN THE CROSS MSU 78-7A X MSU 78-9A, 1981.

	Test	
A	B	C
ns	**	**

**, significant at 1% level
ns, non-significant at 5% level

Significant values (1% level) were obtained for factors B and C in Mather's A, B, C Scaling test suggesting the possibility of epistasis in the expression of petiole thickness (Table 12). This made it necessary to abandon the three parameter model and use a six parameter model outlined by Mather and Jinks (1971) in order to determine the nature of epistatic effects. The six parameter estimates (Table 13) show that dominance gene effects made the major contribution to variation in petiole thickness. Also, additive X dominance epistatic effects were significant (1% level).

TABLE 13 GENE EFFECTS ESTIMATED USING A SIX PARAMETER MODEL ON THE GENERATION MEANS FOR THE CROSS MSU 78-7A X 78-9A, 1981

Effect	Estimate
m	7.35±.008**
a	0.72±.033**
d	7.65±.321**
aa	-0.64±.260
ad	-0.51±.080**
dd	-0.93±.731

**, significantly different from zero

Mather and Jinks (1971) stated that the types of epistatic interaction can be inferred from the relative signs of d and dd. Like signs indicate complementary epistasis whereas opposite signs indicate epistasis of the duplicate, dominant or recessive suppressor types. In this cross, the estimate of d is significantly positive while the dd estimate is negative, suggesting either duplicate, dominant or recessive suppressor epistasis for the expression of petiole thickness.

Two estimates of k were computed, yielding values of 0.58 and 0.63, using Castle's and Burton's methods, respectively. Theoretical F_2 means were calculated, based on the number of factors assumed to be differentiating the parents, after the formulae proposed by Powers, et al, (1950). In these formulae, P_1 is the mean of the dominant parent, P_2 is the mean of the recessive parent, and F_2 is the theoretical F_2 mean.

TABLE 14 THEORETICAL F_2 MEANS FOR ONE, TWO AND THREE GENE PAIRS ASSUMING COMPLETE DOMINANCE, 1981

No. of genes	Theoretical	Observed
1	$(3/4)\bar{P}_1 + (1/4)\bar{P}_2 = 7.2 \pm 1.53$	7.4±1.99
2	$(15/16)\bar{P}_1 + (1/16)\bar{P}_2 = 7.6 \pm 1.51$	7.4±1.99
3	$(63/64)\bar{P}_1 + (1/64)\bar{P}_2 = 7.7 \pm 1.60$	7.4±1.99

Theoretical F_2 means based on one, two and three gene pair hypotheses were not significantly different from the observed F_2 mean (Table 14). The presence of epistatic effects, however, suggest the two gene pair hypothesis.

The F_2 and backcross generations were partitioned into thick and thin types based on the midparent mean (6.6 mm), resulting in a 9:7 segregation pattern. A chi-square was used to test for goodness of fit to a 9:7, two gene epistatic model. Based on the segregation ratios expected from the proposed model, there was a good fit of both the F_2 (P = .50 - .30) and BC2 populations (P = .50 - .10, Table 15).

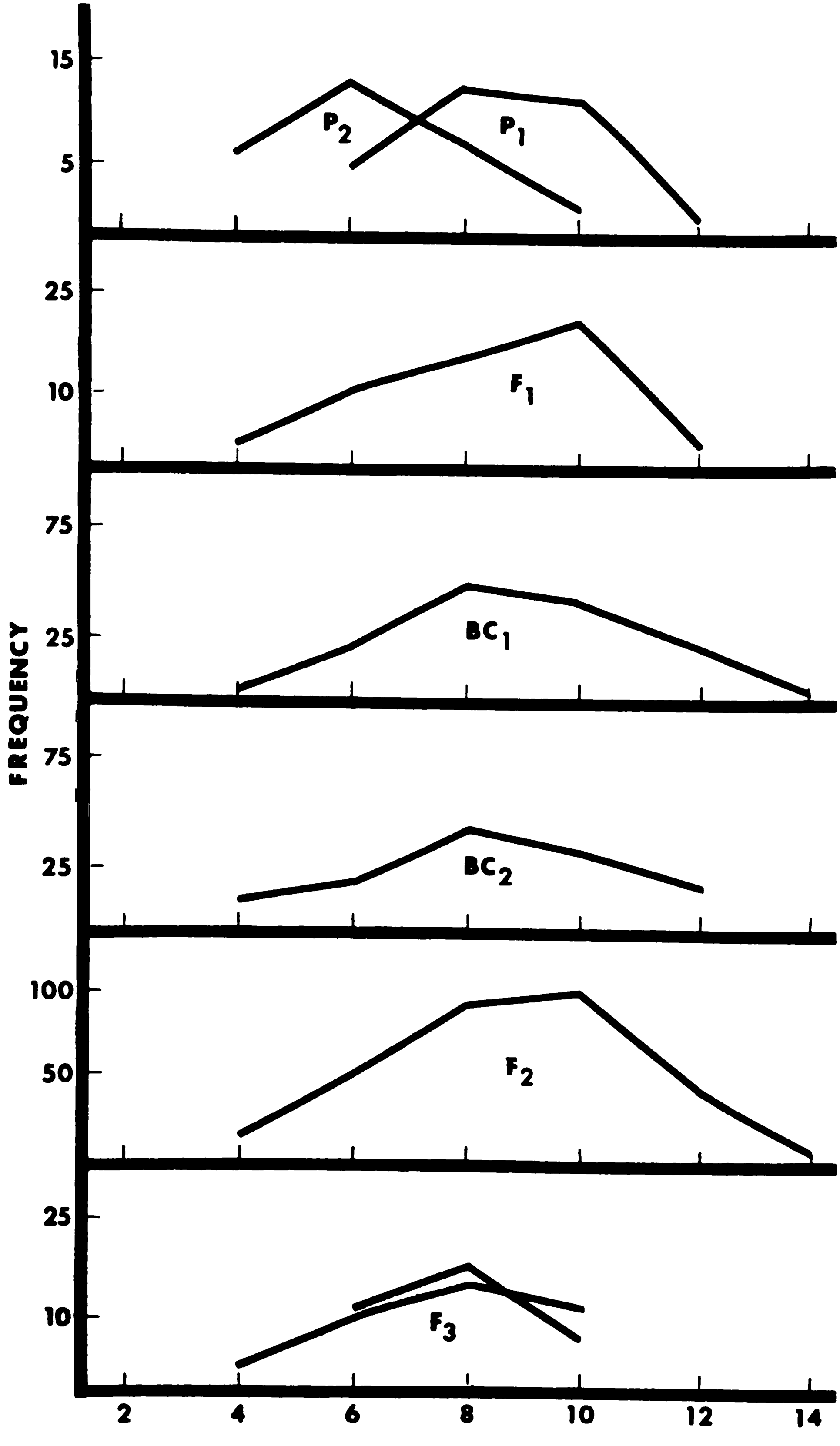
TABLE 15 CHI-SQUARE TEST FOR GOODNESS OF FIT FOR POOLED POPULATIONS FROM THE CROSS MSU 78-7A X MSU 78-9A, BASED ON A TWO GENE, 9:7 SEGREGATION HYPOTHESIS FOR PETIOLE THICKNESS, 1981

Generation	Observed ratio	Theoretical ratio	Chi-Sq.	P
Pooled F_1	103:29	1:0	-	-
Pooled F_2	296:207	9:7	1.01	.50-.30
Pooled BC to P_1	159:36	1:0	-	-
Pooled BC to P_2	45:118	1:3	0.60	.50-.10

Petiole Thickness - 1982

The F_1 and F_2 frequency distributions for petiole thickness were skewed towards the thick parent (P_1) (Figure 5). Approximately fifty-three percent of the F_2 had values higher than the mean of the midparent (7.6 mm), suggesting a partial dominance of thick over thin petioles. The means of the segregating populations support the dominance pattern (Appendix Table 31). The F_1 mean was not significantly higher than the mean of the two parents (F_1 - midparent = .4 mm). The F_2 mean was significantly different (5% level) from the mean of the midparent and also suggested partial dominance. The mean of the BC to P_1 fell between the F_1 and P_1 means,

FIGURE 5 FREQUENCY DISTRIBUTIONS FOR PETIOLE THICKNESS (mm) FROM THE CROSS MSU 78-7A X MSU 78-9A, 1982.


15
5
P2
P1
25
10
F1
75
25
BC1
75
25
BC2
100
50
F2
25
10
F3
FREQUENCY
2
4
6
8
10
12
14
PETIOLE THICKNESS
(mm)

while the BC to P_2 mean fell between the F_1 and P_2 means, and was significantly different from the P_2 mean, but not from the F_1 mean or the mean of the midparent. The two F_3 populations exhibited means of 8.2 mm and 8.7 mm.

Significant values were obtained for factor C in Mather's A, B, C scaling test (1% level), suggesting the possibility of epistasis in the expression of petiole thickness (Table 16).

TABLE 16 SIGNIFICANCE OF THE A, B, C SCALING TEST FOR PETIOLE THICKNESS IN THE CROSS MSU 78-7A X MSU 78-9A, 1982

	Test	
A	B	C
ns	ns	**

**, significant at 1% level
ns, non-significant at 5% level

Six parameter estimates (Table 17) suggest that although there were significant additive effects, dominance gene effects made the major contribution to the variation in petiole thickness, as noted the previous year. However, the estimates for epistatic effects (aa, ad, and dd) were not significant. This could possibly be due to a cancelling out of positive and negative gene effects, or to a level of epistasis too low to be detected by this test.

TABLE 17 GENE EFFECTS ESTIMATED USING A SIX PARAMETER MODEL ON THE GENERATION MEANS FOR THE CROSS MSU 78-7A X MSU 78-9A, 1982

Effect	Estimate
m	8.17±.054**
a	0.83±.046**
d	12.33±.360**
aa	-0.86±.440
ad	-0.05±.822
dd	-0.13±.088

**, significantly different from zero

Theoretical F_2 means were calculated, based on one, two and three gene models and are presented in Table 18. None of the theoretical means were significantly different from the observed mean. Two estimates of k were computed. Estimates of 0.61 and 0.66 were obtained using Castle's and Burton's methods, respectively. These estimates may be biased by epistatic effects, but suggest that a low number of loci are involved in the expression of petiole thickness.

The F_2 and backcross generations were partitioned into thick and thin types based on the mean of the two parents (7.6 mm), resulting in a 9:7 segregation pattern. The F_2 and BC_2 populations showed good fits to the ratios expected from this model (P = .50 - .30, P = .10 - .05, respectively),

TABLE 18 THEORETICAL F_2 MEANS FOR ONE, TWO AND THREE GENE PAIRS ASSUMING COMPLETE DOMINANCE, 1982

No. of genes	Theoretical	Observed
1	$(3/4)\overline{P}_1 + (1/4)\overline{P}_2 = 8.0 \pm 1.54$	8.2±2.05
2	$(15/16)\overline{P}_1 + (1/15)\overline{P}_2 = 8.3 \pm 1.54$	8.2±2.05
3	$(63/64)\overline{P}_1 + (1/64)\overline{P}_2 = 8.4 \pm 1.54$	8.2±2.05

supporting the hypothesis that two major genes control petiole thickness in Pak-Choi (Table 19). The presence of individuals with thin petioles in the F_1 and BC to P_1 population could be due to modifiers affecting this trait.

TABLE 19 CHI-SQUARE TEST FOR GOODNESS OF FIT FOR POOLED POPULATIONS FROM THE CROSS MSU 78-7A X MSU 78-9A, BASED ON A TWO GENE PAIR, 9:7 SEGREGATION HYPOTHESIS FOR PETIOLE THICKNESS, 1982

Generation	Observed ratio	Theoretical ratio	Chi-sq.	P
Pooled F_1	40:14	1:0	-	-
Pooled F_2	160:142	9:7	1.31	.50-.30
Pooled BC to P_1	141:11	1:0	-	-
Pooled BC to P_2	45:96	1:3	3.60	.10-.05

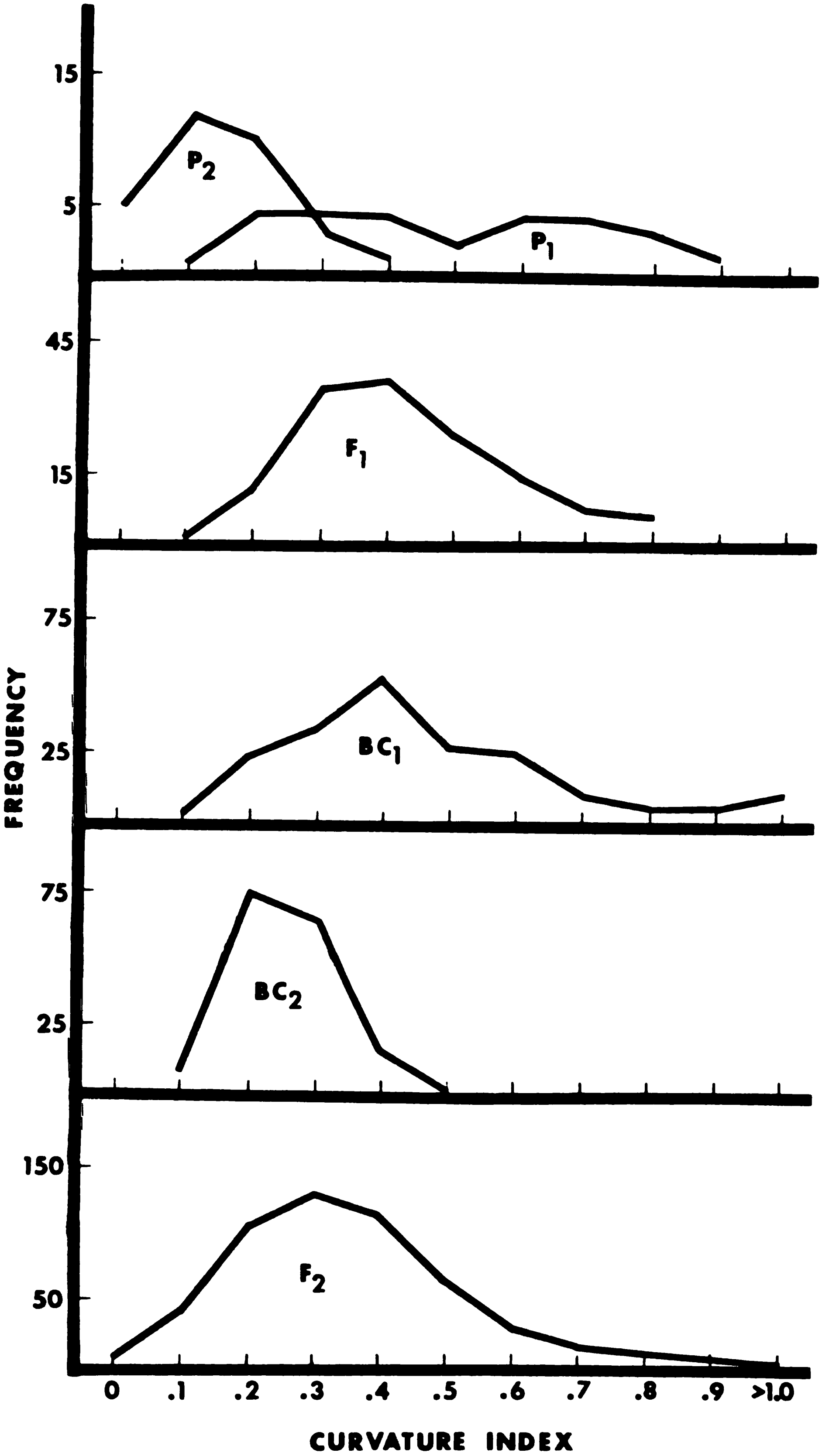
Narrow sense heritability was estimated at 53±5 percent in 1981 and 60±14 percent in 1982, suggesting that improvement can be expected for petiole thickness. Expected gain from selection of the top ten percent of the population was estimated at 10.5 percent in 1981, 13.1 percent in 1982.

The following genetic model is proposed: Two major loci, designated A and B determine petiole thickness. The proposed genotype of MSU 78-7A (P_1) is AABB (thick), while that of MSU 78-9A (P_2) is aabb (thin). The F_1, with a genotype of AaBb, has thick petioles. The observed F_2 and backcross ratios suggest a two gene, 9:7 epistatic model. A_B_ conditions thick petioles. Each gene is epistatic to the other such that recessive homozygosity at either or both loci, conditions thin petioles. Dominance of genes A and B is incomplete, allowing for intermediate petiole thickness. The F_2 and backcross genotypes AABB, AABb, AaBB, and AaBb produce thick petioles, while genotypes AAbb, Aabb, aaBB, aaBb and aabb produce thin petioles.

Petiole Curvature - 1981

The F_1 and F_2 frequency distributions were skewed towards the curved parent (P_1) (Figure 6). Fifty-five percent of the F_2 population had curvature indexes higher than the midparent mean (.32), suggesting partial dominance of curved over flat petioles (Appendix Table 32). The F_1 mean was significantly higher than the midparent mean (F_1 - midparent = .11). The F_2 mean, although not significantly different from the midparent mean, suggested dominance. The mean of BC to P_1

FIGURE 6 FREQUENCY DISTRIBUTIONS FOR PETIOLE CURVATURE FROM THE CROSS MSU 78-7A X MSU 78-9A, 1981


15
5
P2
P1
45
15
F1
75
25
BC1
75
25
BC2
150
50
F2
FREQUENCY
0
.1
.2
.3
.4
.5
.6
.7
.8
.9
>1.0
CURVATURE INDEX

was higher than the P_1 mean, probably due to transgressive segregation. The BC to P_2 mean fell between the F_1 and P_2 means and was significantly different (5% level) from both populations.

TABLE 20 SIGNIFICANCE OF THE A, B, C SCALING TEST FOR ADAXIAL CURVATURE IN THE CROSS MSU 78-7A X MSU 78-9A, 1981.

Test		
A	B	C
ns	**	**

**, significant factors B and C
ns, non-significant

A significant value was obtained for factors B and C in Mather's A,B, C scaling test suggesting the possibility of epistasis in determining petiole curvature. The poor fit to the additive-dominance model made it necessary to use a six parameter model to determine epistatic effects. The six parameter estimates (Table 21) suggest that, while all effects were significant at the 1% level, dominance gene effects made the major contribution to variation in petiole curvature.

Estimates of the number of effective factors controlling adaxial curvature were calculated as 2.38 and 2.09 using Castle's and Burton's methods, respectively. Theoretical F_2 means were calculated based on the number of genes assumed to be differentiating the parents, using the formulae of

TABLE 21 GENE EFFECTS ESTIMATED USING A SIX PARAMETER MODEL ON THE GENERATION MEANS FOR THE CROSS MSU 78-7A X MSU 78-9A, 1981

Effect	Estimate
m	0.349±.0001**
a	0.258±.0010**
d	0.736±.0219**
aa	0.140±.0056**
ad	0.092±.0016**
dd	-0.187±.0252**

**, Significant at 1% level

Powers, et al. None of the resulting theoretical means were significantly different from the observed F_2 (Table 22), however, based on the indication of the presence of epistasis, it appears that more than one gene is responsible for determining adaxial curvature.

TABLE 22 THEORETICAL F_2 MEANS FOR ONE, TWO AND THREE GENE PAIRS ASSUMING COMPLETE DOMINANCE, 1981

No. of genes	Theoretical	Observed
1	$(3/4)\bar{P}_1 + (1/4)\bar{P}_2 = .40\pm.19$	.35 ±.16
2	$(15/16)\bar{P}_1 + (1/16)\bar{P}_2 = .46\pm.21$	.35 ±.16
3	$(63/64)\bar{P}_1 + (1/64)\bar{P}_2 = .48\pm.22$	.35 ±.16

The F_2 and backcross generations were partitioned into curved and flat types based on the midparent mean (.32), resulting in a 9:7 segregation pattern (Table 23). A good fit to a 9:7 epistatic model was observed for both the F_2 (P = .90 - .50) and BC_2 (P = .50 - .10) populations.

TABLE 23 CHI-SQUARE TEST FOR GOODNESS OF FIT FOR POOLED POPULATIONS FROM THE CROSS MSU 78-7A X MSU 78-9A BASED ON A TWO GENE, 9:7 SEGREGATION HYPOTHESIS FOR ADAXIAL CURVATURE, 1981.

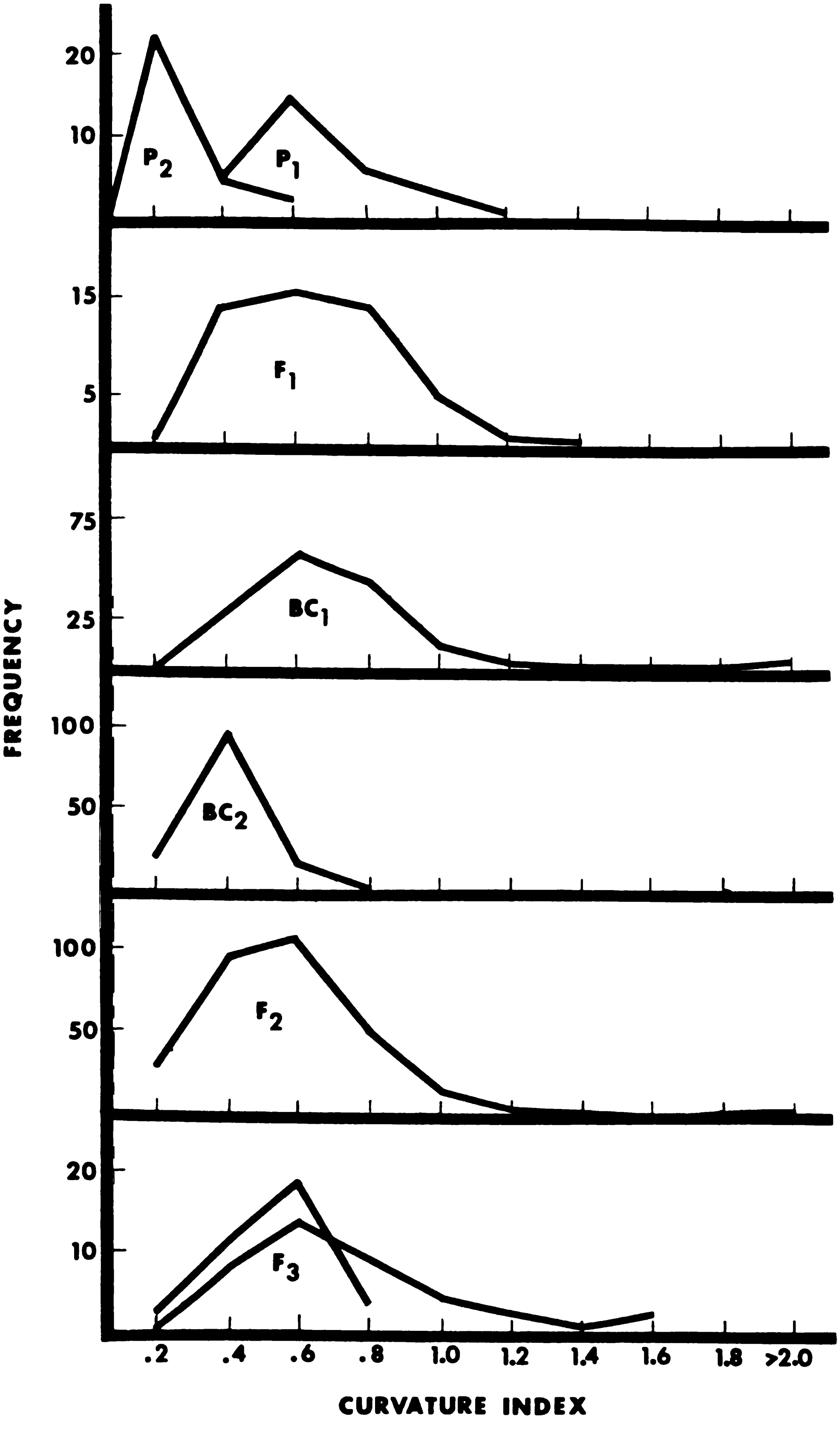
Generation	Observed ratio	Theoretical ratio	Chi-sq.	P
Pooled F_1	120:12	1:0	-	-
Pooled F_2	276:227	9:7	.389	.90-.50
Pooled BC to P_1	156:39	1:0	-	-
Pooled BC to P_2	33:130	1:3	1.974	.50-.10

Petiole Curvature - 1982

As in 1981, the F_1 and F_2 means were skewed towards the curved parent (P_1) (Figure 7). Sixty-three percent of the F_2 had values higher than the midparent mean (.45), suggesting a partial dominance of curved over flat petioles. Similar dominance patterns are discernible from the means of the segregating populations (Appendix Table 33).

The F_1 and F_2 means were higher than the mean of the two parents. The mean of the BC to P_1 was higher than the P_1

FIGURE 7 FREQUENCY DISTRIBUTIONS FOR PETIOLE CURVATURE FROM THE CROSS MSU 78-7A X MSU 78-9A, 1982


20
10
P2
P1
15
5
F1
75
25
BC1
100
50
BC2
100
50
F2
20
10
F3
FREQUENCY
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
>2.0
CURVATURE INDEX

mean, probably due to transgressive segregants as noted in the previous year. The BC to P_2 mean fell between the F_1 and P_2 means and was significantly different (5% level) from the mean of both populations.

TABLE 24 SIGNIFICANCE OF THE A, B, C SCALING TEST FOR ADAXIAL CURVATURE IN THE CROSS MSU 78-7A X MSU 78-9A, 1982

Test		
A	B	C
ns	ns	**

**, significant at 1% level
ns, non-significant at 5% level

A significant value was obtained for factor C in Mather's A, B, C scaling test suggesting the presence of epistasis in the expression of petiole curvature (Table 24). Six parameter estimates (Table 25) showed results similar to the previous year. While all effects were significant, dominance gene effects appeared to be the most important in contributing to variation in petiole curvature.

Two estimates of k were computed. Estimates of 1.22 and 2.02 genes were obtained using Castle's and Burton's methods, respectively. Theoretical F_2 means were calculated using the formulae of Powers, et al., and are presented in Table 26. As in the previous year, none of the theoretical F_2 means were significantly different from the observed mean.

TABLE 25 GENE EFFECTS ESTIMATED USING A SIX PARAMETER MODEL ON THE GENERATION MEANS FOR THE CROSS MSU 78-7A X MSU 78-9A, 1982

Effect	Estimate
m	0.561±.0002**
a	0.320±.0007**
d	2.220±.0158**
aa	-0.948±.0006**
ad	0.088±.0014**
dd	0.291±.0534**

**

TABLE 26 THEORETICAL F_2 MEANS FOR PETIOLE CURVATURE FOR ONE, TWO AND THREE GENES ASSUMING COMPLETE DOMINANCE

No. of genes		Observed
1	$(3/4)\overline{P}_1 + (1/4)\overline{P}_2 = .57 \pm .20$	.56 ±.24
2	$(15/16)\overline{P}_1 + (1/16)\overline{P}_2 = .65 \pm .20$	.56 ±.24
3	$(63/64)\overline{P}_1 + (1/64)\overline{P}_2 = .68 \pm .20$	.56 ±.24

Th F_2 and backcross generations were partitioned into curved and flat types based on the midparent mean (.45), resulting in a 9:7 segregation pattern similar to that observed in 1981. Table 27 presents the results of a chi-square test for goodness of fit to a 9:7, two gene epistatic model.

TABLE 27 CHI-SQUARE TEST FOR GOODNESS OF FIT FOR POOLED POPULATIONS FROM THE CROSS MSU 78-7A X MSU 78-9A BASED ON A TWO GENE, 9:7 SEGREGATION HYPOTHESIS FOR ADAXIAL CURVATURE, 1982

Generation	Observed ratio	Theoretical ratio	Chi-sq.	P
Pooled F_1	45:9	1:0	-	-
Pooled F_2	192:110	9:7	6.58	.05-.01
Pooled BC to P_1	132:20	1:0	-	-
Pooled BC to P_2	43:98	1:3	2.27	.50-.10

The poor fit of the F_2 population to the expected ratio as compared to 1981 was probably due to the differential expression of modifier genes controlling adaxial curvature in 1982. Narrow sense heritability was estimated at 24±6 percent in 1981 and 20±7 percent in 1982. Expected gain from selection of the top 10 percent of the population was estimated at 39 percent in 1981, 48 percent in 1982.

The following genetic model is proposed: Two major loci, designated $\underline{C_1}$ and $\underline{C_2}$, determine adaxial curvature. The proposed genotype of MSU 78-7A (P_1) is $\underline{C_1C_1C_2C_2}$ (curved), while that of MSU 78-9A (P_2) is $\underline{c_1c_1c_2c_2}$ (flat). The observed segregation ratios suggest a two gene 9:7 recessive repressor model, in which the homozygous recessive condition for either or both loci, conditions formation of a flat petiole. $\underline{C_1\_C_2\_}$

conditions curved petioles. The F_1, with the genotype $C_1c_1C_2c_2$, is curved. Dominance of genes C_1 and C_2 is incomplete, allowing intermediate levels of curvature. The F_2 and backcross genotypes $C_1C_1C_2C_2$, $C_1C_1C_2c_2$, $C_1c_1C_2C_2$ and $C_1c_1C_2c_2$ produce curved petioles, whereas the genotypes $C_1C_1c_2c_2$, $C_1c_1c_2c_2$, $C_1c_1c_2c_2$, $c_1c_1C_2c_2$ and $c_1c_1c_2c_2$ produce flat petioles.

Correlation coefficients between the three characters and bolting stage were calculated from F_2 generation data. All correlations were low indicating that there is little or no relation between these characters and bolting. The only significant (.001 level) coefficient obtained was .20 for petiole width and bolting stage. As petiole width increased, there was a tendency towards premature flower formation. This would suggest that difficulties may be encountered in attempting to develop bolt resistant cultivars with wide, thick petioles.

SUMMARY AND CONCLUSIONS

A technique for determining width, thickness and curvature of Pak-Choi petioles was developed. Preliminary studies indicated that valid estimates of these characters could be obtained by sampling the fifth, seventh and ninth petioles, at a distance 9 cm from the base of each petiole. The progenies of crosses between MSU 78-7A and MSU 78-9A were evaluated in two field studies (1981 and 1982) to determine the inheritance of petiole width, thickness and curvature.

Petiole width was determined to be simply inherited, with narrow petioles being dominant over wide. Petiole thickness was found to be controlled by two major genes, with thick petioles partially dominant over thin petioles. Dominance gene effects appeared most important in the expression of petiole thickness, although additive gene effects were also significant (1% level). Additive X dominance effects were significant in 1981, but not in 1982. Narrow sense heritability was estimated at 53±5 percent and 60±14 percent in 1981 and 1982, respectively. Expected gain from selection was estimated at 10.5 percent in 1981 and 13.1 percent in 1982.

Ratios obtained by partitioning the segregating generations into thick and thin types based upon the arithmetic mean of the two parents, suggested a two major gene system controlling petiole thickness. A 9:7 recessive suppressor model best explained the observed ratios. MSU 78-7A (P_1) was designated AABB (thick), while MSU 78-9A (P_2) was designated aabb (thin). The data suggested the presence of modifier genes, which may have affected segregation ratios and estimates of various genetic parameters.

Adaxial curvature of the petiole was also determined to be controlled by two major loci, with curved petioles being partially dominant over flat petioles. Both dominance and additive gene effects were important in the expression of this trait, however, estimates of dominance gene effects were greater in both years. In addition, significant additive X additive, additive X dominance, and dominance X dominance epistatic gene effects were noted in both years. Narrow sense heritability was estimated at 24±6 percent in 1981 and 20±7 percent in 1982. Expected gain from selection was estimated at 39 percent and 48 percent in 1981 and 1982, respectively. Ratios obtained by partitioning the segregating generations into curved and flat types based upon the arithmetic mean of the parental lines, suggested a two major gene system controlling adaxial curvature. A 9:7 recessive supressor model best explained the observed ratios. MSU 78-7A (P_1), was designated $\underline{C_1C_1C_2C_2}$ (curved), MSU 78-9A (P_2) was designated $\underline{c_1c_1c_2c_2}$ (flat).

The results of this study show that petiole width, thickness and adaxial curvature are heritable characters. The information obtained on the genetics of these traits and their relation to one another is essential for the development of cultivars adapted to Michigan growing conditions. Of the three characters investigated in this study, the most important is petiole width. Petiole thickness and curvature, though important, are not as apparent as petiole width. For this reason, plants exhibiting narrow petioles are less desirable since the consumer prefers plants with wide petioles.

Since wide petioles are recessive, following hybridization, one should select for wide petioles for several generations or until such time as the modifiers become homozygous. Selection should include the other characters only after petiole width has been considered. The dominance of thick over thin and curved over flat petioles should aid in the selection of desirable recombinants. Though heritability for petiole curvature was low (20-24 percent), it is the least important of the three characters, since consumers prefer wide, thick petioles. The addition of new germplasm to the Pak-choi breeding program will aid in obtaining the desired recombination of bolting resistance and petiole characteristics.

CHAPTER II

THE INHERITANCE OF THE "UMBRELLA" BRANCHING HABIT IN PEPPER, *CAPSICUM ANNUUM* L.

INTRODUCTION

Increase in harvest costs or lack of available labor may necessitate the development of mechanical harvesters for many vegetable crops. The development of a mechanical harvester for the pepper has been designed based primarily on the architecture of existing pepper cultivars. Problems associated with mechanical harvesting of peppers include difficulty in removing fruit from the plant or from low bearing plants, non-uniform maturity, breakage or branches and uprooting of plants by the action of the harvester.

Modifications of existing harvesters to overcome these problems would be a possible solution. Instead, the plant breeder has been charged with the responsibility of attempting to breed a plant adaptable to the harvester. This would require a plant architype exhibiting concentrated fruit set, whereby the fruit would mature uniformly, and with fruit set high off the ground to facilitate harvest operations. It should also possess the necessary horticultural characteristics, resistance to diseases and insects, etc.

The determinate growth habit reported by Hungarian workers (Kormos and Kormos, 1956; Ferenc, 1970 and Hristov, et al, 1975), would appear to fit the description for a plant architype best suited for mechanical harvest. Whereas most pepper cultivars exhibit a dichotomous growth pattern, with fruits set at branching points, and over a long duration, the Hungarian types exhibit a compact, bunchy habit, with a determinate apex and axillary branches producing clusters of fruit over a short duration. The ideal solution would be to breed a pepper plant of this type, adaptable to harvesting with existing or slightly modified machines.

The possibility of achieving this goal was realized with the appearance of a particular plant habit among the MSU breeding population. These plants exhibited determinate growth, with a cluster of fruit at the apex, and a subsequent branching pattern which resulted in the production of additional clusters of flowers at the apex of each branch, all maturing at approximately the same time.

This plant habit has the advantage of producing the fruit at the periphery of the plant, away from the branch joints. This plant habit could be extremely useful in mechanical harvesting systems, allowing an early hand harvest of the central cluster, followed by a once-over harvest of the remaining fruit upon maturity.

Information on the genetic control of this branching pattern would be helpful in designing an efficient breeding scheme for the development of desirable phenotypes. The objectives of the present study were to determine the inheritance of the "umbrella" branching habit in peppers, and to study the relationship between branching and yield.

REVIEW OF LITERATURE

Yield of crop plants is a complex trait affected by both genetic and environmental factors. Efforts to improve yield through selection of superior genotypes is based upon phenotypic appearance, which can be greatly affected by environment (Singh and Singh, 1974). Consequently, emphasis has been placed upon determining the nature and importance of genetic factors contributing to yield in _Capsicum_ species.

The genus _Capsicum_ includes many cultivated types of peppers, such as bell peppers, pimentoes, small fruited pungent types for fresh market, and large fruited chili and paprika for dehydration. They are grown all over the world under both natural and irrigated conditions (Arya and Saini, 1977).

Due to the fact that peppers are an important part of the diet and spice trade in India, a large portion of the research on various phases of growth and development of _Capsicum_ species has been conducted by researchers in that country. The literature review will be confined to branching and its effects on fruit yield. All studies were conducted using cultivars of Capsicum annuum, unless otherwise stated.

Singh and Singh (1970) conducted a study with chilies on the interrelationships between fruit yield and characters such as plant height, number of primary and secondary forks, and length, width and number of fruit. They found no significant correlations between plant height or numbers of primary and secondary forks with fruit yield, and concluded that these characters may have no direct effect on yield.

In a later study, Singh and Singh (1974) conducted a path coefficient analysis in which data on plant height, number of branches per plant, days to flower, days to maturity, fruit length and thickness, fruit number per plant, and yield per plant were used for analysis. Contrary to the previous study, the results indicated that the number of branches per plant is the most important component of fruit yield in chili.

Soh, et al (1976), in a study of the relationship between yield and its components in chili, produced a seven parent diallel cross population in which they observed days to flower, total number and weight of fruits, weight per fruit, fruit length, width and wall thickness, and plant height. They reported high correlations between total fruit number and yield, and found total number of fruit to be controlled by additive gene action.

Singh and Singh reported conflicting results in two studies regarding gene action for yield and its components in chili. In the first study (Singh and Singh, 1976a), their results indicated that both additive and dominance gene action were equally important in determining the number of branches per plant, while additive gene action was the major contributing factor in determining fruit number. The subsequent study (Singh and Singh, 1976b) indicated that dominance gene effects contributed substantially to number of branches per plant, while both additive and dominance gene effects were important in determining number of fruits per plant. Epistatic effects were also noted, with dominance X dominance interactions acting in determining the number of branches per plant, and additive X dominance interactions present for fruit number.

Awashti, et al, (1976) also studied components of genetic variability in chili, as well as heritability and genetic advance for various characters. Data was recorded for plant height, number of branches per plant, number of fruits per plant, fruit length, diameter and weight, and fruit yield per plant. The results suggested high heritability of all traits except number of fruits per plant, but with low genetic advance for number of branches per plant, indicating non-additive gene action for this trait.

Arya and Saini (1977) on the other hand, obtained high heritability estimates and high genetic advance values for fruit number per plant, and high heritability coupled with moderate genetic advance estimates for number of branches per plant. More recently, Bavaji and Murty (1982) obtained high heritability and genetic advance values for both number of branches and number of fruits per plant. Yield was significantly correlated with both traits.

Mishra, et al, (1976) observed eight parental lines and their F_1's for several yield contributing traits, among them, number of primary and secondary branches per plant, and number of fruits per plant. The increase in vigor of the F_1's over the better parent was significant for all three characters. Dominance was observed for both primary and secondary branches per plant. Positive association was observed between yield per plant, number of fruits per plant and number of primary branches per plant.

Path coefficient analysis conducted by Dutta, et al, (1979) in chili, indicated that the number of fruits per plant exercises high positive direct effects on fruit yield, while number of primary branches exhibits negative direct effects on yield. In contrast, Rao and Chhonkar (1981) found both number of branches and fruit number per plant to be positively and significantly associated with ripe fruit yield in chili, indicating that yield can be improved either by selection of plants with more branches or plants with more fruits.

Several investigations of the inheritance of other traits in peppers have been reported. Dale (1931) studied the inheritance of a dwarf plant habit arising from a cross between the cultivars Coral Gem and Anaheim, and determined the trait to be a simply inherited recessive character. Deshpande (1944) conducted an analysis of the inheritance of bunchy habit in chili. This mutant was described as bushy and compact with shortened internodes, and flowers and fruit produced in clusters. The bunchy character was shown to be recessive, and was later termed fasciculate (fa) by Lippert, et al, (1965, 1966).

Kormos and Kormos (1956) crossed a fasciculate type of pepper with various non-fasciculate types and recovered F_2 progeny exhibiting completely determinate growth. In these plants, the main axis stopped growing early in the season and produced a cluster of fruit, after which no lateral shoots developed. This character was found to be recessive. This plant habit was considered ideal for mechanical harvesting, and a breeding program was begun in Hungary to incorporate the determinate trait into desired genotypes. According to Ferenc (1970), the resulting plant types attain a height of 20 to 25 cm, terminate growth, and produce a large number of flowers, from which clusters of fruit develop, and ripen over a short period of time (two to three weeks). Continued selection resulted in the release of an early, simultaneously ripening, determinate cultivar 'Buketen,' suitable for once-over mechanical harvest (Hristov, 1975).

The inheritance of bearing habit in *C. frutescens*, L. was determined from a cross between two tabasco type cultivars, LP-1 and Almeda, in which the characters cluster vs. non-cluster fruit set were studied. Results indicated that the cluster habit was controlled by a single recessive gene (Barrios and Mosokar, 1972).

Two genetic studies have been conducted on branching in peppers. Bergh and Lippert (1975) studied three species, *C. baccatum* L., *C. chinense* Jacq. and *C. frutescens* L., for the inheritance of axillary shooting prior to the first bifurcation or point of branching. They observed mutant plants of *C. chinense* with extensive prebifurcation axillary shoots and results of intra- and inter-specific crosses with these plants indicated a monogenic recessive basis for the trait, which they termed compact (*ct*). Considerable environmental effects on the expression of axillary shooting were observed.

Shifriss and Hakim (1977) studied the inheritance of prebifurcation shooting in *C. annuum* L. They crossed Santaka, a Japanese cultivar with many axillary shoots developing acropetally along the main stem, and exhibiting the fasciculate bearing habit, with Csokros Fellalo, an Hungarian bush fasciculate cultivar, devoid of axillary shoots, and Yolo-Wonder Y, with few axillary shoots prior to the first bifurcation. In the F_1 and F_2 from Santaka X Csokros Fellalo, the progenies showed partial dominance of many over few axillary shoots, while in the F_1 and F_2 from Santaka X Yolo-Wonder Y, the opposite occurred, i.e., partial dominance of few over many shoots. They concluded that prebifurcation shooting, though a quantitative character, is controlled by relatively few genes with different action, and modified by environmental conditions.

MATERIALS AND METHODS

Three inbred Capsicum annuum L. lines, MSU 78-101, MSU 79-221 and MSU 74-230 were used in this study (Figure 8). MSU 78-101 is an upright, dwarf banana pepper carrying the "fasciculate" or clustered gene (fa). MSU 79-221 was a selection from the cross MSU 74-190, a yellow long banana pepper, X Csokros Fellalo, a Hungarian upright, yellow bell, also carrying the fasciculate gene. It was selected on the basis of its unique branching habit, termed "umbrella." Upon attaining a height of approximately 15 cm, the apex terminates in a cluster of 2-6 fruits followed by initiation of several lateral branches, each of which produces a terminal cluster of fruit, that mature uniformly. The umbrella phenotype has been designated (um).

MSU 74-230, a yellow, long banana, was an F_5 selection from the cross between Avelar, and a yellow long banana MSU selection. It is an indeterminate, non-clustered fruiting, yellow banana type, with a prolific branching habit, and produces fruit continuously and, therefore, matures over an extended period.

FIGURE 8 PLANT HABIT OF THE THREE PARENTAL LINES

Top, MSU 78-101, Dwarf. (ctctdtdtfafaSuSu)

Center, MSU 79-221, Umbrella. (ctctdtdtfafasusu)

Bottom, MSU 74-230, Indeterminate
(ctctDtDtFaFasusu)

Hybridization

Crosses were made in the greenhouse to produce reciprocal populations for the genetic studies. One plant of each parental line was selected for hybridization with the other two parents. All generations were produced using these single plants and their F_1's. In the case of MSU 78-101, flowering occurred over a 10-14 day period, followed by very little vegetative development and occasional flowering. Therefore, it was impossible to obtain backcross progenies using MSU 78-101.

Seeds of parents and progenies were sown in vermiculite on April 13, 1982, transplanted into peat pots on May 1 and 2, and into the field in June, 1982. A completely randomized design with three replications was used.

MSU 78-101 X MSU 79-221

Due to a short period of flowering of the MSU 78-101 parent, it was impossible to obtain reciprocal generations for this study. Using the dwarf as the female parent, F_1, F_2 and BC_2 populations were produced. Each replication consisted of 12 plants of each parent, 12 of each F_1 family, 72 of the backcross to MSU 79-221, and 96 of the F_2 population. Rows were spaced 1.07 m apart, with plants spaced at intervals of 0.60 m in the row. Cultural practices utilized were those recommended for pepper production in Michigan

Plants were classified by growth habit (indeterminate vs. determinate) and fruit bearing habit (non-cluster vs. cluster). The means of reciprocal populations were tested for homogeneity prior to analysis of the data.

MSU 79-221 X MSU 74-230

Each replication consisted of 12 plants of each parent, 24 of each F_1 family, 36 of each backcross population and 96 of each F_2 family. Cultural practices were identical to those described for the previous cross as were procedures of data collection and analysis. The means of reciprocal populations were tested for homogeneity prior to analysis of the data. The possibility of linkage necessitated the use of a x^2 contingency test in which the test is separated into three components using the following formulae (Bonnier, 1942):

Aa segregation component $$x^2 = \frac{a+b - 3(c+d)\ ^2}{3N}$$

(1° of freedom)

Bb segregation component $$x^2 = \frac{a+c - 3(b-d)\ ^2}{3N}$$

(1° of freedom)

Linkage component $$x^2 = \frac{(a - 3b - 3c + 9d)^2}{9N}$$

(1° of freedom)

Where classes a, b, c and d = phenotypes AB, Ab, aB, and ab, respectively.

Linkage intensities were calculated using the product method (Fisher and Balmukand, 1928).

MSU 78-101 X MSU 74-230

Reciprocal populations of F_1 and F_2 were produced for use in this study. However, the F_1 was backcrossed only to MSU 74-230 due to an absence of flowers caused by the short duration of flowering in the dwarf parent (MSU 78-101). Each replication consisted of 12 plants of each parent, 12 of each F_1 family, 72 of the backcross to MSU 74-230, and 96 of each F_2 population. All procedures of data collection and analysis were identical to those described previously.

Branching and Fruit Number

Data were recorded prior to frost for number of fruit at the apical cluster, number of primary, secondary and tertiary branches, and number of fruit per respective branch. Primary branches were identified as those arising directly from the main axis. While secondary branches were those arising from primary branches and tertiary branches those arising from secondary branches. Total fruit per plant (branch fruit plus apical cluster fruit) was calculated for each plant.

The F_2 population was separated by plant habit and level of branching in order to determine the relationship between branching and the number of marketable fruit produced. Determination of fruit marketability was based upon the size of the mature fruits on the individual plant.

The resulting classes were tested for significant differences in number of marketable fruit by means of a two-tailed t-test (Steel and Torrie, 1960).

RESULTS AND DISCUSSION

Plant Type and Bearing Habit

MSU 78-101 X MSU 79-221

The segregating populations were separated on the basis of plant habit prior to genetic analysis. The F_2 generation segregated into 103 dwarf : 40 indeterminate : 47 umbrella, approximating a 9:3:4 ratio (x^2 = .682, P = .80-.70, Table 34). The expected ratio for the backcross to the umbrella parent would be 2 umbrella : 1 dwarf : 1 indeterminate. Out of 188 plants, a ratio of 99 : 49.5 : 49.5 would be expected. The data show a good fit to the expected ratio (P = .30-.20, Table 34). The observed F_1 ratio could not be tested due to the zero expectation for the umbrella class.

TABLE 34 CHI-SQUARE TEST FOR GOODNESS OF FIT FOR POOLED GENERATIONS FROM THE CROSS MSU 78-101 X MSU 79-221

Generation	Observed	Theoretical	Chi-sq.	P
Pooled F_1	34:9	1:0	-	-
Pooled F_2	103:40:47	9:3:4	.682	.80-.70
Pooled BC to P_2	89:59:50	2:1:1	2.838	.30-.20

There appear to be four genes involved in the expression of the umbrella habit. Two genes, dt and ct affect plant habit. The dt gene is a recessive gene conditioning determinate growth, while ct is a recessive gene controlling the number of axillary shoots (Bergh and Lippert, 1975). Dt and Ct are dominant genes conditioning indeterminate growth, and appear to be epistatic to one another, such that, in the homozygous dominant or heterozygous conditions, Ct is epistatic to the expression of dt, while Dt is epistatic to the expression of ct. A third gene, fa, controls the fasciculate or clustered fruit bearing habit. Fa causes non-clustered fruit set.

Assuming that the genotype of MSU 69-221 is ctctdtdtfafa, and that of MSU 78-101 is CtCtdtdtfafa, the expected F_2 ratio would be 3 dwarf : 1 umbrella. However, the appearance of indeterminate plants in the F_2 suggests the presence of an additional factor(s) in determining the umbrella habit. Modifying the genotype of the dwarf parent to include an additional gene, Su, a dominant suppressor, would result in a 9:3:4 segregation pattern. In this case, the genotype of MSU 79-221 would be ctctdtdtfafasusu, that of MSU 78-101, CtCtdtdtfafaSuSu. The Su gene would act to suppress the epistatic action of Ct. The genotypes Ct--dtdtfafaSu-- would produce dwarf plants, genotypes *ctctdtdtfafaSu--* and *ctctdtdtfafasusu* would produce umbrella types, and genotypes *Ctdtdtfafasusu* and *Ctctdtdtfafasusu* would produce indeterminate types.

The presence of 9 umbrella plants out of 43 F_1 plants is probably due to the effect of modifiers on the expression of the *ct* gene. The genotype of the F_1 would be *CtctdtdtfafaSusu*. Assuming the supressor gene inhibits the action of the *Ct* gene, modifiers affecting the expression of the *ct* gene could alter the amount of branching in a given plant, based on the interaction of these modifiers and the *ct* gene, resulting in a misclassification of a plant as an umbrella type. The proposed genotypes and phenotypes expected from this cross are presented below:

CtCtdtdtfafaSuSu	9	Dwarf
CtctdtdtfafaSuSu		
CtCtdtdtfafaSuSu		
CtctdtdtfafaSuSu		
CtCtdtdtfafasusu	3	Indeterminate
Ctctdtdtfafasusu		
ctctdtdtfafaSuSu	4	Umbrella
ctctdtdtfafaSusu		
ctctdtdtfafasusu		

MSU 79-221 X MSU 74-230

Plant type and fruit bearing habit were used to separate the F_2 and backcross progenies into distinct classes for genetic analysis. The F_1 plants were indeterminate and non-clustered, suggesting that the umbrella habit was a recessive character. In the F_2, the plants segregated into 4 classes: indeterminate, non-clustered; indeterminate, clustered; determinate, non-clustered and determinate, clustered. Plant habit appeared to be under a 2 gene dominant epistatic control, resulting in a segregation of 15 indeterminate : 1 determinate. Also, the non-clustered vs. clustered characters did not fit the expected 3 : 1 ratio. A preponderance of parental types suggested linkage between the determinate and fasciculate genes. This was supported by the poor fit of the data to the proposed (15:1) (3:1) model (x^2 = 106.45, P = <.001, Table 35). However, this model gave the best fit of all models tested.

The backcross of the F_1 to the umbrella parent also showed a poor fit to the expected ratio (P = <.001, Table 35). The preponderance of parental types over recombinants in the backcross generation further suggested linkage between the genes determining plant growth habit and bearing habit. The backcross of the F_1 to the dominant parent shows a good fit to the expected ratio.

TABLE 35 CHI-SQ. TEST FOR GOODNESS OF FIT FOR THE CROSS MSU 79-221 X MSU 74-230, BASED ON A 4-GENE, EPISTATIC MODEL

Generation	Observed	Theoretical	Chi-sq	P
Pooled F_1	136:0	1:0	-	-
Pooled F_2	440:31:19:20	45:15:3:1	106.45	<.001
Pooled BC to P_1	245:43:30:94	3:3:1:1	203.26	<.001
Pooled BC to P_2	394:0	1:0	-	-

TABLE 36 SEPARATION OF THE X^2 TEST FOR GOODNESS OF FIT INTO ITS COMPONENTS

Aa component x^2 (indeterminate vs determinate	=2.17, P=.50-.10
Bb component x^2 (non-clustered vs clustered)	=59.89, P= <.001
Linkage component x^2	=33.91, P= <.001

Separation of the x^2 test into its components showed a good fit to the expected 15:1 segregation for plant habit, but a poor fit for bearing habit (Table 36). Also, a significant value was obtained for the linkage component. Linkage studies using the product method indicated a crossover value of 10.45 ± 3.82 percent. Therefore, it appears that the poor fit of the data to the proposed model is most likely due to the tight linkage between the genes conditioning indeterminate plant habit and non-clustered fruit bearing habit.

Within the determinate class of the F_2 and BC_1 populations, both umbrella and dwarf types were recovered. The following genetic model is proposed: 3 major genes are involved in the inheritance of the umbrella habit. The proposed genotype of the umbrella parent is ctctdtdtfafasusu, where ct is a recessive gene controlling the number of axillary shoots (Bergh and Lippert, 1975). The dt and fa genes are recessive genes for determinate growth and clustered bearing habit, respectively. The proposed genotype of MSU 74-230 is *CtCtDtDtFaFasusu*. *Dt* and *Ct* are dominant genes causing indeterminate growth. It appears that, in the homozygous or heterozygous conditions, *Ct* is epistatic to the expression of *dt*, while *Dt* is epistatic to the expression of *ct*. However, it is also possible that both dominant genes are inherited independently, resulting in a 9:3:3:1 segregation ratio for plant habit, but due to an inability to distinguish the intermediate classes from the dominant class, a 15:1 ratio is observed. The dominant suppressor, *Su*, is in the homozygous recessive condition (*susu*) in both parents and thus has no bearing on the expression of these characters in this cross. The proposed genotypes and phenotypes of the F_2 generation are tabulated below:

CtCtDtDtFaFasusu	45	Indeterminate, non-clustered
CtCtDtDtFa susu		
CtCtDtdtFaFasusu		
CtCtDtdtFafasusu		
CtCtdtdtFaFasusu		
CtCtdtdtFafasusu		
CtctDtDtFaFasusu		
CtctDtDtFafasusu		
CtctDtdtFaFasusu		
CtctDtdtFafasusu		
CtctdtdtFaFasusu		
Ctctdtdtfafasusu		
ctctDtDtFaFasusu		
ctctDtDtFafasusu		
ctctDtdtFaFasusu		
ctctDtdtFafasusu		
CtCtDtDtfafasusu	15	Indeterminate, clustered
CtCtDtdtfafasusu		
CtCtdtdtfafasusu		

CtctDtDtfafasusu CtctDtdtfafasusu Ctctdtdtfafasusu ctctDtDtfafasusu ctctDtdtfafasusu	15 (cont'd)	Indeterminate, clustered (cont'd)
ctctdtdtFaFasusu ctctdtdtFafasusu	3	Determinate, non-clustered (Umbrella and dwarf)
ctctdtdtfafasusu	1	Determinate, clustered (Umbrella and dwarf)

Dwarf plants arising from this cross would have the genotype ctctdtdtfafasusu or ctctdtdtFa--susu but would have reduced axillary shoots due to the action of modifier genes. Recombination of modifiers associated with ct would allow for varying numbers of axillary shoots in different genetic backgrounds, resulting in dwarf plants with few or no axillary branches.

MSU 78-101 X MSU 74-230

The plants in the segregating generations were classified by plant type and fruit bearing habit. The F_1 plants were indeterminate and non-clustered, suggesting these characters to be dominant to the dwarf, clustered habit, as previously reported. The F_2 segregated into 363 indeterminate, non-clusted : 53 determinate, clustered plants.

Analysis of each of these two characters showed a segregation ratio of 13:3 for plant type ($x^2 = 4.33$, $P = .05-.01$) and 3:1 for bearing habit ($x^2 = 2.95$, $P = .10-.05$), suggesting that bearing habit is controlled by a single gene, as reported by Deshpande (1944), while plant type appears to be controlled by two genes. As discussed in the previous crosses, the Ct and Su genes are present in both parents and are presumably involved in determining plant habit in this cross. The proposed genotype of MSU 78-101 is CtCtdtdtfafaSuSu, that of MSU 74-230 is CtCtDtDtFaFasusu. A cross involving parents with these genotypes would result in a segregation ratio of 39 indeterminate, non-clustered; 13 indeterminate, clustered; 9 determinate, non-clustered; 1 determinate, clustered. A chi-square test for this model gave a poor fit (x^2 = 48.27, P = <.001, Table 37).

TABLE 37 CHI-SQUARE TEST FOR GOODNESS OF FIT TO A 9:3:3:1 EXPECTED RATIO FOR THE CROSS MSU 78-101 X MSU 74-230

Generation	Observed	Theoretical	Chi-sq.	P
Pooled F_1	72:0	1:0	-	-
Pooled F_2	363:68:70:53	39:13:9:3	48.27	<.001
Pooled BC to P_2	428:0	1:0	-	-

The predonderance of parental types in the segregating generations suggested the presence of linkage between the genes for determinate plant habit and fasciculate fruit set. In separating the x^2 test into its components, a significant value was obtained for the linkage component, supporting this view (Table 38).

TABLE 38 SEPARATION OF THE X^2 TEST FOR GOODNESS OF FIT INTO ITS COMPONENTS

Aa component x^2(indeterminate vs determinate)= 4.33,P=.05-.01

Bb component x^2(non-clustered vs clustered) = 2.95,P=.10-.05

Linkage component x^2 =40.99,P= <.001

Linkage studies using the product method indicated a crossover value of 31.70 ± 2.58 percent.

In the F_2 generation, the proposed genotypes and phenotypes expected are tabulated below:

CtCtDtDtFaFaSuSu	39	Indeterminate, non-clustered
CtCtDtDtFaFaSusu		
CtCtDtDtFaFasusu		
CtCtDtDtFafaSuSu		
CtCtDtDtFafaSusu		
CtCtDtDtFafasusu		
CtCtDtdtFaFaSuSu		
CtCtDtdtFaFaSusu		
CtCtDtdtFaFasusu		
CtCtDtdtFafaSuSu		
CtCtDtdtFafaSusu		
CtCtDtdtFafasusu		
CtCtdtdtFaFasusu		
CtCtdtdtFafasusu		
CtCtDtDtfafaSuSu	13	Indeterminate, clustered
CtCtDtDtfafaSusu		
CtCtDtDtfafasusu		
CtCtDtdtfafaSuSu		
CtCtDtdtfafaSusu		
CtCtDtdtfafasusu		
CtCtdtdtfafasusu		
CtCtdtdtFaFaSuSu	9	Determinate, non-clustered
CtCtdtdtFaFaSusu		
CtCtdtdtFafaSuSu		
CtCtdtdtFafaSusu		

CtCtdtdtfafaSuSu CtCtdtdtfafaSusu	3	Determinate, clustered

Branching and Fruit Number

MSU 78-101 X MSU 79-221

The F_2 population was separated into the following classes: dwarf (branchless); dwarf with 1-2 primary branches; indeterminate without secondary branches; indeterminate without tertiary branches; umbrella without secondary branches and umbrella without tertiary branches. The umbrella phenotypes exhibited primary branches which arose from axillary nodes rather than from bifurcation of the apical meristem. Significant differences in number of marketable fruit per plant were observed between the branchless dwarf classes and all other classes. There was no significant difference in the mean number of marketable fruit per plant between the dwarf class with primary branches and the indeterminated class without secondary branches. No significant differences were observed between the other classes for mean number of marketable fruit per plant (Table 39). All differences were significant at the .05 level.

TABLE 39 - MEAN NUMBER OF MARKETABLE FRUIT AND BRANCHES PER PLANT FOR THE VARIOUS PLANT TYPES, FROM THE CROSS MSU 78-101 X MSU 79-221

Plant type	No	Fruit/plant	PB/plant	SB/plant	TB/plant
(a) Dwarf (branchless)	63	7.4 0.27a	-	-	-
(b) Dwarf (PB)	40	9.2 0.18b	1.3	-	-
(c) Indeterminate (No SB)	7	13.5 1.75bc	4.5	-	-
(d) Indeterminate (No TB)	33	15.5 0.86c	4.0	4.3	-
(f) Umbrella (No SB)	13	14.9 0.72c	4.7	-	-
(g) Umbrella (No TB)	34	17.7 0.21c	4.4	3.7	-

B - primary branches

SB - secondary branches

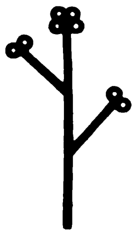
TB - tertiary branches

(a-g) from Figure 9.

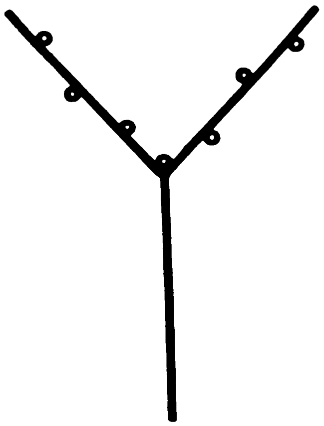
FIGURE 9 SCHEMATIC REPRESENTATION OF THE VARIOUS PLANT TYPES AND LEVELS OF BRANCHING

a. Dwarf (branchless).
b. Dwarf with 1-2 primary branches.
c. Indeterminate without secondary branches.
d. Indeterminate without tertiary branches.
3. Indeterminate with tertiary branches.
f. Umbrella without secondary branches.
g. Umbrella without tertiary branches.
h. Umbrella with tertiary branches.

a



b



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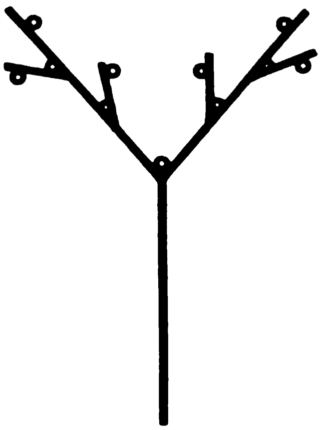

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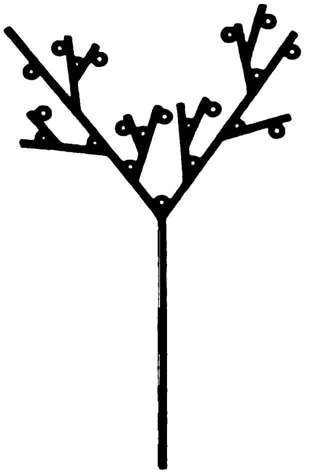

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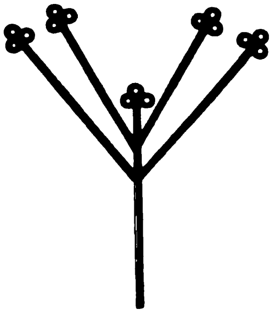

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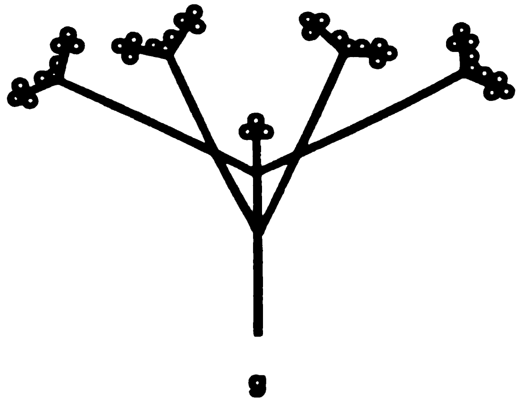
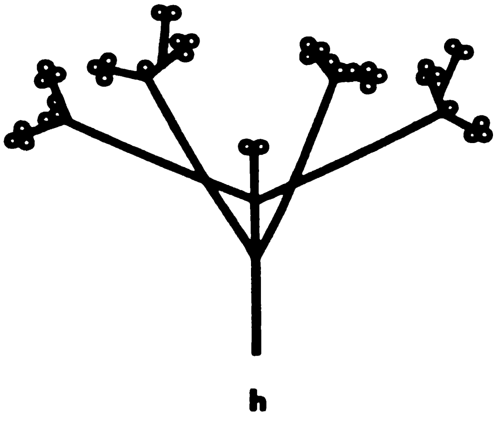


g



h

MSU 79-221 X MSU 74-230

The F_2 population was separated into the following classes: dwarf (branchless); indeterminate without secondary branches; indeterminate without tertiary branches and umbrella with tertiary branches. There were no umbrella plants without secondary branches. Significant differences in the mean number of marketable fruit per plant were observed between the dwarf class and all other classes. The indeterminate class without secondary branches was also significant from all other classes. No significant differences were observed between the indeterminate class without tertiary branches and the two umbrella classes, nor between the indeterminate class with tertiary branches and the umbrella class without tertiary branches. All differences were significant at the .05 level (Table 40).

While the indeterminate class with tertiary branches produced the highest number of marketable fruits, these fruits were borne singly and continuously as the plant developed, and exhibited variable maturity. The umbrella plant, however, produced clusters of fruit which matured uniformly, making this plant habit very desirable for mechanical harvesting.

The highest yielding umbrella plant type exhibited branching on two levels, primary and secondary. Clusters of fruit developed at the end of primary branches, followed by

TABLE 40 MEAN NUMBER OF MARKETABLE FRUIT AND BRANCHES PER PLANT FOR THE VARIOUS PLANT TYPES, FROM THE CROSS MSU 79-221 X MSU 74-230

Plant type	No	Fruit/plant	PB/plant	SB/plant	TB/plant
(a) Dwarf (branchless)	15	6.3 0.48a	-	-	-
(c) Indeterminate (No SB)	81	12.0 1.78b	4.3	-	-
(d) Indeterminate (No TB)	243	19.6 0.44c	4.7	5.1	-
(e) Indeterminate (TB)	189	27.0 0.58d	4.7	6.8	2.7
(g) Umbrella (No TB)	19	22.8 2.41cd	5.6	6.2	-
(h) Umbrella (TB)	5	20.0 1.32c	3.8	6.8	2.0

PB - primary branches

SB - secondary branches

TB - tertiary branches

(a-h) from Figure 9.

the initiation of short secondary branches terminating with a cluster of fruit, giving the appearance of one large cluster at the apex of each primary branch. An ideal phenotype would be one exhibiting 4-6 primary branches, each producing 2 secondary branches with clusters of fruit (Figure 9g).

MSU 78-101 X MSU 74-230

The F_2 population was separated into the following classes: dwarf (branchless); dwarf with 1-2 primary branches; indeterminate without secondary branches; indeterminate without tertiary branches and indeterminate with tertiary branches. There were no significant differences in the mean number of marketable fruit per plant between the two dwarf classes and the indeterminate class with only primary branches (Table 41). This indeterminate class had primary branches which produced fruit continuously throughout the season, without the development of secondary branches. The dwarf classes and the indeterminate class without secondary branches were significantly lower in mean number of marketable fruit per plant than the indeterminate classes with and without tertiary branches. Significant differences in the mean number of marketable fruit per plant were observed between the indeterminate classes with and without tertiary branches. All differences were significant at the .05 level.

TABLE 41 MEAN NUMBER OF MARKETABLE FRUIT AND BRANCHES PER PLANT FOR THE VARIOUS PLANT TYPES, FROM THE CROSS MSU 78-101 X MSU 74-230

Plant type	No	Fruit/plant	PB/plant	SB/plant	TB/plant
(a) Dwarf (branchless)	30	6.3 0.33a	-	-	-
(b) Dwarf (PB)	93	5.7 0.31a	1.9	-	-
(c) Indeterminate (No SB)	23	5.9 0.64a	2.8	-	-
(d) Indeterminate (no TB)	336	14.2 0.29b	4.2	3.5	-
(e) Indeterminate (TB)	72	18.0 0.63c	4.3	4.2	1.6

PB - primary branches

SB - secondary branches

TB - tertiary branches

(a-e) from Figure 9.

SUMMARY AND CONCLUSIONS

Three inbred lines, MSU 78-101, MSU 79-221 and MSU 74-230 were used to determine the inheritance of the "umbrella" branching habit in peppers. MSU 79-221, exhibiting the umbrella phenotype, was crossed with MSU 78-101 and MSU 74-230. Segregating populations were separated on the basis of plant growth habit and fruit bearing habit.

The results of genetic analysis suggested that the umbrella phenotype was controlled by three recessive genes, <u>ct</u> and <u>dt</u> determining plant habit, and <u>fa</u> determining fruit bearing habit. When the dominant alleles <u>Dt</u> and <u>Ct</u> are in the homozygous dominant or heterozygous condition, they effect a dominant epistasis which results in an indeterminate phenotype. A fourth gene, <u>Su</u>, is a dominant suppressor which acts to suppress the epistatic action of the <u>Ct</u> gene. Modifiers were involved in the control of branching in the umbrella plants. Linkage was also noted between the genes for indeterminate plant habit and non-clustered bearing habit.

Studies of the relationship between the mean number of marketable fruit per plant and the level of branching suggested that the yield of the umbrella phenotype was comparable to that of indeterminate types. Fruit position and uniform maturity within a 10-14 day period make the umbrella phenotype attractive for mechanical harvesting. With the information gained from this study, the breeder will have a better understanding of the problems ahead, and the manner in which he may attempt to overcome them.

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APPENDIX

TABLE 28 FREQUENCY DISTRIBUTION FOR PETIOLE WIDTHS (mm) FOR THE CROSS MSU 78-7A X MSU 78-9A, 1981

		Petiole Width (mm)											No. of
Pedigree	Generation	10	15	20	25	30	35	40	45	50	Mean	s	Plants
MSU 78-7A	P_1	4	12	9	2						16.2a	3.63	27
MSU 78-9A	P_2			2	8	6	5	7	1	1	30.7e	9.32	30
MSU 78-7A X MSU 78-9A	F_1		30	65	34	3					20.4c	3.48	132
F_1 self	F_2	30	125	197	92	39	13	5	1	1	20.5c	5.93	503
F_1 X P_1	BC_1	21	63	74	29	7					18.4b	4.64	195
F_1 X P_2	BC_2		3	45	68	41	6				25.1d	4.01	163

TABLE 29 FREQUENCY DISTRIBUTION FOR PETIOLE WIDTHS(mm) FOR THE CROSS MSU 78-7A X MSU 78-9A, 1982

Pedigree	Generation	Petiole Width (mm) 10	15	20	25	30	35	40	45	50	Mean	s	No of Plants
MSU 78-7A	P_1	1	16	10	2						16.8a	3.22	29
MSU 78-9A	P_2		1	3	5	4	3	7	3	2	33.9d	9.34	28
MSU 78-7A X MSU 78-9A	F_1		7	21	17	8	1				23.0c	4.63	54
F_1 self	F_2	6	40	88	105	39	12	9	1	1	23.7c	6.53	302
F_1 X P_1	BC_1	2	28	76	39	7					20.7b	3.77	152
F_1 X P_2	BC_2		1	8	34	51	38	9			30.1d	4.85	141
F_2 self	F_3	1	5	22	10	2					20.8b	3.75	40
F_2 self	F_3		9	24	4						19.5b	2.56	37

TABLE 30 FREQUENCY DISTRIBUTION FOR PETIOLE THICKNESS (mm) FOR THE CROSS MSU 78-7A X MSU 78-9A, 1981

Pedigree	Generation	Petiole Thickness (mm) 2	4	6	8	10	12	14	Mean	s	No. of Plants
MSU 78-7A	P_1			8	15	3	1		7.8a	1.56	27
MSU 78-9A	P_2	1	15	12	2				5.3c	1.44	30
MSU 78-7A X MSU 78-9A	F_1		17	56	49	9	1		7.1ab	1.65	132
F_1 self	F_2	3	73	165	164	85	12	1	7.4a	1.99	503
F_1 X P_2	BC_1	2	21	58	71	38	4		7.6a	1.91	195
F_1 X P_2	BC_2	3	40	75	6	9			6.8ab	1.49	163

TABLE 31 FREQUENCY DISTRIBUTION FOR PETIOLE THICKNESS (mm) FOR THE CROSS MSU 78-7A X MSU 78-9A, 1982

Pedigree	Generation	Petiole Thickness (mm)							Mean	s	No. of Plants
		2	4	6	8	10	12	14			
MSU 78-7A	P_1			5	12	10	2		8.5a	1.54	29
MSU 78-9A	P_2		6	13	7	1			6.6c	1.53	28
MSU 78-7A X MSU 78-9A	F_1		3	11	16	21	3		8.0ab	1.70	54
F_1 self	F_2		15	50	91	98	43	5	8.2a	2.19	302
F_1 X P_1	BC_1		3	23	56	45	22	3	8.3a	1.99	152
F_1 X P_2	BC_2		25	41	39	19	12		7.5b	1.66	141
F_2 self	F_3		3	10	15	12			8.2z	1.92	40
F_2 self	F_3			12	18	7			8.7a	1.28	37

TABLE 32 FREQUENCY DISTRIBUTION FOR ADAXIAL CURVATURE INDEXES FOR THE CROSS MSU 78-7A X MSU 78-9A, 1981

		Adaxial Curvature Index													
Pedigree	Generation	0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0	Mean	s	No. of Plants
MSU 78-7A	P_1		1	4	4	4	2	4	4	3	1		.48	.218	27
MSU 78-9A	P_2	5	11	10	3	1							.15	.091	30
MSU 78-7A X MSU 78-9A	F_1		1	11	34	36	23	14	7	6			.43	.151	132
F_1 self	F_2	6	40	104	127	114	61	29	11	6	4	1	.35	.164	503
F_1 X P_1	BC_1		3	23	34	54	28	26	8	4	4	10	.51	.450	195
F_1 X P_2	BC_2		7	75	65	15	1						.26	.071	163

TABLE 33 FREQUENCY DISTRIBUTION FOR ADAXIAL CURVATURE INDEXES FOR THE CROSS MSU 78-7A X MSU 78-9A, 1982

		Adaxial Curvature Index												No. of
Pedigree	Generation	.2	.4	.6	.8	1.0	1.2	1.4	1.6	1.8	2.0	Mean	s	Plants
MSU 78-7A	P_1		4	15	6	3	1					.68a	.204	29
MSU 78-9A	P_1	22	4	2								.22e	.181	28
MSU 78-7A X MSU 78-9A	F_1	1	14	16	14	6	2	1				.65ab	.208	54
F_1 self	F_2	31	97	106	53	10	2	1	0	1	1	.56bc	.238	302
F_1 X P_1	BC_1	1	29	57	44	11	5	1	1	1	2	.72a	.304	152
F_1 X P_2	BC_2	24	98	18	1							.40d	.097	141
F_2 self	F_3	1	8	13	9	4	2	1	2			.75a	.305	40
F_2 self	F_3	2	14	18	3							.50c	.157	37