THE INHERITANCE OF CARPEL SEPARATION IN MATURE FRUITS OF PICKLING CUCUMBER

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This is to certify that the

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ABSTRACT

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Progenies of crosses between the pickling cucumber (*Cucumis sativus* L.) lines SC601H and MSU381 were evaluated to determine the inheritance of mature fruit carpel separation. Reciprocal cross differences for carpel separation were not detected. Weak carpel suture strength, as expressed by carpel separation, exhibited dominance over non-separation. Additive genetic variance exceeded dominance variance, and a significant non-genetic or environmental component of variation was observed. Estimates of narrow-sense heritability ranged from 39 to 45% suggesting that carpel suture strength, and consequently fruit quality, could be improved through selection. Although a genetic model consistent with the observed frequency distributions was not found, the data can be interpreted as a 2-gene, or at the most a 3-gene, system with low heritability. High frequencies of carpel separation were not necessarily associated with gynoecious or high yielding phenotypes.

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Guidance Committee:

The body of this thesis has been condensed into a manuscript intended for publication in the Journal of the American Society for Horticultural Science.

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INTRODUCTION

Carpel separation in mature fruits of the pickling cucumber (Cucumis sativus L.) is expressed when the sutures of the 3 fused carpels separate forming a hollow or void which runs through part or the entire length of the fruit (Fig. 1).

Economically, this character is important because it is associated with carpel separation in the immature fruits used for pickling (Fig. 2). At present approximately 45% of the pickling cucumbers harvested in the USA is utilized immediately in various pasteurized, fresh pack products (11). Carpel separation lessens the consumer appeal of these products lowering their economic value. The remaining 55% is cured by fermentation in brine for later processing. Early workers (8) suggested a causal relationship between green stock characteristics and bloater formation during curing of salt stock. Later, researchers showed that carpel suture strength was positively correlated with the brining quality of pickling cucumbers (7,15). As carpel suture strength increased, the frequency of green stock carpel separation decreased, and likewise the frequency of balloon bloater formation during fermentation decreased. It has been reported that bloater formation resulted in a 5 million dollar loss to the pickle industry in the 1971-72 packing season (11).

Figure 1. Cross-sections of mature cucumber fruits exhibiting separation of the carpels.

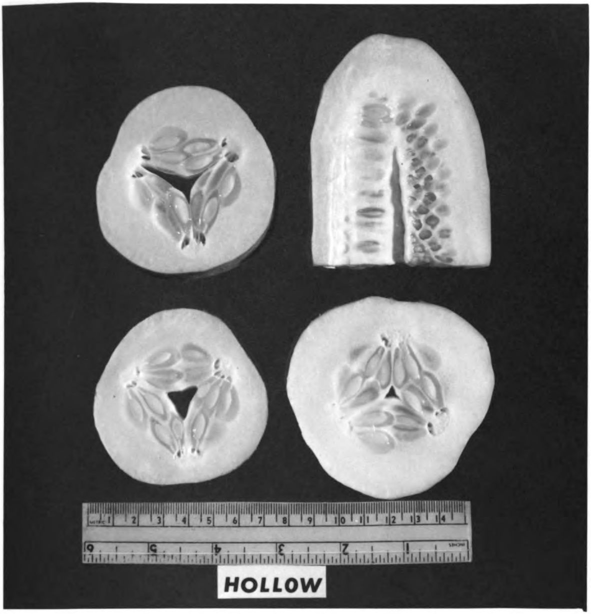

HOLLOW

Figure 2a. Longitudinal sections of immature cucumber fruits showing carpel separation.

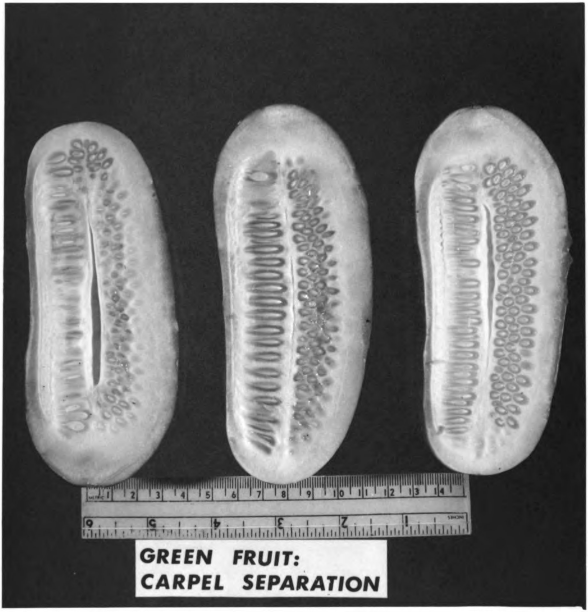
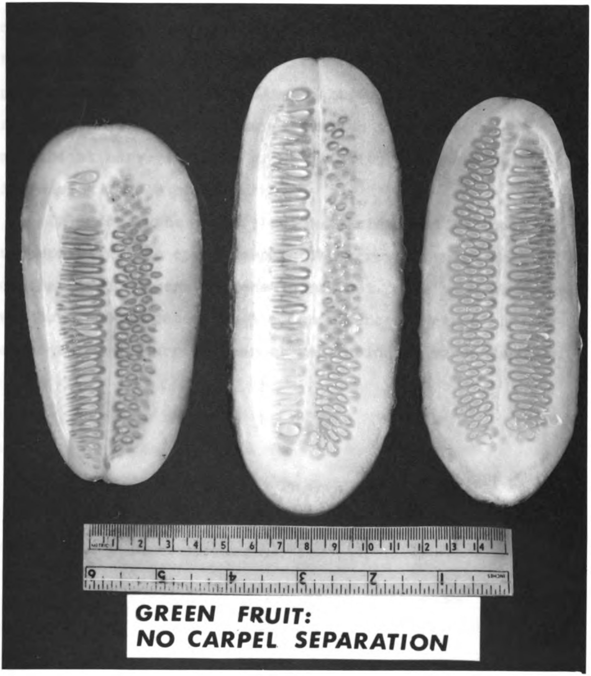

GREEN FRUIT:
CARPEL SEPARATION

Figure 2b. Longitudinal sections of immature cucumber fruits showing no carpel separation.



GREEN FRUIT:
NO CARPEL SEPARATION

The frequency of carpel separation is determined by a number of factors. It has been demonstrated that percent carpel separation was associated with length of processing time and delay of processing after harvesting of the raw product (13) and with the date of harvest (14). Carpel separation was markedly increased with each step in mechanical harvesting and grading (9,10) and sometimes by increasing levels of impact (5).

In each of the above studies, varietal differences in susceptibility to carpel separation were suspected or demonstrated suggesting genetic control. The present study was designed to determine the inheritance of carpel suture strength as measured by carpel separation in mature fruits.

MATERIALS AND METHODS

It is difficult to determine objectively the degree of carpel separation in immature fruits suitable for processing. The informal "thumb test", by which one estimates the force necessary to separate the carpels of a cross-sectional slice with the thumb, is too subjective. In contrast, the technique utilizing the Instron Universal Testing Machine [Hooper, et al. (6)], although sensitive and objective, cannot be conveniently used when large numbers of fruits must be evaluated. Therefore, in this study susceptibility to carpel separation was judged by the degree of this defect in mature fruits. The use of mature fruits permitted full expression of the character being studied. The rating of up to 3 fruits per plant allowed sampling of fruits which developed under different environments. This partly offset the observation that carpel separation ratings of fruits on the same plant may differ with environmental conditions during fruit development.

Preliminary Investigation (1968). Two parent lines were used. SC601H (P_1), a monoecious line developed at Clemson University, produced mature fruits which were predominantly non-hollow with apparent resistance to carpel separation. The second parent, MSU381G (P_2), was a gynoecious line characterized by a high degree of separation in both the immature and mature fruits. Seeds of the parents, F_1, F_2, and reciprocal backcross generations were produced by hand pollinations in the greenhouse. Each generation was made up of seed bulked from several plants. All populations were field grown near Dansville, Michigan, in a randomized complete block design with 4 replications. Each replicate consisted of one or more 3.05 m (10 ft) rows of each generation spaced 61 cm (2 ft) between rows, 15.2 cm (6 in) between plants giving 107,593 plants per hectare (43,560 per acre). Fertilizer and irrigation schedules approximated those recommended for commercial pickle production.

When the majority of the fruits had reached maturity, data were collected from the first and, whenever possible, from the second fruit of each plant. Only mature fruits were evaluated. Each fruit was cut transversely through the center and visually classified for degree of carpel separation using the following rating scale:

Class	Log_{10}	Class Description
1	0.00	No separation between adjacent carpels.
2	0.30	Separation only at the vertex juncture of the 3 carpels.
3	0.48	Any separation greater than the above but involving less than one-half of each carpel suture.
4	0.60	Any separation greater than above.

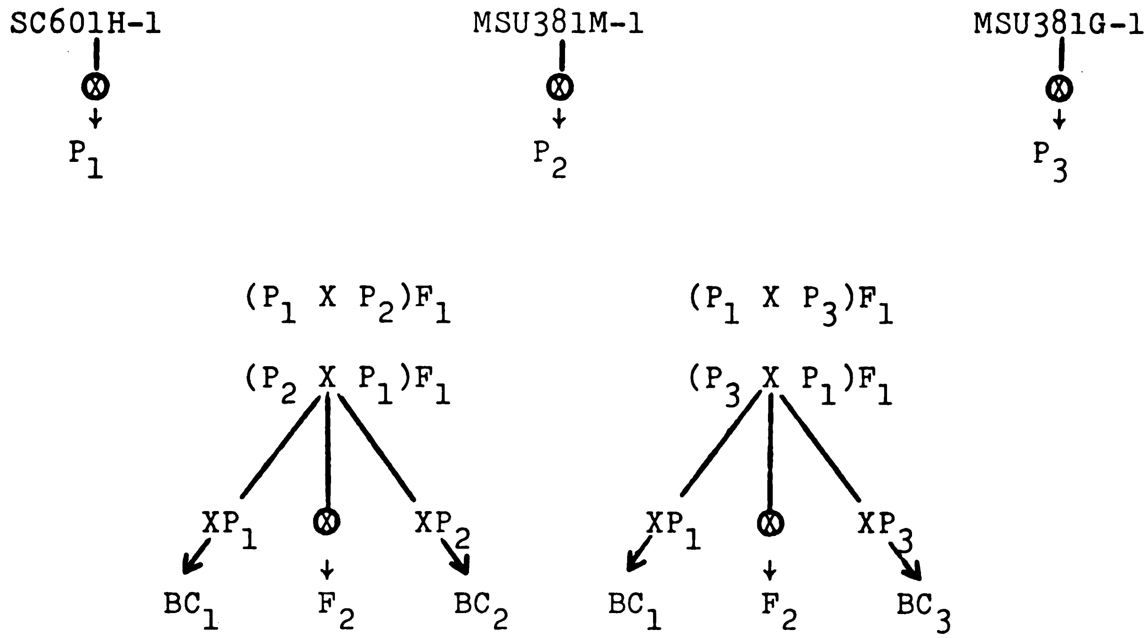
Although flood damage caused poor stands and variable fruit maturation, the data collected were sufficient to permit tentative conclusions concerning the inheritance of carpel separation and to indicate the magnitude of the environmental effects on this character. The need for a more detailed study utilizing a larger population was apparent.

Detailed Investigation (1970). Three parents were used to produce populations for study. The P_1 and P_2 generations were selected from the S_1 generations of SC601H and MSU381G used in the preliminary investigation. The P_3, MSU381M, was a monoecious line isogenic to gynoecious P_2, differing from it only by sex expression.

Genetic families (Fig. 3) were originated from single plant crosses by hand pollinations. The F_1 and reciprocal F_1 generations were made both between P_1 and P_2 and between P_1 and P_3. Three such single plant families were created and utilized.

Parents and progeny were field grown near Dansville, Michigan, in a randomized complete block design with 3 replications. Commercial varieties were included in each replication for comparison. Cultural practices used in the preliminary study were followed. In July a randomly chosen sample of 417 plants from the parental, F_1, and F_2 generations was labeled for use in comparing immature and mature

Figure 3. Typical family derived from cross of two single plants for use in the inheritance study.



fruit carpel separation. Grade size 3 (3.8 to 5.1 cm dia.) immature fruits were cut longitudinally and scored visually as being either carpel separated or non-separated.

In August, all plants in all generations were observed for mature fruit carpel separation. Data were collected from at least 1, and whenever possible from 2 or a maximum of 3, mature fruits on each plant. Each fruit was cut cross-sectionally into 4 segments so that the center, blossom end, and stem end could be classified according to the rating scale given previously. Thus a plant could be measured by as few as 3 determinations to as many as 9 readings. The mean of these 3, 6, or 9 determinations was used to measure the carpel separation of each plant.

<u>Data Analysis</u>. The non-parametric Mann-Whitney U- and Kruskal-Wallis tests as well as parametric analyses of variance were employed for comparing distributions or means.

The distributions of the segregating generations were continuous, exhibiting no clear-cut modes which would permit division into phenotypic classes. Consequently, data were analyzed biometrically using the methods outlined by Mather and Jinks (12). The original data were transformed to natural logarithms, common logarithms, and square roots. Mather's ABC scaling test (12) was applied to each transformation to determine on which the additive-dominance model was adequate.

The ratio of additive genetic variance to total phenotypic variance was used to estimate narrow-sense heritability. The minimum number of genes differentiating the parents was computed using the methods reported by Castle (3), Wright (16), Burton (2), and Mather and Jinks (12).

RESULTS AND DISCUSSION

Preliminary Investigation. Original data were transformed to common logarithms because this transformation best conformed to the assumptions of Mather's additive-dominance model for partitioning of variance. Means and variances for carpel separation were calculated (Table 1) for the parents, F_1, F_2, and backcrosses. The means of the F_1 and F_2 generations fell between the means of the two parents. The means of the BC with P_1 approached the mean of P_1; likewise the mean of the BC with P_2 approached P_2. No reciprocal cross differences were detected for the BC_1 generation.

Dominance for weak carpel suture was suggested by the fact that the F_1 mean exceeded the midparent value (Table 2). However, the comparatively higher variance of the BC with P_2 than the BC with P_1 suggested that P_1, the strong carpel sutured parent, carried a predominance of the dominant genes.

The estimated values for the components of variance (Table 2) suggest that additive and dominant effects as well as environmental effects were important in the inheritance of mature fruit carpel separation. Relatively high estimates for degree of dominance and heritability were obtained. Estimates of k suggest that a minimum of 2 gene pairs conditioned this character.

Detailed Investigation. In both the non-parametric and parametric tests no differences (5% level) were found

Table 1. Means, standard errors, and variances for mature fruit carpel separation ratings in the family SC601H X MSU381G, preliminary study.

Pedigree	Gen	Population		
		No of Plants	Mean[z]	Total Phenotypic Variance
SC601H	P_1	15	0.00 ± .000	0.000
MSU381G	P_2	13	0.42 ± .023	0.007
SC601H X MSU381G	F_1	23	0.25 ± .035	0.028
F_1 self	F_2	48	0.20 ± .030	0.042
P_1 X F_1	BC_1	66	0.12 ± .019	0.023
F_1 X P_1	BC_1recip	59	0.10 ± .021	0.026
P_2 X F_1	BC_2	32	0.27 ± .033	0.035

[z]Data transformed to $\log_{10}$.

Table 2. Estimates of components of variation, degree of dominance, heritability, and probable number of effective factors for mature fruit separation in the family SC601H X MSU381, preliminary and detailed studies.

	Preliminary	Detailed
Environmental variance (E)	0.017	0.010
Additive variance (D)	0.051	0.015
Dominance variance (H)	0.019	0.009
Degree of dominance $(\sqrt{\frac{H}{D}})$	0.614	0.750
Midparent value	0.212	0.283
F_1 mean	0.253	0.387
Narrow-sense heritability (h^2)		
In F_2		0.39
In F_2 and BC gen	0.62	0.45
Number of effective factors (k)		
Castle (1921)	1.6	1.4
Wright (1934)		1.9
Burton (1951)	1.6	1.6
Mather and Jinks (1971)		1.2

between P_2 and P_3, between reciprocal F_1's, and between plants maturing 1 and 3 or more fruits. Data were pooled accordingly. Original data were transformed to common logarithms as in the preliminary study.

Immature-Mature Fruit Carpel Separation Comparison. Frequency distributions comparing carpel separation ratings of mature fruits harvested from plants producing separated immature fruits and those producing non-separated immature fruits were developed (Fig. 4). Plants scored as non-separators in the immature fruit stage had an average mature fruit carpel separation rating of 0.14; whereas plants having separated immature fruits produced mature fruits with a 0.44 average mature fruit carpel separation rating. The difference between these two means was highly significant (.01 level), showing that there was good agreement between mature and immature carpel separation. Consequently, degree of carpel separation in the mature fruits seemed a reliable indicator of the potential for this defect in the immature fruits used for pickling.

This conclusion is reinforced by the work of Hooper (4) in which the carpel suture strength of immature fruits of SC601H (P_1) and MSU381 ($P_{2\&3}$) was measured with an Instron puncture technique (6). Using 6 mm slices from No. 3 fruits, he found that a mean force of 318.6 ± 55.1 g was required to separate the carpels of SC601H; whereas the carpel suture of MSU381 required only 222.7 ± 32.2 g.

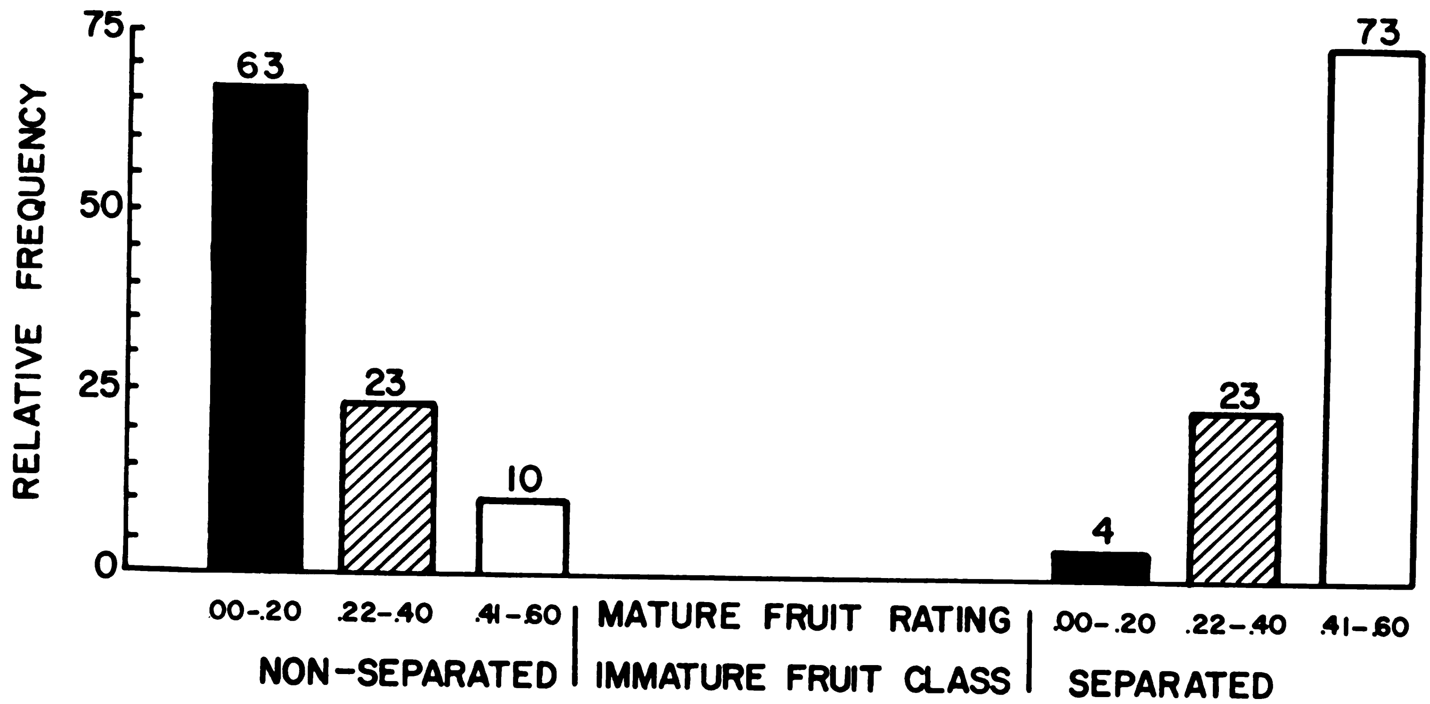


Fig. 4. Frequency distributions (%) comparing carpel separation in mature fruits of cucumber plants with early immature carpel separation ratings.

<u>Genetics of Mature Fruit Carpel Separation</u>. The relative frequency distributions for mature fruit carpel separation were prepared (Table 3). Commercial varieties have been included for comparison. A large percentage of fruits from the hybrid variety Pioneer were distributed in the strong carpel classes, whereas the majority of the fruits from the hybrid variety Spartan Progress were in the weak carpel suture or large carpel separation classes. Fruits of the open-pollinated monoecious variety Pixie were intermediate for carpel separation.

The distributions of the generations of the pooled family are also presented in histogram form (Fig. 5). The distributions of P_1 and $P_{2\&3}$ overlapped in the central portion of the scale. The F_1 was skewed strongly towards the weak carpel sutured $P_{2\&3}$, as was the F_2 although to a lesser degree. The BC to $P_{2\&3}$ was skewed more toward its recurrent parent than was the BC with P_1. These distribution patterns indicated that weak carpel suture, as measured by large carpel separation ratings, was dominant. The means and variances of the different populations (Table 4) substantiate this dominance pattern. The F_1 mean approached the mean of $P_{2\&3}$; the F_2 mean was intermediate but shifted slightly towards $P_{2\&3}$. The mean of the BC to $P_{2\&3}$ was closer to the mean of $P_{2\&3}$ than was the mean of the BC to P_1. Dominance of weak carpel suture was also indicated by the facts that the F_1 mean exceeded the

Table 3. Relative frequency distributions (%) for mature fruit carpel separation in cucumber from the pooled family of SC601H X MSU381 compared to established varieties; detailed study.

Pedigree	Gen	Class centers of carpel separation ratings[z]								
		No separations →							Large hollows	
		0.03	0.10	0.17	0.23	0.30	0.37	0.43	0.50	0.57
SC601H	P_1	49.0	21.0	4.0	13.0	7.0	4.0	2.0	0.0	0.0
MSU381	$P_{2\&3}$	0.0	1.2	0.6	1.2	4.8	13.1	25.0	46.4	7.7
SC601H X MSU381	F_1	0.8	1.2	2.7	6.8	14.5	20.2	32.0	21.1	0.6
F_1 self	F_2	6.2	6.9	9.4	14.4	16.0	14.8	15.4	14.8	2.1
F_1 X P_1	BC_1	13.6	12.3	13.6	18.0	15.5	11.9	10.6	4.2	0.2
F_1 X $P_{2\&3}$	BC_2	1.5	1.0	2.5	6.1	14.7	16.2	24.4	24.9	8.6
Pioneer	F_1	23.3	8.3	1.7	10.0	28.3	18.3	5.0	5.0	0.0
Spartan Progress	F_1	0.0	0.0	0.0	4.3	10.6	10.6	34.0	38.3	2.1
Pixie	Variety	6.3	10.0	14.0	21.3	19.3	13.7	12.0	3.3	0.0

[z]Ratings on a 1 to 4 scale, with 1 designating no separation, transformed to $\log_{10}$.

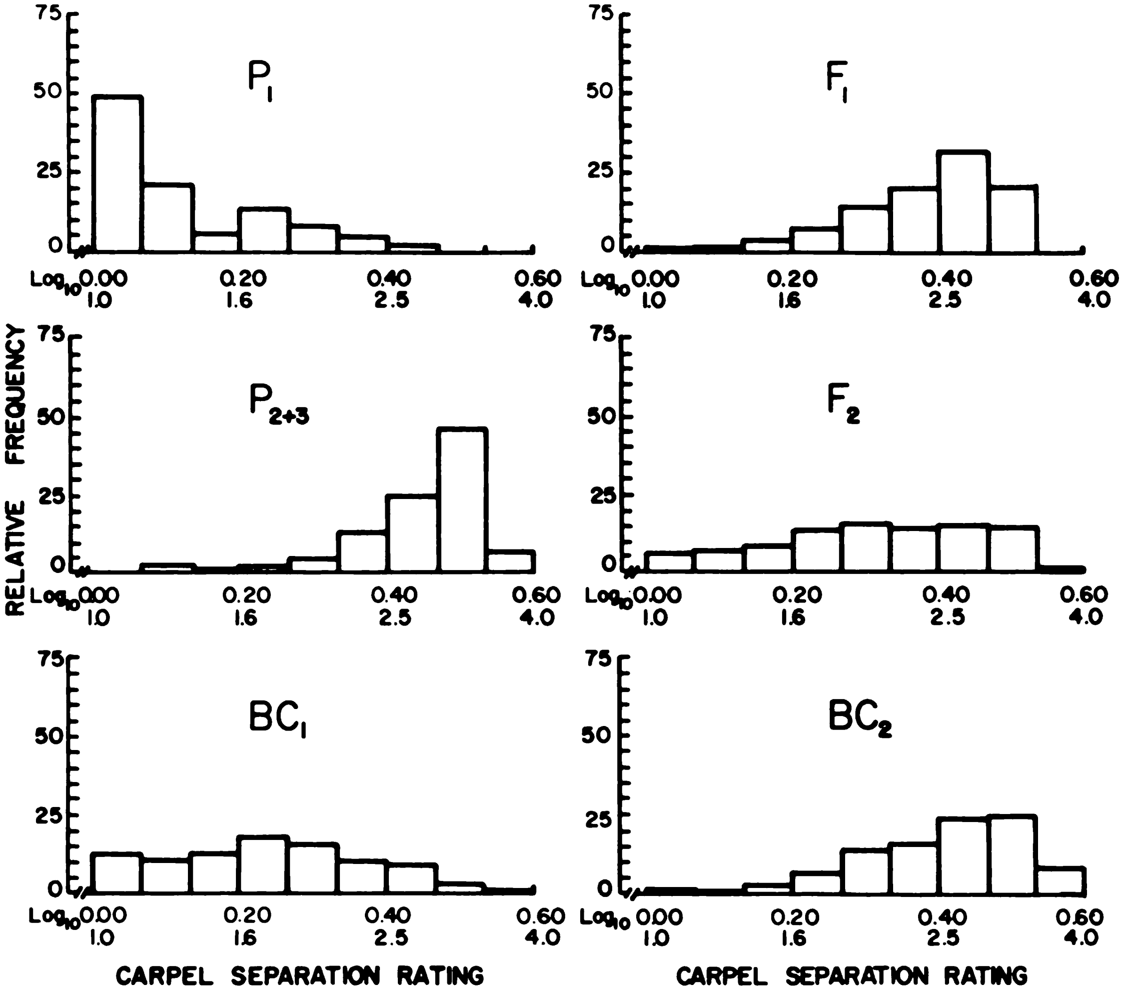


Fig. 5. Frequency distributions (%) for carpel separation in mature fruits of cucumber from the family of SC 601H x MSU 381.

Table 4. Means, standard errors, and variances for mature fruit carpel separation in cucumber from the pooled family of SC601H X MSU381; detailed investigation.

Pedigree	Gen	Population		
		No of Plants	Mean[z]	Total Phenotypic Variance
SC601H	P_1	100	0.11 ± .012	0.014
MSU381	$P_{2\&3}$	168	0.45 ± .006	0.006
SC601H X MSU381	F_1	484	0.39 ± .004	0.009
F_1 self	F_2	723	0.31 ± .005	0.020
F_1 X P_1	BC_1	528	0.24 ± .006	0.019
F_1 X $P_{2\&3}$	BC_2	394	0.41 ± .006	0.013
Pioneer	F_1	60	0.28 ± .013	0.010
Spartan Progress	F_1	47	0.43 ± .011	0.006
Pixie	Variety	300	0.27 ± .007	0.014

[z]Data transformed to $\log_{10}$.

midparent value (Table 2) and the BC to P_2 exhibited a lower variance than the BC to P_1.

Estimated values of components of variation, degree of dominance, heritability, and minimum number of effective factors were computed (Table 2). The additive portion of the variance exceeded the dominance variance but was almost equaled by the environmental, or non-heritable variance. This value for environmental variance was large, but realistic. The results of the initial analysis of variance in which environmental variance was measured by the differences between replications was highly significant and accounted for a large portion of the total phenotypic variation in carpel separation (Table 5).

The calculated degree of dominance suggested partial dominance. Narrow-sense heritability, which reflects the effectiveness of selection for carpel suture strength, ranged from 39 to 45%. Four estimates of k, the minimum number of effective factors controlling carpel separation, were computed. Each gave a value between 1 and 2. This is an underestimate of the actual number of gene pairs involved because a comparison of the s(dh) and $\sqrt{DH}$ (12) indicated that one or more of the following was true: the increments due to each gene were unequal, the distribution of genes was not completely isodirectional, linkage was present, or the genes involved could not be phenotypically distinguished.

Table 5. Analysis of variance for mature fruit carpel separation in cucumber for parent and F_1 generations of the pooled family SC601H X MSU381; detailed investigation.

Sources of Variation	Degrees of Freedom	Mean Squares	F
Total	751		
Generations	2	76.28	345.7**
Replications	2	5.17	23.4**
Error	747	0.22	

**$P < 0.01$.

The values calculated suggested that a 2 gene pair system was in operation. A large number of gene models were tried and rejected because of low probabilities in chi-square tests for goodness of fit. However, the data suggest that segregation at two loci, or at the most 3 loci, accounted for most of the variation in carpel separation in the crosses studied. A clear-cut dihybrid ratio may have been obscured by incomplete penetrance and possibly by incomplete dominance, linkage, and genotype x environment interactions.

The Relationship of Carpel Separation to Sex Expression and Yield. Recently it has been implied by growers and processors that predominantly female cucumber hybrids produced on gynoecious seed parents, when compared to monoecious varieties, have more carpel separation and higher frequencies of bloated fruits in brine stock. The isogenic lines used as P_2 and P_3 were compared with each other in terms of carpel separation ratings. No differences (5% level) were found between P_2 and P_3, nor between the F_1, F_2, or backcross populations resulting when each was crossed with P_1.

Segregating populations resulting from the cross P_2 X P_1 (MSU381G X SC601H) contained gynoecious segregates whereas those resulting from the cross P_3 X P_1 (MSU381M X SC601H) contained only monoecious plants. Nonetheless, the populations containing gynoecious segregates did not have significantly higher levels of mature fruit carpel separation than those populations containing no gynoecious segregates. These data suggest that weak carpel suture strength is not necessarily associated with gynoecious sex expression, and are in agreement with Barnes (1), who analyzed data collected over several seasons, and concluded that F_1 hybrids made with gynoecious seed parents brined as well as their respective monoecious male parents.

Tests for significance also indicated no differences ($P > .05$) in degree of carpel separation between those plants maturing one fruit and those maturing 3 or more fruits. Since the number of mature fruits per plant is an indication of yield capacity, these results suggest that weak carpel strength is not always associated with high yielding capacity.

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