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INHERITANCE OF PARTHENOCARPIC YIELD IN
GYNOECIOUS PICKLING CUCUMBER (CUCUMIS SATIVUS L.)

presented by

Ibrahim Ibrahim Soliman El-Shawaf

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Horticulture

J R Baker
Major professor

Date 4 May 1979

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INHERITANCE OF PARTHENOCARPIC YIELD

IN

GYNOECOUS PICKLING CUCUMBER (*CUCUMIS SATIVUS* L.)

By

Ibrahim Ibrahim Soliman El-Shawaf

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

1979

ABSTRACT

INHERITANCE OF PARTHENOCARPIC YIELD

IN

GYNOECIOUS PICKLING CUCUMBER (CUCUMIS SATIVUS L.)

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The advent of a mechanical harvest technology for pickling cucumber during the last decade has stimulated research efforts for high yields to enhance the feasibility of this once-over destructive harvest system. The advantages of superior quality and high yield potential of parthenocarpic over seeded cucumbers encouraged cucumber breeders to research the development of parthenocarpic cvs. However, little is known about the genic system which controls the parthenocarpic yield in pickling cucumbers for open-field production. The present research was undertaken to elucidate the genetic system which conditions parthenocarpy in gynoecious pickling cucumber grown out-of-doors.

Relatively high GCA and SCA effects for parthenocarpic yield indicated that both additive and non-additive gene effects were important. Dominance was partial for low parthenocarpic yield with K = 1 to 2. Many recessive genes were controlling

high yields as measured by fruit numbers. However, the heritability estimates for yield were relatively low (0 to 32%) depending on the measurement.

High phenotypic and genotypic correlations were detected between flowering time and nodal position of first-pistillate flower and between the latter and yield (fruit number). Accordingly, selection for early flowering and lower nodal positions for the first-pistillate flower could be used as criteria to select for high yields. Complete dominance was found for flowering time with a moderately high heritability (64%); whereas, the degree of dominance was partial for nodal position of the first-pistillate flower with a high heritability (63%). Heterosis, heterobeltiosis, and inbreeding depression were all detected for parthenocarpic yield which suggested that hybrid vigor could be utilized to increase the yield of parthenocarpic cvs.

Gynoecious expression is a prerequisite for parthenocarpy to preclude pollination. The heritability for gynoecious expression was relatively high (73%) for an array of 17 topcrosses derived from gynoecious by hermaphroditic crosses. The degree of dominance was expressed as over-dominance for gynoecious expression.

Thus, gynoecious inbred lines might be improved for parthenocarpic yields by recurrent selection in a breeding program because of the quantitative inheritance of yield. Moreover, transgressive segregation might occur for parthenocarpy yield by selfing highest

yielding individual plants and selecting in subsequent segregating populations. The parthenocarpic hermaphroditic lines (pollen parents) could be developed by using the backcross method to transfer the single gene, m, for hermaphroditic expression into gynoecious parthenocarpic recurrent parents with high yield. Thus, high yielding parthenocarpic cvs. with necessary gynoecious expression could be produced from the cross of unrelated gynoecious parthenocarpic with hermaphroditic parthenocarpic parent lines.

DEDICATION

I dedicate all of these efforts with unlimited affection and gratitude to:

1. My parents who raised me with affection and love, while instilling in me self-independence during the early years of my life.

2. My wife, Salwa, and my son, Hytham, who were patient and tolerant during this period of study.

3. My beloved country, EGYPT, and the EGYPTIAN People who provided all of the financial support for my graduate study.

4. I dedicate this work also to the Egyptian-American friendship that is based on mutual interests and a progressive relationship for the good of mankind.

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Special thanks go to my colleagues: Messrs. M. Tasdighi, M. Dessert, J. Parrot, L. Yarger, and G. Lester for their willing assistance with the many research plots.

Thanks also goes to Mr. Amos Lockwood and Marshall Pollok of the Horticultural Research Center for their help with cultural practices. And my thanks go to all of the undergraduate students who helped to harvest all the research plots.

Guidance Committee:

This thesis has been condensed into the format suited and intended for publication in the Journal of the American Society for Horticultural Science.

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PART I

Performance of Hermaphroditic Pollen Parents in Top Crosses With Gynoecious Lines

Abstract. The top crosses method was used to judge the performance of 17 hermaphroditic lines (pollen parents) for yield and associated characters. Hybrid yields of parthenocarpic fruit averaged from 2.9 to 5.8 fruits/plant with 67.7 to 99.5 percent of desired gynoecious expression. Seven hermaphroditic lines were judged outstanding based on their hybrid performance for both high yields and gynoecious expression. Significant correlations were detected between days-to-flower and nodal position of first-pistillate flower; and between the latter and yield. Heritabilities were 64%, 63%, and 73% for days-to-flower, nodal position of the first-pistillate flower, and gynoecious expression, respectively. The heritability for yield (no. of fruit/plant) of parthenocarpic fruits was 20%. Accordingly, plant breeders might exercise selection gains for associated characters, but realize somewhat less success for yield (fruit no.).

INTRODUCTION

Inbred lines may be evaluated for yield and other economic characters by testing them in a series of hybrid crosses for combining ability. The line-variety (top cross) method was long ago used to test the general combining ability (GCA) of parental lines (3). Since then, the top cross method has been used in

many crops, e.g., muskmelon, watermelon, corn and sweet corn (2,6,11,12,13,17,20,30,31,32). Moreover, the type and number of tester(s), the use of tester female parents, and the use of hand pollinations to derive top crosses were also ascertained and elucidated (11,13,17,30,32). Obviously, the merit of the tested lines can be determined most accurately in single-cross hybrid combinations. However, because of the limited number that can be tested in single crosses (6), the top cross method is more practical. Then, the selected outstanding line(s) can be carefully evaluated in single-cross hybrid combinations.

The advent of mechanical harvesting in pickling cucumber production necessitated the development of a technology to concentrate yields for a destructive once-over harvest system (1,4, 18,35). The average yield under this system ranges from 1 to 2 fruits/plant (18). The breeding of parthenocarpic gynoecious hybrid cultivars capable of producing high numbers of fruits per plant has been suggested as a means to increase yields for once-over harvest regimes (1,4,22,23,24). Accordingly, the utilization of high yielding parthenocarpic lines as gynoecious seed parents crossed with comparable hermaphroditic male parents to produce hybrids which are both parthenocarpic and gynoecious is a breeding research strategy to increase yields for once-over harvest.

Fruit no. has been used to judge cucumber cultivar productivity (10,24,28,29). There is a correlation between fruit no. and fruit weight (9,35) and between yield (no. fruits/acre) and

dollars/acre (28). Genotypic and phenotypic correlations for fruit no. and dollar values were high which suggested selection pressure for high fruit numbers would be effective in increasing crop value. However, the heritabilities of full-sib families for dollar value and number of fruit were 19 and 17%, respectively, which is sufficient for selection (29).

A highly female hybrid (100% gynoecious) is a prerequisite for parthenocarpic fruiting (22,24). The genetics of femaleness has been reported (14,15,25,26) and gynoecious lines have been developed (14,21). Gynoecious hybrids (100% pistillate flowers) were produced from crosses of gynoecious by hermaphroditic lines (1,14,22). However, the phenotypic stability of gynoecious expression in cucumber is subjected to environmental influences which may enhance or suppress female expression (1,5,25,26,34).

Importantly, flowering time is a simply inherited character (19,27) which is highly correlated with maturity (9,19), but affected by various environmental factors (16,19,25,27). The nodal position of the first-pistillate flower is also a good measure of both female tendency and maturity (25), but it is strongly influenced by environment (19,25).

The objective of our research was to select among an array of hermaphroditic male parents for parthenocarpic yield and associated components based on GCA. The top cross method was used to judge the performance of the hermaphroditic lines for parthenocarpic yield and associated components (gynoecious expression, days to flowering, and nodal position of the first-pistillate flower).

MATERIALS AND METHODS

An array of 17 hermaphroditic pollen parents was evaluated for combining ability by the use of a "controlled" top cross. Crosses were made in the fall of 1976, in the greenhouse, between the hermaphroditic pollen parents and gynoecious seed parents (Table 1). Each of the 17 hermaphroditic pollen parents was represented by 12 plants grown in 20 cm clay pots. The seed parents were spaced 30 cm apart on raised soil benches with routine cultural practices to maximize seed yields. Each of the 6 gynoecious seed parents was represented by 136 plants; 8 of which were crossed with each pollen parent.

The gynoecious seed parents were rogued for predominantly female (PF) plants. At flowering time, the bisexual flowers from each hermaphroditic line were collected daily; and then randomly used to cross-pollinate by-hand to the 6 gynoecious seed parents. Plants of the seed parents developed 2 or 3 fruits which were harvested at maturity. Several hundred seeds of each cross (6 gynoecious x 17 hermaphrodites) were obtained.

A total of 17 "controlled" top crosses representing each hermaphroditic pollen parent were obtained by randomly mixing 70 seeds from each of the 6 hybrids together for each pollen parent.

Table 1. Description of parental cucumber lines used to study heritability and combining ability for parthenocarpic yield and associated characters in gynoecious hybrids under out-of-door conditions.

MSU No.	Pedigree description
Hermaphroditic pollen parents (♂).	
661H	Sib increase from (SC40A x MSU 7154H) F_{10}
662H	" " " (SC40A x MSU 7154H) F_{11}
663H	" " " (MSU 844G x MSU 4108H) F_9
664H	" " " (MSU 844G x MSU 4108H) F_8
665H	" " " (SC40A x MSU 7154H) F_{12}
666H	" " " (SC40A x MSU 7154H) F_{12}
667H	" " " (MSU 844G x MSU 4108H) F_9
668H	" " " (MSU 844G x MSU 4108H) F_9
669H	" " " (MSU 844G x MSU 4108H) F_{10}
319H	" " " (SC40A x MSU 7172H) F_8
530H	" " " (MSU 364G x 4108H) F_2 x (MSU 364G)BC_2 S_3
581H	" " " (MSU 394G x 4108H) F_2 x (MSU 394)BC_2 S_3
532H	" " " (MSU 394G x 4108H) F_5
591H	" " " (SC40A x MSU 7152H) F_9
4108H	" " " USSR Accession (P.I. 351140) S_7
7152H	" " " USSR Accession '1031' S_7
HP-61	" " " USSR Accession 'HP-61' S_2
Gynoecious seed parents (♀).	
Gy3	Mass increase from breeders stock; Clemson Univ. release.
Gy14	Mass increase from breeders stock; Clemson Univ. release.
92G	Sib increase from cross (MSU 713-5, MSU 35G, Spotvrige) F_9
364G	Mass increase from cross (MSU 35G, MSU C-14, MSU 5711, MSU 5612, and Spotvrige)F_6
402G	Sib increase from Poland Accession 'Skieriewicki' S_4.
921G	Mass increase from cross (Gy3, MSU 713-5, MSU 35G, and Spotvrige) F_7.

This created a population with 420 seeds equally represented by each hybrid. A "controlled" S_1 population (check) was likewise derived by blending an equal number of seeds from the 6 gynoecious seed parents.

The assumption was made that, on the average, all of the individuals of the top cross had an equal female parentage; i.e., an equal and random sample of female gametes (an equal basis). So, progenies of each top cross consisted of both full-sib and half-sib families but averaging half-sib family in their relationships; and consequently, all the crosses were composed of half-sib families. Accordingly, the genetic variation among the top crosses is due to the genetic differences among the hermaphroditic pollen parents. Such genetic differences can be computed as a ratio (heritability estimate) of the total phenotypic variation as follows: h^2 of half-sib family means = $6^2_G/(6^2_G+6^2_E)$ where 6^2_G = additive genetic variance, 6^2_E = error variance, and $6^2_G+6^2_E=6^2_p$ = Total phenotypic variance; (33). These variances can be estimated from the expected mean squares (EMS) as follows:

Source of variation	d.f.	EMS
Replications (R)	5	$6^2_E + 17\ 6^2_R$
Top crosses (T)	16	$6^2_E + 6\ 6^2_G$
RxT (error)	80	6^2_E
Total	101	

The 17 top crosses were evaluated in a field experiment during the summer of 1977. The seeds of each controlled top cross population were divided equally into 7 lots of 60 seeds. Six lots of each controlled top cross were planted and one lot was saved for remnant. The experimental design was a randomized complete block with 6 blocks and single plots to represent each population. The seeds were planted on June 22 at the Horticultural Research Center of Michigan State University near East Lansing. Data were collected on an individual plant basis for days-to-flowering, node of the first-opened flower and sex expression. The data for yield (mean number of fruits/plant) were obtained by dividing the total number of fruits/plot by the number of plants/plot. Individual plots were harvested when 10-20% of the fruits were observed to be oversized (>5 cm diam.). Routine cultural practices were used.

Data were statistically analyzed for variance components, multiple comparisons, correlation coefficients and regression coefficients (8) for yield and associated characters.

RESULTS

The ANOVA for the 17 top crosses (Table 2) produced highly significant differences (1% level) for all characters. Therefore, genetic differences among the hermaphroditic parents were probable.

Days-to-flowering. The analysis of variance for days-to-flowering (Table 2) was highly significant ($P<0.01$). The mean days-to-flowering (Table 3) for the 17 top crosses (38.7 days)

Table 2. ANOVA for yield components and parthenocarpic yield of cucumber from top crosses involving 17 hermaphroditic pollen parents.[z/]

Source of variation	d.f.	Mean Squares			
		Days	Nodes	% Gynoecious	No. fruits
Replication	5	13.17**	0.32	9.24^{ns}	4.46^{ns}
Top crosses	16	29.99**	1.11**	336.10**	3.21**
Error	80	2.53	0.10	19.10	1.27
Total	101	7.41	0.27	68.84	1.74

[z/] **indicates highly significant differences at 1% level; *significant at 5% level, and ns not significant at 5% level.

Table 3. Performance of the progenies from 17 top crosses and the gynoecious parental blend (check) for yield components and yield in parthenocarpic cucumber.[z/]

Hermaphroditic MSU line No.	Days to flower (No.)	Node first flower (No.)	Gynoecious (%)	Yield (No. fruit)
661H	37.1 ± 0.4	3.2 ± 0.1	99.2 ± 0.5	4.3 ± 0.5
662H	36.9 ± 0.3	2.2 ± 0.1	94.0 ± 1.3	5.7 ± 0.7
663H	37.9 ± 0.5	2.1 ± 0.1	95.8 ± 1.4	4.5 ± 0.4
664H	40.1 ± 0.8	2.5 ± 0.1	98.4 ± 1.6	3.8 ± 0.7
665H	38.0 ± 1.0	2.2 ± 0.1	97.6 ± 2.0	3.9 ± 0.4
666H	36.2 ± 0.9	2.2 ± 0.1	96.4 ± 1.6	5.2 ± 0.3
667H	41.0 ± 1.1	2.2 ± 0.1	93.5 ± 2.8	4.4 ± 0.5
668H	39.2 ± 0.7	2.2 ± 0.1	98.4 ± 0.7	4.6 ± 0.6
669H	36.7 ± 0.8	2.2 ± 0.2	99.5 ± 0.5	4.2 ± 0.6
319H	38.9 ± 0.6	3.4 ± 0.2	98.1 ± 0.9	5.3 ± 0.6
530H	45.0 ± 0.6	3.1 ± 0.1	92.6 ± 2.7	4.3 ± 0.5
581H	39.5 ± 0.5	2.8 ± 0.2	98.7 ± 0.8	5.8 ± 0.4
532H	38.4 ± 0.4	2.2 ± 0.1	99.5 ± 0.5	4.4 ± 0.6
591H	35.0 ± 0.6	2.2 ± 0.1	98.0 ± 1.0	3.9 ± 0.1
4108H	39.7 ± 1.0	3.3 ± 0.1	99.4 ± 0.6	4.7 ± 0.3
7152H	38.9 ± 0.4	3.0 ± 0.3	97.8 ± 0.8	2.9 ± 0.4
HP-61	39.2 ± 1.0	2.7 ± 0.2	67.7 ± 4.4	4.2 ± 0.5
Check	38.6 ± 1.0	3.1 ± 0.2	90.2 ± 7.2	4.5 ± 0.5
Mean	38.7 ± 0.5	2.5 ± 0.1	95.6 ± 2.8	4.5 ± 0.2

[z/] Each value is the mean and standard error of the mean.

was equal to the check mean (38.6 days). The mean days-to-flower (Table 4) for the hermaphroditic parents ranged from 35 (591H) to 45 (530H) days. Two hermaphroditic lines were significantly different from the check. These were the early line (35 days), 591H, and the late line (45 days), 530H. Moreover, significant differences occurred among the hermaphroditic lines (Table 3) for flowering time which could be classified into 5 subsets (Table 4). These subsets contain the early, intermediate, and late lines. The relatively high heritability for the hermaphroditic lines was 64.4% (Table 6) for this trait.

Node of first-female flower. Highly significant differences among the progenies of the 17 top crosses suggested genetic differences among the hermaphroditic lines for this trait (Table 2). A range of 1.1 nodes was detected among the means.

Ten hermaphroditic lines (663H, 669H, 668H, 662H, 591H, 666H, 532H, 667H, 665H, and 661H) opened first-pistillate flowers on lower nodes than the check (Table 4). The lines were divided into 4 subgroups. The first group included 13 of the 17 lines. A relatively high heritability of 62.9% was found (Table 6) for this trait.

Gynoecious. A parthenocarpic hybrid with a high gynoecious frequency (99 to 100%) is desirable in order to avoid pollination and permit parthenocarpic fruit set. Highly significant differences were found among the top crosses (Table 2) which suggested genetic differences among the male parents. The hermaphroditic lines crossed with gynoecious seed parents produced F_1 hybrids which ranged from 68 to 99% gynoecious expression

Table 4. Combining ability of hermaphroditic cucumber lines for parthenocarpic yield components in top crosses and a gynoecious parent blend (check) in a 1977 field experiment.[z/]

Hermaphroditic MSU line no.	Flowering			Sex expression	
	Number plants	Days	Node first flower	Number plants	Gynoecious (%)
661H	156	37.1abc	2.3a	213	99.2a
662H	154	36.9abc	2.2a	191	94.0a
663H	155	37.9abc	2.2a	203	95.8a
664H	151	40.1cd	2.5ab	218	98.4a
665H	155	38.0abcd	2.2a	240	97.6a
666H	147	36.2ab	2.2a	162	96.4a
667H	132	41.0d	2.2a	159	93.5a
668H	152	39.2bcd	2.2a	179	98.4a
669H	150	36.7ab	2.2a	203	99.5a
319H	145	38.9bcd	3.4d	170	98.1a
530H	136	45.0e	3.1bcd	195	92.6a
581H	154	39.5bcd	2.8abcd	171	98.7a
532H	142	38.4abcd	2.2a	188	99.5a
591H	152	35.0a	2.2a	169	98.0a
4108H	127	39.7bcd	3.3cd	151	99.4a
7152H	156	38.9bcd	3.0bcd	230	97.8a
HP-61	143	39.2bcd	2.7abc	174	67.7b
Check	138	38.6	3.1	156	90.2

[z/]Separation between means by Tukey's multiple range test, 5% level.

(Table 3). The check averaged 90.2% gynoecious plants with a high standard deviation (17.6). However, most of the crosses with hermaphroditic lines ranged from 92.6 (530H) to 99.5% (532H) gynoecious plants with relatively small standard deviations in relation to those of the check and HP-61. Only one line (HP-61) was significantly different from the check; as well as, from the 16 hermaphroditic lines (Table 4). The heritability was high (73.4%; Table 6).

Yield (average number fruits/plant). The analysis of variance for yield revealed a highly significant difference among the progenies of the 17 top crosses (Table 2). Yields ranged from 2.9 (7152H) to 5.8 (581H) fruits/plant (Table 3). The mean number of fruits/plant was 4.5 for both the 17 top crosses and the check. Four hermaphroditic lines were found to exceed 5 fruits/plant (581H, 662H, 319H, 666H). The remaining 13 lines yielded from 2.9 to 5.0 fruits/plant (Table 5). Two lines (581H and 662H) were significantly higher for yield than the other lines which indicated high GCA. The heritable variation among the hermaphroditic lines as estimated by the heritability was 20% (Table 6).

Relationships between characters. Correlation and regression coefficients were calculated to characterize the relationships among the four characters to better select hermaphroditic parents for yield and gynoecious expression. A highly significant positive correlation (0.37**) was found between days-to-flower and the node of the first-pistillate flower (Table 7). However, a significant negative correlation (-0.21*) was found between node of first-pistillate flower

Table 5. Combining ability for parthenocarpic yield from 17 top crosses and a gynoecious parental blend (check). Hermaphroditic parents are ranked by their parthenocarpic yields.

Hermaphrodite parents	Number of progenies	No. of fruits[z/]
581H	171	5.8 a
662H	191	5.7 a
319H	170	5.3 ab
666H	162	5.2 ab
4108H	151	4.7 ab
668H	179	4.6 ab
663H	203	4.5 ab
532H	188	4.4 ab
667H	159	4.4 ab
530H	195	4.3 ab
661H	213	4.3 ab
HP-61	174	4.2 ab
669H	203	4.2 ab
591H	196	3.9 ab
665H	240	3.9 ab
664H	218	3.8 ab
7152H	230	2.9 b
Check	156	4.5

[z/] Separation between mean no. of fruits/plant of the hermaphrodite parents by Tukey's multiple range test; 5% level.

Table 6. Heritability of yield components and yield from half-sib family means of parthenocarpic cucumber based on 17 hermaphroditic top crosses in outdoor production.[z/]

Character	Genetic Variance (6^2_G)	Phenotypic Variance (6^2_p)	h^2 (%)
Days to first flower	4.58	7.11	64.4
Node first flower	0.17	0.27	62.9
No. fruits/plant	0.32	1.59	20.2
% Gynoecious	52.8	71.9	73.4

z/ All values were computed from the ANOVA described in Materials and Methods section.

and yield. All other relations between characters were not significant.

Three regression analyses were done to identify dependency of a certain variable and its significant relationship with another variable. Since the node of the first-pistillate flower was highly correlated with days-to-flower and, yield was significantly correlated with node of the first-pistillate flower; regression analysis was done for both cases. Regression analysis for yield and % gynoecious was also done because of its importance for parthenocarpic pickling cucumbers. Regression analyses were displayed graphically (Fig. 1, 2 and 3). The regression coefficient for days-to-flowering and node of the first-pistillate flower was highly significant ($b = 0.07 \pm 0.02$). A significant regression coefficient was shown ($b = -0.52 \pm 0.23$) for yield and the position of the first-pistillate flower (Fig. 2). The regression coefficient was not significant for yield and % gynoecious plants (Fig. 3). The gynoecious expression accounted for only 2% of the variability in yield.

Selection for outstanding hermaphroditic parents. Because of the importance of both high % gynoecious expression and high yields for parthenocarpic cucumbers, a weighted scheme was used to select better hermaphroditic lines that produced hybrid combinations with 4.5 or more fruits per plant with 98 to 100% gynoecious expression (Fig. 3). Only 4 hermaphroditic lines fit these selection criteria; vis., 4108H, 581H, 668H, and 319H. However, when yield

Table 7. Correlations amongst yield components and yield of parthenocarpic cucumbers from 17 hermaphroditic top crosses in outdoor conditions.

Characteristic		Coefficients[z/] (1)	(2)	(3)	(4)
Days to first flower	(1)	1.00	0.37** r^2= 0.13	-0.13^{ns} r^2=0.02	0.08^{ns} r^2=0.01
Node first flower	(2)		1.00	-0.16^{ns} r^2=0.03	-0.21* r^2=0.04
% Gynoecious	(3)			1.00	0.15^{ns} r^2=0.02
No. fruits/plant	(4)				1.00

z/**indicates highly significant at 1% level; *significant at 5% level, and ns not significant at 5% level.

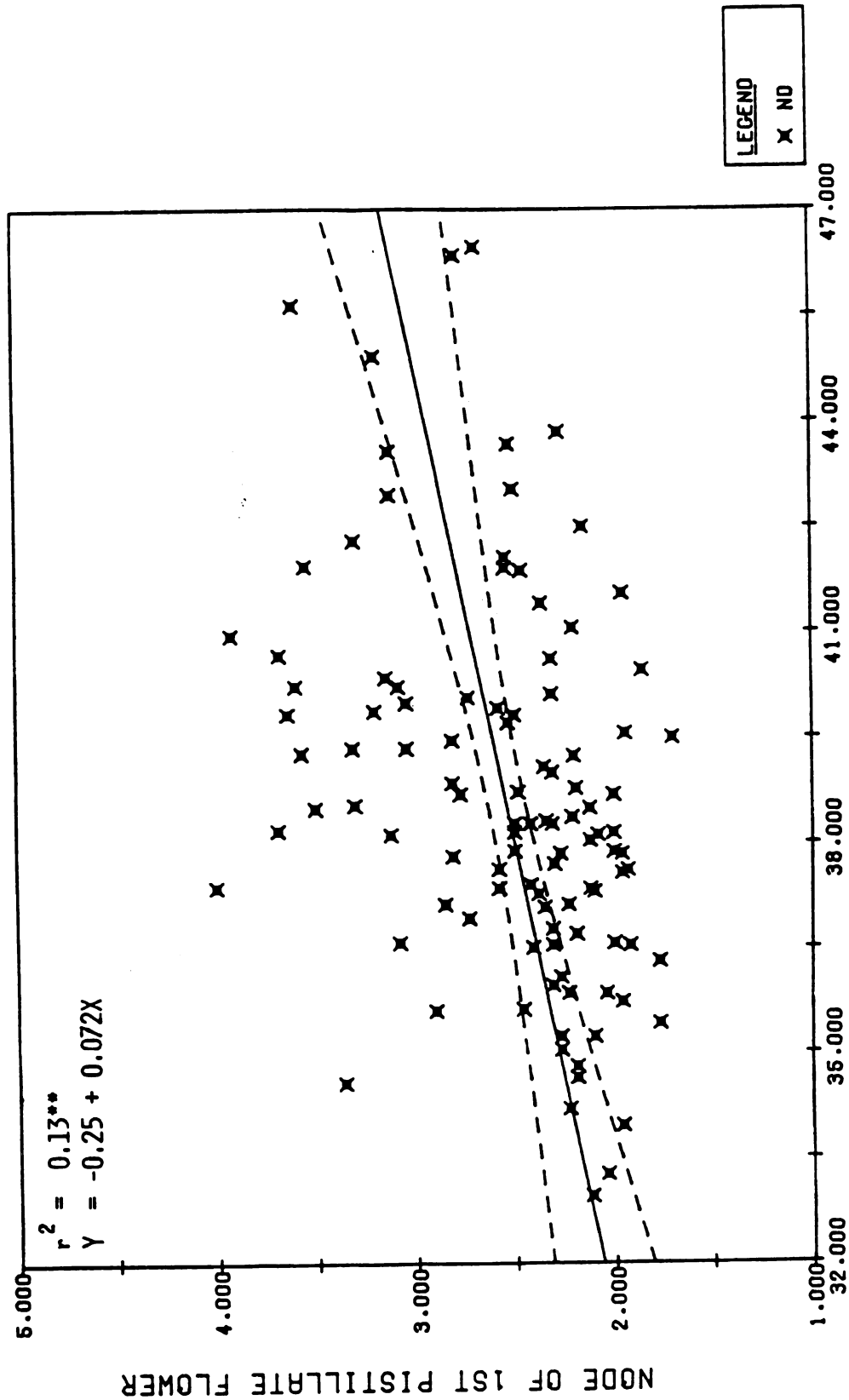

FIG. 1. RELATIONSHIP BETWEEN FLOWERING TIME AND FIRST-PISTILLATE FLOWER IN PARTHENOCARPIC PICKLING CUCUMBER.

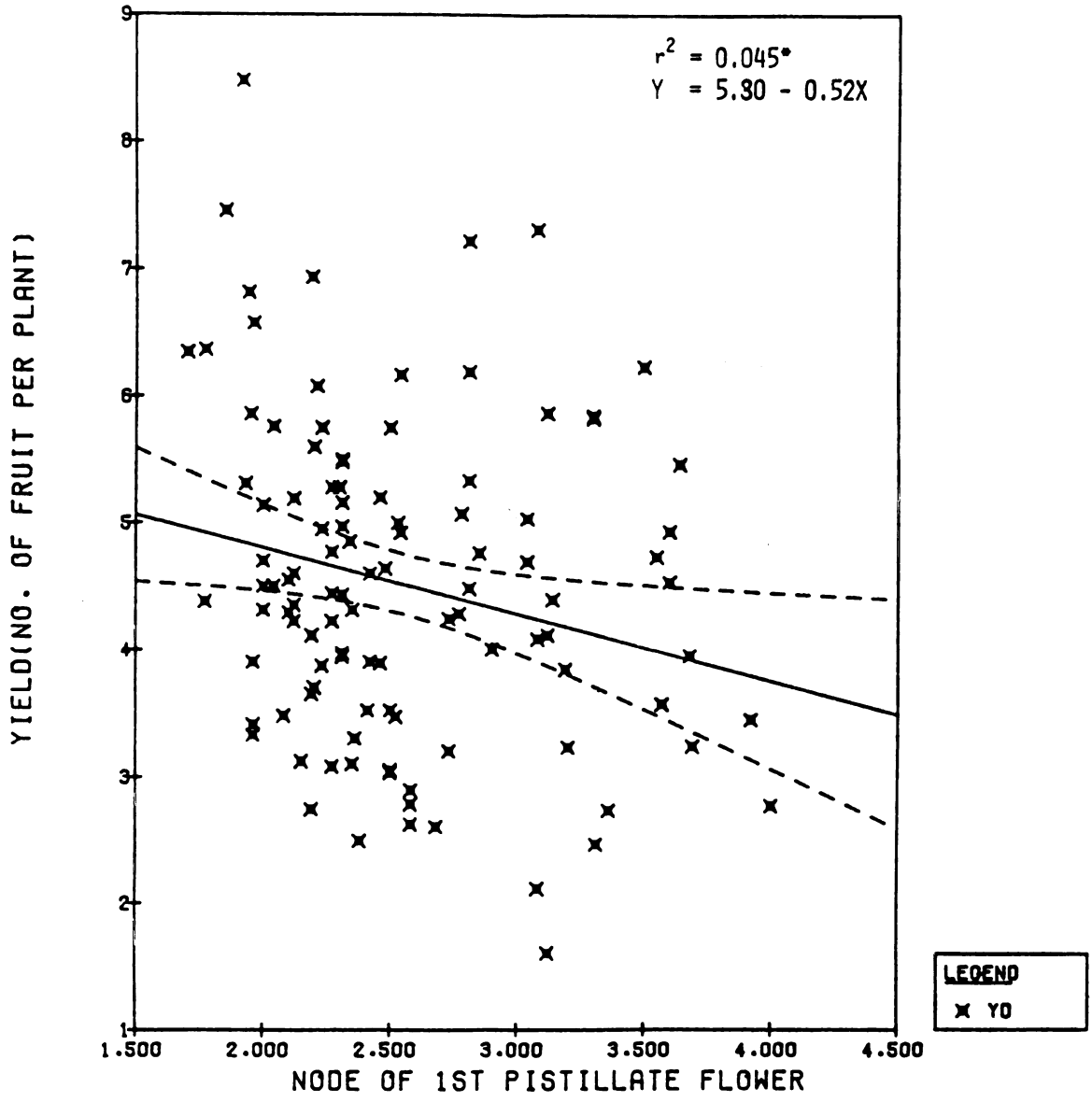

FIG. 2. RELATIONSHIP OF FIRST-PISTILLATE FLOWER TO PARTHENOCARPIC YIELD (FRUIT NO.) IN GYNOECIOUS CUCUMBER.

was arbitrarily decreased to 4.2, 7 hermaphroditic lines were over the limit of 98% gynoecious plants (Tables 4 and 5; Fig. 3).

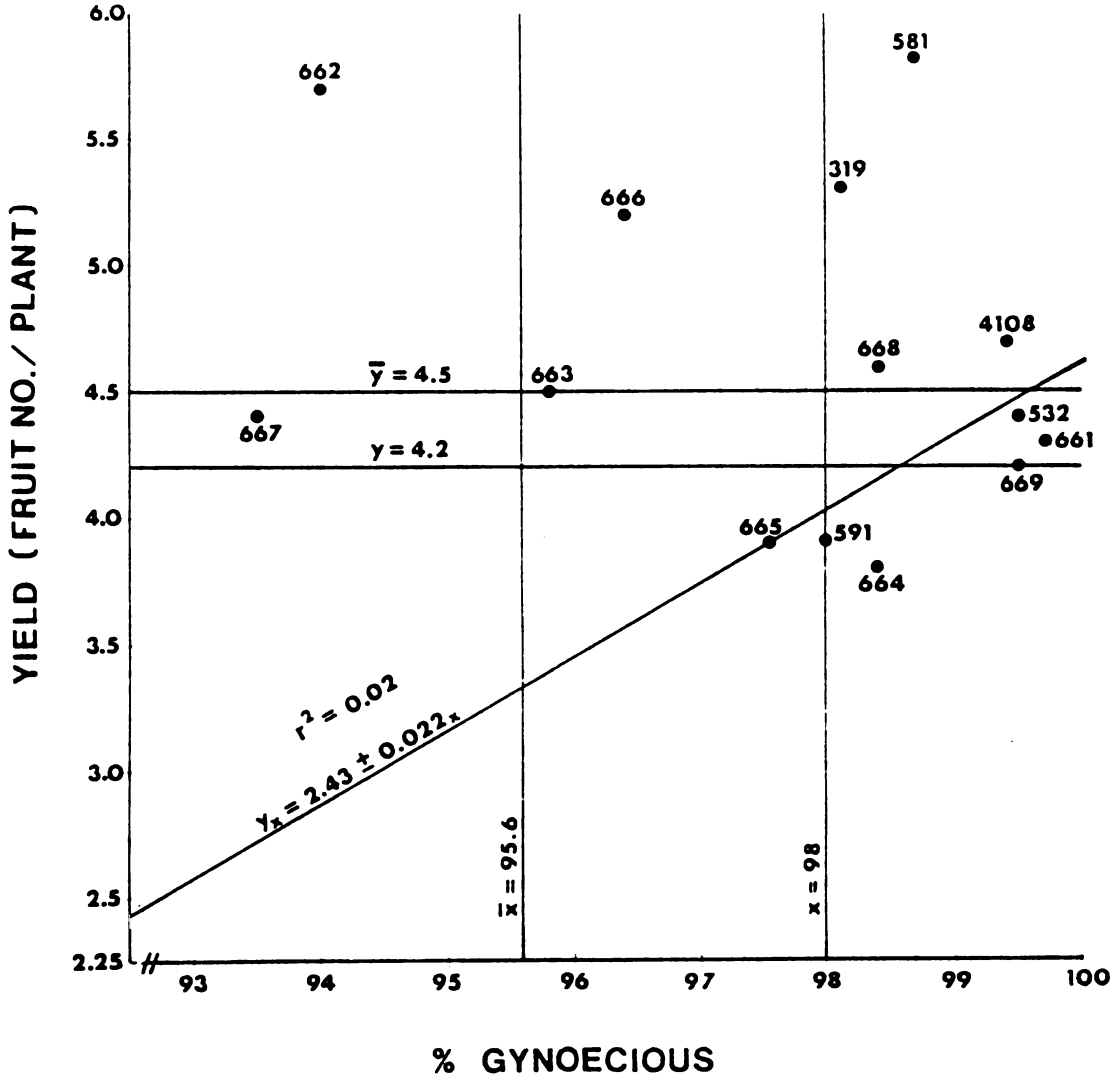

Fig. 3 : Effects of gynoecious expression on parthenocarpic yield and selection for out - standing hermaphroditic cucumber lines.

DISCUSSION

The top cross method has been used extensively in corn and other crops to evaluate and select inbred lines according to their GCA for yield and other economic characteristics (2,3,6,11,12,20, 30,32). Both the efficiency of the top cross method and type of tester(s), as well as number of testers, have been established for several different crop species (6,11,12,13,17,30,31).

In the present study, a modification of the top cross method was made by controlling the crosses and then creating so-called "controlled" top crosses. This reduced the time and cost from a practical standpoint for the evaluation of a relatively large array of parent lines in a hybrid cucumber program. The analysis of variance revealed highly significant differences among the hermaphroditic pollen parents for the number of days to first-pistillate flower, node no. of the first-pistillate flower, yield, and % gynoecious plants.

Days-to-flowering. Flowering time (days to first-pistillate flower) had a moderately high heritability estimate of 64% which approximated a previous report (19). Moreover, this yield characteristic was previously found controlled by one dominant gene (26) or else relatively few partially dominant genes (19).

Estimation of maturity via days to first-pistillate flower was the best prediction criterion with a high correlation (r=.84, 9; r=.82,19). According to the relatively high heritability (64%; Table 6) for flowering time among the hermaphroditic pollen parents and the dominance of this character, selection could be effectively used to develop parthenocarpic hybrids with different maturities.

Node of first-pistillate flower. The hermaphroditic pollen parents demonstrated differences for the nodal position of the first-pistillate flower on the main stem, which suggested genetic control of this trait as reported earlier (9,19,25). The nodal position for the first-pistillate flower occurred with a moderately high heritability ratio of 0.63 which was higher than previously reported (19). These researchers estimated a ratio of 0.11 to 0.26; however, they reported that the character was simply inherited and the minimum no. of effective factors was 1 to 3 genes. As with time of flowering, no. of nodes to first-pistillate flower was a reasonably good measure of maturity (25). Accordingly, selection among the hermaphroditic pollen parents for early, intermediate, and late maturity "combiners" could be accomplished through selection for flowering on appropriate nodes.

Gynoecious expression. Hybrids with 99.5% pistillate flowers (gynoecious) were obtained from crosses between gynoecious seed parents and hermaphroditic pollen parents (Table 4). This is considered advantageous for hybrid cultivar development based on the use of hermaphroditic parents (14,22,24). All of the hermaphroditic lines, except HP-61, combined well for gynoecious

expression (93 to 99% gynoecious, Table 4).

Selection among the hermaphroditic lines for those which combine well for gynoecious expression when crossed with gynoecious lines could be quite effective. The relatively high heritability of 73% suggested that the environment played a minor role in the expression of gynoecious expression. The expected gain in gynoecious expression was from 1.8 to 2.9% more than the mean of the top crosses when selection was exercised on the hermaphroditic lines that produced crosses with 98 and 99.5% gynoecious progenies, respectively. For the same hermaphroditic lines, the expected increase ranged from 5.7 to 6.8% over the mean for the gynoecious parents (check).

Yield (average number fruits/plant). Fruit number was used to judge the productivity and to evaluate the yield performance of the hermaphroditic male parents in the top crosses. Fruit number was used instead of weight since time-of-harvest influenced fruit weight. Fruit number was also used by other investigators to estimate cucumber yields (9,24). Moreover, the use of fruit no. was highly correlated with dollar/acre values on a once-over harvest basis ($r=.84$; 28). Furthermore, the genetic and phenotypic correlation between fruits no. and dollar/acre value was also high (29).

Genetic variation for yield among the hermaphroditic parents, due to additive genetic effects, was about 20% of the phenotypic variance. Hence, the no. of parthenocarpic fruit/plant was inherited as a quantitative trait which agrees with a recent report for seeded

fruit yields (29). They indicated the genetic variance for fruit no. was additive with a heritability of 17% based on full-sib families. However, they reported a high genotype by environment interaction variance. Other data (24) demonstrated differences in fruit counts for F_1 hybrid plants derived from crosses of two hermaphroditic with two gynoecious lines. The present study found a wide range for yield of almost 3 fruit/plant among the progenies of the hermaphroditic lines. This variation for parthenocarpic yield suggests the development of high yielding parthenocarpic hybrids. These hybrids could be produced by crossing hermaphroditic pollen parents with high GCA for yield by gynoecious seed parents with high yields.

Relationships between characters. The linear relationship between days-to-flowering and node of the first-pistillate flower indicated that the early pollen parent lines bear the first-pistillate flowers on lower nodes in comparison to intermediate and late lines (Table 3; Fig. 1). These data could be used to predict and select parent lines to produce hybrid cultivars with different maturities in a breeding program as suggested previously (25).

Days to flowering was not associated with femaleness (Table 7). Therefore, selection for differing maturities could be practiced while maintaining the desired sex expression. Recent workers also found that flowering time and femaleness were not associated (19).

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PART II

Diallel Analysis Among Six Gynoecious Lines

Abstract. Six gynoecious inbred lines were evaluated using two diallel analysis programs. A complete diallel of F_1 and half-diallel of F_2 generations, including parents, were used to elucidate the genetic system based on 3 parthenocarpic yield characters. Genetic differences among the 6 parental lines were apparent for all characters. Highly significant differences for GCA and SCA effects were found for all characters which suggested that both additive and non-additive genic effects were important. However, additive effects were determined more important. Tests for reciprocal differences were not significant for any of the yield characters indicating no maternal effects on yield.

According to the diallel analysis procedure of Jinks and Hayman, recessive genes were acting in the direction of higher yields and dominant genes in the direction of lower yields. The heritability estimates were low for all 3 yield characters (0 to 32%).

Significant ratios for heterosis and heterobeltiosis were obtained for all 3 yield characters. However, the estimates for inbreeding indicated that only fruit number on the main stem seemed to display significant depression. Accordingly, the development of parthenocarpic hybrid cvs. with high yield potential would require that both parents possess genotypes with high yield ability.

INTRODUCTION

The combination of gynoecious expression with parthenocarpic fruiting for out-of-door production was suggested by cucumber breeders. The advent of mechanical harvest in a once-over destructive system dictates a uniform set with high yields of fruits. Parthenocarpic pickling cucumbers are suggested to produce higher yields and quality than conventional seeded cultivars (2,7,24).

However, relatively little is known about the inheritance of parthenocarpic yield in gynoecious cultivars under outdoor conditions. A number of studies were made with glasshouse cultivars under glasshouse conditions. Hawthorn and Wellington (1930) suggested that parthenocarpy behaved as a recessive trait. However, Pike and Peterson (1969) suggested one gene with incomplete dominance. Juldasheva (1973) and Meshcherov and Juldasheva (1974) assigned a single recessive gene for parthenocarpy. Moreover, Kvasnikov et al. (1970) reported parthenocarpy under the control of many incompletely recessive genes. A recent report by Ponti and Garretsen (1976) suggested that 3 independent, isomeric major genes with additive action, together with non-allelic interaction were responsible for parthenocarpy. They used a partial diallel under greenhouse

Recently, Ponti and Garretsen (1976), in Holland, used a partial diallel under greenhouse conditions to study parthenocarpy. They concluded that both additive and non-allelic interaction of the genes were important. Moreover, they reported a high heritability estimate of 0.88; however, the scope of the experiment was limited to 5 replicates with 3-plant samples.

Hybrid vigor is well documented in cucumber. Yield of the F_1 generation was found to exceed the high parent in many cases (3,4,9, 11,14,26,27). A recent report (9) showed an inbreeding depression for yield in pickling cucumber. Basic information about the genetic system for parthenocarpy would assist plant breeders in choosing an efficient breeding program for this trait. Diallel cross analysis (12,15,16) could provide valuable information on both the genetic and environmental components of variation for parthenocarpic yield. Diallel analysis for combining ability (10) can be used as a tool for evaluating an array of inbred lines in hybrid combinations. Moreover, it provides information on the amount and relative magnitude of the additive and non-additive gene effects.

The objectives of this study were to evaluate gynoecious cucumber lines for parthenocarpic yield and elucidate the genetic system which conditions parthenocarpic yield. This would be useful information for choosing an appropriate method for breeding programs to improve parthenocarpic pickling cucumber.

MATERIALS AND METHODS

A complete diallel was constructed from 6 cucumber genotypes by controlled pollinations under greenhouse conditions in 1976. The gynoecious lines were Gy3, Gy14, MSU 92G, MSU 364G, MSU 402G and MSU 921G and were previously described by El-Shawaf and Baker (8). Staminate flowers were produced on gynoecious plants by recommended procedures with $GA_{4/7}$ application (23) to produce an abundance of F_1 seed. Seed of each of the 30 F_1 crosses in the diallel was produced from 8 plants of the seed parent cross-pollinated by 8 plants of the pollen parent. The 6 sib (S_1) generations were similarly produced. The F_2 seeds were readily obtained by selfing the half-diallel following $GA_{4/7}$ treatment.

The S_1, F_1, and F_2 seeds were planted in the field at the Horticultural Research Center near E. Lansing on July 7, 1977, in a randomized complete block design with six replicates. Thus, each block/replicate consisted of 51 single-row plots spaced 152 cm apart and 7.6 m in length. A total of 60 seeds for each generation was sown per plot and seedlings were blocked to 30 cm. Standard cultural practices were used with sprinkler irrigation (22).

Staminate flower buds were removed daily from infrequent predominantly female (PF) plants to avoid seeded fruit set. A sample of 15 plants was randomly selected from each plot for eventual yield measurements. Plants were harvested individually when the largest fruit reached 5 cm in diameter. Individual plants were pulled at the time of harvest and fruits counted from the main stem and from the laterals separately. Fruits from sizes 2 to 5 cm diam were counted; then, all fruits per plant were weighed. All large fruits ($\geq$5 cm diam) from individual plants were cut to confirm parthenocarpic fruitation. Plants with any fruits that contained one or more seeds were discarded from further analysis.

Firstly, the complete diallel was subjected to the analysis of variance of combining ability. The procedures of Griffing (1956) Method 1, Model 1, were utilized. Secondly, data of both F_1 and F_2 generations were subjected to diallel cross analysis (Jinks - Hayman Method). A computer program developed by Lee and Kaltsikes (1971) was used to compute all of the statistics for diallel regression analysis and variance-covariance components and their standard errors. The mean values were obtained for the diallel table in each block (replicate). Each block was then treated as a complete experiment to obtain the variance and covariance components and the diallel regression analysis. The means of the variances and the covariances over replicates were used to obtain variance components estimates and standard errors.

The variances and covariances of the diallel (Hayman, 1954; Jinks and Hayman, 1953; Jinks, 1954) were:

Vp = variance of the parents = D + E

$\bar{V}r$ = mean variance of the arrays =

$$\tfrac{1}{4}D + \tfrac{1}{4}H_1 - \tfrac{1}{4}F + (E + \tfrac{1}{2}(n-1)E')/n$$

$V\bar{r}$ = The variance of the means of the arrays =

$$\tfrac{1}{4}D + \tfrac{1}{4}H_1 - \tfrac{1}{4}H_2 - \tfrac{1}{4}F + (E + \tfrac{1}{2}(n-2)E')/n$$

$\bar{W}r$ = mean covariance between the parents and the arrays =

$$\tfrac{1}{2}D - \tfrac{1}{4}F + \frac{1}{n}E$$

The genetic components estimated by the Jinks and Hayman Model in the computer program were D, H_1, H_2, and F. These can be defined as follows:

D = component of variation due to additive effects of the genes = Vp - E.

F = the mean of the covariation of additive and dominance effects over the arrays = 2 Vp - 4 $\bar{W}r$ - 2(n-2)E/n.

H_1 = component of variation due to the dominance effects of the genes = Vp - 4 $\bar{W}r$ + 4 $\bar{V}r$ -(3n-2)E/n.

H_2 = H_1 $(1-(u-v)^2)$ = dominance indicated asymmetry of positive and negative effects of genes = $4\bar{V}r - 4V\bar{r} + 2E$, and

E = the expected environmental component of variation.

Gene action and dominance were also interpreted from Wr/Vr regression of each trait (Mather and Jinks, 1971). The limiting parabola for graphing was constructed by plotting Vr, $Wr^2 = (VrxVp)^{\frac{1}{2}}$ points.

RESULTS

Heterosis and inbreeding depression. The overall means for each parent and its hybrid combinations were calculated (Table 1). Significant differences among the parental lines were detected for all 3 yield measurements. Yields of fruits per main stem ranged from 2.7 (921G) to 4.5 (364G) and fruits on laterals ranged from 0.6 (402G) to 9.7 (364G). Yields as fruit weight ranged from 332 (Gy3) to 480 g (364G) per plant.

The F_1 reciprocal means were pooled as there were no differences between reciprocals (Table 2). The F_1 hybrids displayed higher means than the midparents for all characters (Table 1). The F_1 means also exceeded the F_2 means for fruit numbers on the main stem and fruit weight/plant, but did not exceed the F_2 mean for fruit numbers on the laterals.

Estimates for heterosis were relatively high at 54%, 28%, and 22% for fruits on the main stem and laterals and their weight per plant, respectively (Table 1).

Heterobeltiosis, calculated as the percent difference between the F_1 and its higher parent average, was 18 and 8% for fruit number on main stem and weight/plant, respectively. Inbreeding depression was estimated at 40% for fruits on the main stem, but approximated zero and 4% for fruits on the laterals and fruit weight per plant, respectively.

Table 1. Parthenocarpic yield evaluation from 6-parent diallel of gynoecious pickling cucumbers grown in the field during the summer of 1977.

MSU parent line no.	Yield per plant[z/]								
	Fruit no. on main stem			Fruit no. on laterals			Total weight (g)		
	$\bar{P}$	$\bar{F}_1$	$\bar{F}_2$	$\bar{P}$	$\bar{F}_1$	$\bar{F}_2$	$\bar{P}$	$\bar{F}_1$	$\bar{F}_2$
Gy3	3.3b	5.2a	3.3a	5.2b	8.3c	7.3a	331.7a	490.1a	480.1a
Gy14	2.9a	5.3a	2.9a	5.4b	8.4c	8.4b	400.4b	545.0a	515.8a
92G	3.4b	5.1a	3.1a	6.7bc	6.3b	6.0a	479.7c	493.1a	514.4a
364G	4.5c	5.7b	3.4a	9.7d	8.5c	9.0b	485.0c	552.9a	541.2a
402G	3.5b	5.1a	3.4a	0.6a	3.9a	5.4a	466.2cb	555.1b	503.5a
921G	2.7a	5.1a	3.0a	7.6c	9.5c	8.8b	433.3b	523.9a	483.8a
Mean	3.4	5.3	3.2	5.9	7.5	7.5	432.7	526.7	506.5
Avg. % heterosis[y/]	54.4**			27.8**			21.7*		
Avg. % heterobeltiosis	17.7**			-22.6**			8.5		
Inbreeding depression (%)	39.6**			0.0			3.8		

[z/] Means within columns followed by the same letter are not significantly different at the 0.05 level probability according to Tukey's Multiple Range Test.

[y/] * and ** are significantly different from zero at the 5 and 1% levels of probability, respectively. Average % heterosis = $(\bar{MF}_1 - \bar{MP}/\bar{mp}) \times 100$; average % heterobeltiosis = $(\bar{MF}_1 - \bar{HP}/\bar{HP}) \times 100$; and % inbreeding depression = $(\bar{MF}_2 - \bar{MF}_1/\bar{MF}_1) \times 100$.

Combining ability. The ANOVA for the 3 yield characters was conducted on the mean performance of the complete diallel (6x6) based on Griffing's (1956) Method 1 with Model 1 (Table 2). Significant differences were found for all yield characters as regards GCA and SCA effects, but not for reciprocal effects. The mean squares for GCA were greater than SCA for all yield characters. The ratios of 6^2 GCA: 6^2 SCA were estimated at 16:1, 46:1, and 8:1, for fruits on the main stem, fruits on the laterals, and fruit weight/plant, respectively.

The estimation of GCA effects (Table 3) from the diallel showed that 364G had the higher value (+0.39) for fruit number on main stem; whereas 921G was a poor combiner for that trait. The GCA effects for fruits on main stems were not significant for the other parents.

For parthenocarpic fruits on the laterals, 4 lines displayed positive and significant values for GCA effects. The line, 921G, had the greatest GCA (1.96) followed by 364G (1.50), Gy14 (0.65) and Gy3 (0.59). The poorest combiner was 402G (-3.85) followed by 92G (-0.86).

The highest GCA values for fruit weight/plant were exhibited by 364G (30.5) and 402G (29.1); whereas, Gy3 and 92G were considered poor combiners with significant negative values.

The SCA effects for parthenocarpic yield were also estimated from the 6-parent diallel (Table 3). However, only one of the F_1 crosses displayed significant positive effects for fruit number on the main stem, Gy3 x 921G (0.80). There were two F_1 crosses

Table 2. ANOVA for GCA, SCA and reciprocal effects of parthenocarpic yield estimates from a complete diallel (6x6) of pickling cucumber.

Source	d.f.	Mean squares[z/]		
		Main stem	Laterals	Weight
GCA	5	0.5 *	53.7**	10722.5*
SCA	15	0.2 *	7.4**	8583.0*
Reciprocals	15	0.07	1.5	2832.1
Error[y/]	2124	0.07	0.8	1463.7
6^2GCA:6^2SCA		16:1	46.1:1	7.7:1

[z/] * and ** are significant at the 0.05 and 0.01 level of probability, respectively.

[y/] The error term was estimated from the variance within plots divided by 60 (number of replications x number of plants per plot).

Table 3. Combining ability for parthenocarpic yield in pickling cucumber from a complete diallel (6x6) of gynoecious hybrids grown in the summer of 1977.

Parent	Yield of fruits	SCA effects[z/]						GCA effects[z/]
		Gy3	Gy14	92G	364G	402G	921G	
Gy3	No./main stem	0.12	-0.10	-0.30	-0.70*	0.10	0.80*	-0.03
	No./laterals	3.23	-2.10*	0.80	-0.10	0.60	3.90*	0.59*
	Wt./plant	86.02	22.30	4.90	-20.70	129.50*	-5.10	-46.70*
Gy14	No./main stem		-0.22	-0.10	0.20	0.20	0.01	-0.06
	No./laterals		-3.14	-0.16	2.40*	1.27*	1.68*	0.65*
	Wt./plant		-130.28	47.60*	77.90*	55.60*	-28.50	9.70
92G	No./main stem			0.33	0.30	-0.13	-0.12	-0.08
	No./laterals			1.23	0.48	-1.00	-1.40*	-0.86*
	Wt./plant			9.05	28.30	-91.80*	2.10	-50.30*
364G	No./main stem				0.50	-0.20	-0.23	0.39*
	No./laterals				-0.51	-1.80*	-0.50	1.50*
	Wt./plant				-87.13	-46.70*	48.30*	30.50*
402G	No./main stem					0.40	-0.42*	-0.04
	No./laterals					1.09	-0.21	-3.85*
	Wt./plant					-103.20	56.50*	29.10*
921G	No./mainstem						-0.20	-0.18*
	No./laterals						-3.50	1.96*
	Wt/plant						-73.22	-2.30

	Main stem	Laterals	Weight
SE(gi)	0.07	0.23	10.10
SE(Sii)	0.22	0.72	31.90
SE(Sij)	0.16	0.52	23.00

[z/] *is significantly different from zero at the 0.05 level of probability.

which exhibited significant negative effects for SCA; viz., Gy3 x 364G (-0.70) and 402G x 921G (-0.42). Four of the 15 F_1 combinations showed significant positive SCA effects for fruit number on laterals. One of the F_1 parents was Gy14 which was involved in 3 of the 4 crosses, Gy14 x 364G, Gy14 x 402G and Gy14 x 921G. The other and highest cross for SCA was Gy3 x 921G (3.90). There were 3 crosses with significant negative effects for SCA of yields on laterals. Six of the 15 crosses showed significant positive effects for yield based on fruit weight/plant. The parents, Gy14 and MSU 402G, accounted for 5 of the crosses. The cross of Gy3 x 402G had the highest value of 129.5 for SCA effects. Only two crosses had significant negative effects for SCA; viz., 92G x 402G and 364G x 402G.

Diallel cross analysis. Complete validity of Jinks-Hayman's diallel cross analysis is based on fulfillment of several assumptions. These assumptions are: (1) homozygous parents, (2) diploid segregation, (3) no reciprocal-cross differences, (4) no multiple alleles, (5) no epistasis, (6) independent gene distributions, and (7) no genotype-environment interactions within locations and years. The failure of the fulfillment of any of these assumptions limits the analysis to some degree (Crumpacker and Allard, 1962). Accordingly, the assumptions were tested to determine the adequacy of the model. For assumptions 1 and 2, Cucumis sativus is a diploid (2n=14) which segregates in a diploid pattern (6,27).

Since the gynoecious lines used in this investigation have been inbred for several generations and are phenotypically homogeneous, they are assumed to be homozygous. The test for reciprocal differences (Table 2) indicated no significant differences due to maternal parents for these 3 yield traits which fulfills the third assumption. Moreover, two general tests were used (20). These tests were:

(1) The ANOVA for the quantity (Wr-Vr); where, Vr is the array variances and Wr is the parent-offspring covariances. This test was conducted for 6 arrays in each of 6 replications for F_1 and F_2 generations (Table 4). The value of Wr-Vr was, as expected, constant over arrays. Thus, all the assumptions of the diallel cross analysis were valid and the environmental effects were zero (1,15,20). Mather and Jinks (1971) reported that if Wr-Vr values were constant, the additive-dominance model with independent gene distribution is adequate. Moreover, the constancy of Wr-Vr values indicated the absence of epistasis (1).

(2) The regression coefficient of (Wr,Vr) is expected to be significantly different from 0, but not significantly different from 1.0 if all assumptions are valid. The regression coefficients for these 3 yield traits for both the F_1 and F_2 generations were not significantly different from 1 except for fruit number on the laterals in the F_2

Table 4. The ANOVA for Wr-Vr values involving parthenocarpic yields of gynoecious pickling cucumber in out-of-doors production.

Source of variation	d.f.	No. of fruit per plant				Yield (g)/plant	
		Main stem		Laterals			
		F_1	F_2	F_1	F_2	F_1	F_2
Replication	5	0.3092	0.98	88.18	349.54	337108716.3**	110714407.8
Array (Lines)	5	0.1762	0.19	61.96	246.10	13874918.0	49650910.7
Error	25	0.0861	0.36	39.94	152.99	33977759.5	57682923.5

z/** is significant at the 0.01 level of probability.

Table 5. (Vr, Wr) regression coefficients.

Yield measurement	Generation	Coefficient	t-values b = 0	t-values b = 1
1 - Fruit no. main stem	F_1	0.78	0.89	0.31
	F_2	0.98	10.40**	0.19
2 - Fruit no. laterals	F_1	0.98	1.40	0.03
	F_2	0.40	2.70	3.98**
3 - Weight (g)/plant	F_1	0.43	0.78	1.02
	F_2	0.55	2.07	1.72

**Significant at the 0.01 level of probability.

generation (Table 5); neither were they significantly different from 0 except for fruit number on the main stem in the F_2 generation. Therefore, fruit number on the main stem in the F_2 generation was the yield trait which satisfied the test while the other 2 were partially fulfilled. The estimation of population parameters are possible with partial fulfillment (Hayman, 1954), but these estimates will be less reliable than those traits which completely satisfy this assumption $1 \geq b > 0$.

Mean estimates of genetic variances (D,F,H_1, and H_2) were calculated for both F_1 and F_2 generations (Table 6). The value of F was positive for number of fruit on the main stem in both generations which indicated a preponderance of dominant alleles. Conversely, F was negative for fruit number on laterals and for fruit wt/plant which indicated a majority of recessive alleles for these 2 yield traits. The value of D-H_1 for fruit number on the main stem indicated that additive gene effects were more important than dominance effects.

The average degree of dominance $(H_1/D)^{\frac{1}{2}}$ was 0.62 and 0.83 for fruit no. on the main stem in the F_1 and F_2 generations, respectively (Table 7). The crude estimate for frequency of negative (v) versus positive (u) alleles ($H_2/4H_1$) at loci which exhibit dominance in the parents (Crumpacker & Allard, 1962) is expected to be 0.25 if equally distributed among the parents. For this study, the number of fruits

Table 6. Genetic variance components for parthenocarpic yield of gynoecious pickling cucumber in outdoor culture.

Genetic parameter[z]	Yield[y]					
	Fruit number on					
	Main stem		Laterals		Weight (g)	
	F_1	F_2	F_1	F_2	F_1	F_2
D	0.71**	0.75**	-0.27	-1.20	-5573	-2667
H_1	-0.27	-0.51	1.69	68.66*	8206	7599
H_2	-0.26	-1.15*	2.14	75.50**	11914	25563**
F	0.32	1.78**	-17.47**	-23.40**	-12232	-15792**
D-H_1	0.98**	1.26**	-1.96	-68.85**	13778*	-10267*
E	1.01**	0.97**	12.71**	13.63**	15145**	12240**

[z] D = additive effects of genes; H_1 = dominance effects of genes; H_2 = dominance indicated asymmetry of positive and negative effects of genes; F = covariance of dominance and additive effects; E = error.

[y] **indicates highly significant at 1% level; *significant at 5% level.

on the main stem exhibited a ratio of 0.24 indicative of a symmetrical distribution of positive and negative alleles at the "non-additive" loci of the parental lines (Table 7). Asymmetric distributions of positive and negative alleles were noted among the parental lines for fruit no. on laterals and fruit weight/plant. The ratios for $H_2/4H_1$ were 0.31 and 0.36 for both characters, respectively.

The ratio of K_D/K_R for the F_1 generation indicated that more dominant than recessive alleles were present for fruit no. on the main stem ($K_D/K_R>1$). Conversely, the ratio of K_D/K_R was <1 for fruit number on laterals and fruit weight. This indicated an equal distribution of dominant and recessive alleles that control these 2 characters.

The number of groups of genes that exhibit dominance were estimated as K (Table 7). Values of 1.4, 1.3, and 2.5 were obtained for fruit no. on the main stem, on the laterals, and fruit weight/plant, respectively.

The narrow sense heritability ratios were .17 and .32 for fruit number on the main stem in the F_1 and F_2 (Table 7), respectively. The heritability ratios for fruit no. on laterals and fruit weight were negative and very small for both characters. They were not significantly different from 0; and were therefore set to zero (Table 7).

Table 7. Heritability parameters for parthenocarpic yield in gynoecious pickling cucumber for outdoor culture.

Genetic components[z/]	Yield: Fruit Number: Main stem F_1	Yield: Fruit Number: Main stem F_2	Yield: Fruit Number: Laterals F_1	Yield: Fruit Number: Laterals F_2	Yield: Weight (g) F_1	Yield: Weight (g) F_2
$(H_1/D)^{\frac{1}{2}}$	0.62	0.82	2.52	7.59	1.20	1.68
$H_2/4H_1$	0.24	0.56	0.31	0.27	0.36	0.84
K_D/K_R	2.13	-5.52	-0.86	-0.13	0.05	-0.27
Heritability	0.17	0.32	0.00	0.00	0.00	0.00
K	1.43	-0.19	1.36	0.15	2.5	0.61

[z/] $(H_1/D)^{\frac{1}{2}}$ = Average degree of dominance, $H_2/4H_1$ = average frequency of negative vs positive alleles, $K_D/K_R = \frac{(4DH_1)^{\frac{1}{2}} + F}{(4DH_1)^{\frac{1}{2}} - F}$ is the ratio of dominant to recessive alleles. Heritability is $\frac{1}{4}D/(\frac{1}{4}D - \frac{1}{4}F + \frac{1}{4}H_1 + E)$; $K = h^2/H_2$, an estimate of number of groups of genes exhibiting dominance, where $h^2 = 4(ML1-MLo)^2-4(n-1)E/n^2$, and (ML1-MLo) is the difference between the mean of the parents and the mean of their n^2 progeny.

The Wr/Vr graphs (Fig. 1-3) are the regressions of Wr (parent-offspring covariances) on Vr (parental array variances) and their limiting parabola in the 6-parent diallel for partheno-carpic yield. The (Wr,Vr) graph provides tests of significance for the presence of dominance ($b \neq o$) and the average degree of dominance (the sign of a); where b is the slope of the regression line and a is the intercept of b on Wr axis. According to the diallel theory (12,16), the regression of Wr on Vr is a straight line of unit slope (b is not significantly different from unity, but signi-ficantly different from zero). As indicated by Jinks (1954) and Hayman (1954), the position of the array points along the regression line depends on the relative proportion of dominant and recessive alleles present in the common parent of each array. Accordingly, the more recessive parents will be located farther from the origin because of a large array variance and covariance; whereas, parents with a preponderance of dominant alleles will have a low array variance and covariance which locates them nearer the origin.

The regression of Wr on Vr for fruit number on the main stem (Fig. 1) revealed that the slope ($b = 0.74 \pm 0.84$) was not signi-ficantly different from either 1 or zero ($t = 1.17$ and 0.39, respectively). Hence, the assumption of no genic interaction was not valid. The gynoecious lines Gy3 and 921G could be responsible for the slope not being different from zero. However, the array point for 364G indicated a preponderance of recessive genes for this yield trait; whereas, gynoecious lines Gy14, 402G, and 92G contain high frequencies of dominant genes.

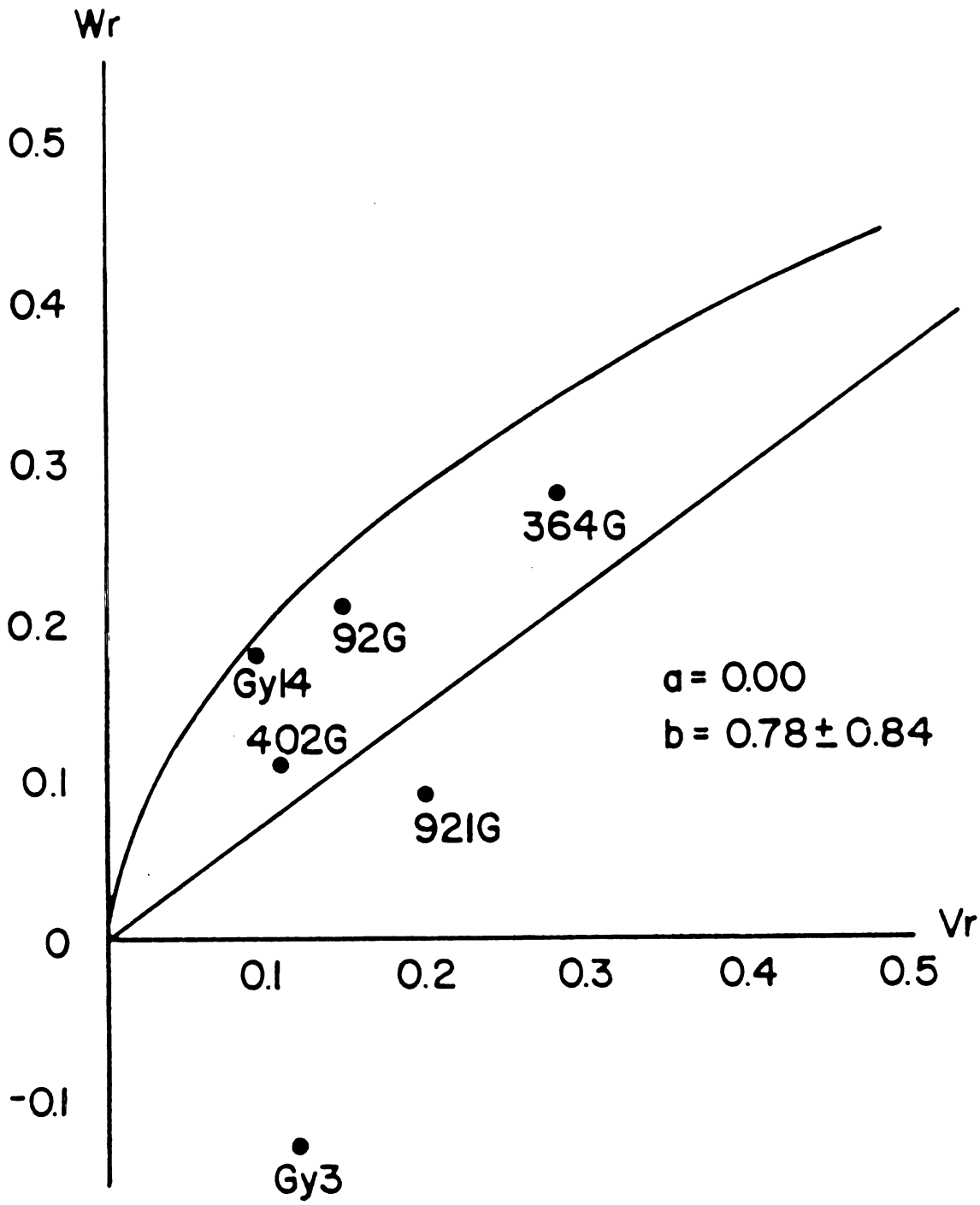

Figure 1. Wr, Vr regression for Fruit no. on main stem of F_1 parental arrays.

The Wr/Vr regression coefficient for yield as fruit number on laterals was neither significant from unity nor from zero (Fig. 2). The regression line intercept is below the origin (a = -2.9) which indicated over-dominance. However, the intermediate slope value is indicative of genic interaction which could obscure simpler genic effects. Line Gyl4 appeared to cause a deviation in the regression line. However, the position of the array point for 364G lies near the far right end of the regression line which suggested that 364G contains a preponderance of recessive genes. Conversely, Gy3 contains a preponderance of dominant genes. The remaining 2 lines (921G and 402G) contained slightly more dominant alleles than recessive; while, 92G contains a balanced proportion of dominant and recessive genes.

The regression of Wr on Vr for fruit weight per plant (b = 0.43 $\pm$ 0.55) was not significantly different from either zero or unity which again indicated possible genic interaction (Fig. 3). The array points were scattered on the graph. The negative large value of "D" (-5573) in Table 5, upsets the Wr/Vr graph. However, the two lines Gy3 and Gyl4 appeared to possess recessive genes responsible for relatively low yields (weight per plant).

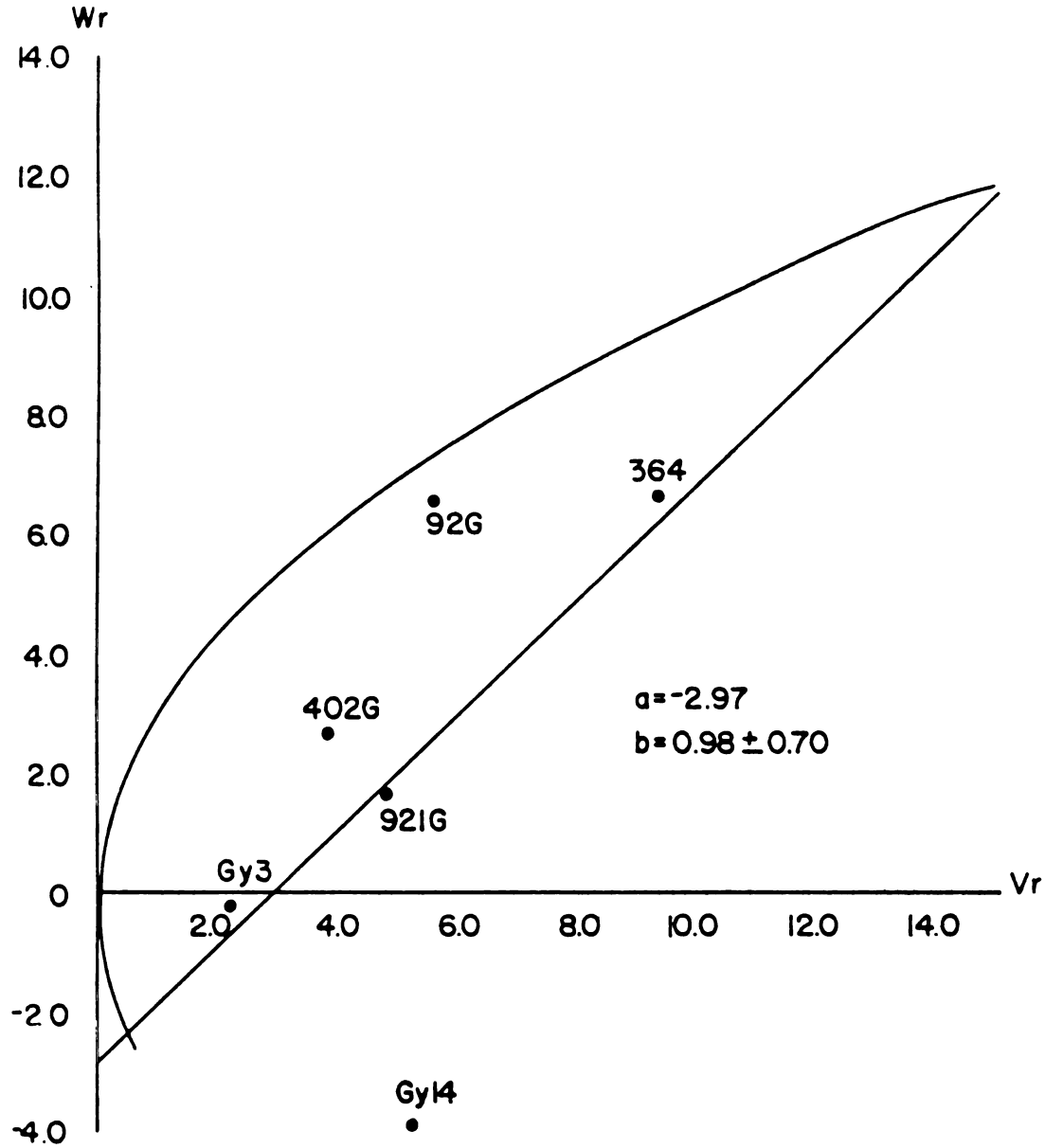

Figure 2. Wr, Vr regression for Fruit no. on Laterals of F1 parental arrays.

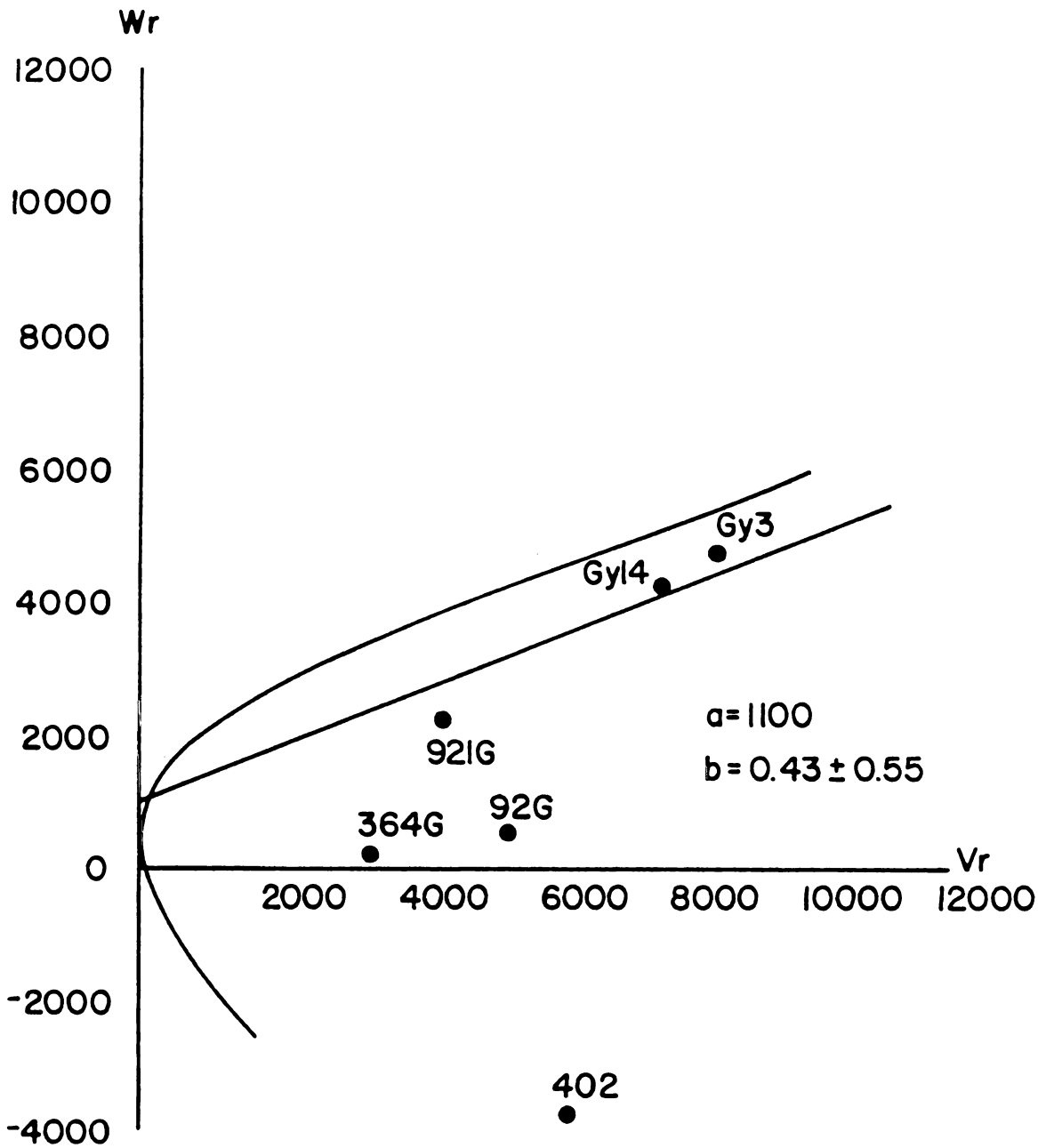

Figure 3. Wr, Vr regression for yield weight (g)/plant of F1 parental arrays.

DISCUSSION

Ample genetic variation among the gynoecious lines for parthenocarpic yield was evident. The mean squares for GCA and SCA were significant for all three yield determinants. This suggested both additive and non-additive genetic effects were responsible for the variability among the gynoecious lines. However, a comparison of the relative magnitudes of 6^2GCA vs 6^2SCA effects revealed that GCA was more important than SCA for all the parthenocarpic yield characters (Table 2). The magnitudes and directions of GCA and SCA effects were used to further elucidate the genetic system for parthenocarpic yield in the parents. Based on desirable horticultural characteristics and a high yield performance as parent lines and hybrid crosses (Tables 1 and 3), 4 lines were selected; namely, Gyl4, 364G, 402G, and 921 G for further evaluation in crosses with hermaphroditic lines.

Diallel analysis (12,15,16) provided further information about the nature of the genetic system conditioning parthenocarpic yield in gynoecious cucumber. However, partial fulfillment of the assumptions for analysis dictated caution in imposing interpretations.

For parthenocarpic fruiting on the main stem, genes with additive effects were important since D and D-H were significantly different from zero (P>0.01) in both the F_1 and F_2 generations (Table 6). Dominance was also involved (K = 1 to 2; number of groups of genes exhibiting dominance). However, the degree of dominance was partial and the magnitude and direction of dominance was -0.32. Moreover, the parental line 364G produced higher yields than the other 5 lines on the main stem. This high yield was controlled by a preponderance of recessive genes as shown from its position on the Wr/Vr regression lines (Figs. 1,2). Furthermore, the correlations between the parental order of dominance (Wr+Vr) and parental measurements (main diagonal) were high (0.49 and 0.82) for the F_1 and F_2 generations, respectively, which suggested that most of the recessive alleles in the parents were conditioning high yield. This agrees with Russian research (18) which showed that parthenocarpy was controlled by many recessive genes.

The remaining two yield characters; viz., fruit number on laterals and fruit weight per plant, were strongly influenced by genic interactions which likely obscured the additive and dominance gene effects. Therefore, the interpretation of the diallel analysis for these characters (Table 6 and 7, Fig. 2 and 3) must be cautiously extrapolated to other cucumbers and will not be discussed in detail.

Based on the information obtained from combining ability analysis (Griffing, 1956) and diallel cross analysis (Jinks, 1954;

and Hayman, 1954), the inheritance of parthenocarpic yield is quantitative with a heritability ratio somewhere between 0 and .32 depending on the yield trait in question. Parthenocarpic yield was controlled by both additive and non-additive gene effects. The same conclusion was drawn recently from an investigation of glasshouse cucumbers in The Netherlands (25). However, an earlier study (23), which proposed that one gene with incomplete dominance conditioned parthenocarpy, should not be confused with parthenocarpic yield, but demonstrated genetic control for parthenocarpic or non-parthenocarpic fruitation.

The presence of high levels of heterosis for the parthenocarpic yield characters together with an inbreeding depression for fruit number on the main stem were not surprising. Heterosis for yield was reported long ago (11) for seeded cucumber. Heterosis were also reported for various other cucumber characters (4,11,14, 26,27). Recently, Ghaderi and Lower (9) reported heterosis and an inbreeding depression were found for fruit number and weight and a fruit-bearing index in seeded fruitation of cucumber.

Based on the present study and previous reports, hybrid vigor can be utilized to improve the yield of parthenocarpic pickling cucumber. Therefore, gynoecious lines could be improved for parthenocarpy by using a recurrent selection breeding program followed by testing of inbred lines in hybrid combinations.

Superior parent lines and hybrid combinations with high parthenocarpic yields could be identified. If gynoecious-hermaphroditic crosses are used for hybrid cultivars, then a backcross program could be used to improve the parthenocarpic yield of the hermaphroditic (pollen) parent as a single gene is responsible for the difference in gynoecious and hermaphroditic expression (17).

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PART III

Combining Ability and Genetic Variances of G x H F_1 Hybrids

Abstract. The yield performance of 20 gynoecious parthenocarpic hybrids of pickling cucumber, obtained by crossing 4 gynoecious (G) lines (seed parents) with 5 hermaphroditic (H) lines (pollen parents) was determined in the field. Additive genetic variance was greater than non-additive genetic variance for all yield and associated characters, except gynoecious expression where non-additive was more important. The GCA for harvesting-time, gynoecious expression, and yield of the female parents was greater than that of the male parents in this population. The converse was true for flowering time. The dominance estimates indicated complete dominance for early flowering and over-dominance for gynoecious expression. The remaining characters appeared to be under the control of genes with additive effects and partial dominance. Narrow sense heritability ratios of half-sibs (males or females) differed considerably and were moderately high for some traits. Genetic and phenotypic correlations for flowering time and nodal position of first-pistillate flower and between the latter and yield of first harvest could be due to linkage and/or pleiotropic effects of genes that control these characters.

INTRODUCTION

The breeding and development of parthenocarpic cultivars of pickling cucumber with gynoecious expression for out-of-doors production has received increasing attention from cucumber breeders (1,6,17,25,26). The advantages of higher yield potentials and better quality of parthenocarpic over seeded cultivars seem apparent (1,6,17, 25,26,31).

Environmental conditions such as low light, short daylength, low night temperature and late season enhance parthenocarpic fruit set in pickling cucumber especially on well developed vines (11,24, 26,31,36). This phenomenon was confirmed experimentally by growing cucumber under controlled conditions (31). It was reported that genetically parthenocarpic and non-parthenocarpic lines produced more parthenocarpic fruit under short day and low night temperatures. This agreed with a previous report (26). In the latter study, the number of parthenocarpic fruits was dramatically increased in the last two weeks of the harvest when daylengths became short (12 hr).

Plant growth regulators, auxins, and auxin transport inhibitors, can also increase parthenocarpic fruit set in cucumbers (2,3,11,24).

The expression of parthenocarpic fruiting as a trait was suggested to be under monogenic control with incomplete dominance (25) for parthenocarpy. This was in agreement with an early report (13). Conversely, Juldasheva (15) suggested one recessive gene might be responsible for the expression of parthenocarpy. Moreover, Kvasnikov et al. (19) suggested that parthenocarpy was controlled by many recessive genes. Currently, Ponti and Garretsen (27) have assigned 3 independent, isomeric major genes with additive action together with non-allelic interaction as being responsible for this same trait. However, their model was based on data from glasshouse experiments with multiple harvests.

The heritability and genetic variances (nature and magnitude) for yield in parthenocarpic gynoecious pickling cucumbers for once-over mechanical harvest under field conditions are not reported. Such knowledge would be valuable to cucumber breeders to make breeding programs more efficient towards the development of parthenocarpic cultivars. The purpose of this investigation was to estimate genetic variance components and combining ability for yield and related characters in parthenocarpic gynoecious pickling cucumber from gynoecious-hermaphroditic crosses.

MATERIALS AND METHODS

Five hermaphroditic (H) parental lines from the MSU breeding program (661H, 669H, 319H, 581H and 532H) were crossed with four gynoecious (G) inbred lines (Gy14, 921G, 364G, and 402G) to make 20 F_1 (GxH) hybrids. These parental lines were described earlier (7,8). The 20 F_1 hybrids and 4 gynoecious lines were seeded in a randomized complete block design with five replications on June 22, 1978 at the Horticultural Research Center of Michigan State University near East Lansing. Each experimental plot was 7.6 M in length by 1.8 M in width. Plants were thinned to spacing of 25 cm in the row with a minimum no. of 20 plants/plot. Standard cultural practices were used (23) with sprinkler irrigation.

The field was isolated from other cucumbers by at least 3 miles. Before flowering, 10 plants were chosen at random to obtain data on flowering time, sex expression and nodal position of the first-pistillate flower. All plants were rogued daily for staminate floral buds. Plants which produced one or more staminate flowers were considered predominantly female (PF). Plots were hand-harvested when 10% of the fruits in a plot were judged over-sized (>5 cm diam) as suggested for once-over harvest (20) for two consecutive harvests. Data on both harvest-time and yield (avg no. and wt (g) fruit/plant) were obtained from plot yields.

Data from the G x H hybrids were analyzed using a two-way classification model with interaction to obtain general combining ability (GCA) and specific combining ability (SCA) estimates.

The sums of squares for the interactions, rep x male and rep x female, were pooled with the error term since these interactions were not significant. So, the formula for the statistical model was:

$$Y_{hijk} = \mu + \alpha i + \beta j + (\alpha\beta)ij + R_h + E_{hijk}$$

Where, Y_{hijk} = the observation for the k-th full-sib progeny in a plot of the h-th replication of the i-th hermaphroditic pollen parent and the j-th gynoecious seed parent. And, μ = the constant which is common to all observations; and αi and βj are the random effect of the i-th male parent and the j-th female parent, respectively; $(\alpha\beta)ij$ = random effect of the interaction of male and female parents; R_h = fixed effect of the h-th replication; and E_{hijk} = environmental effect and the remainder of the genetic effect between full sibs on the same plot and the following analysis of variance was used to estimate the genetic and phenotypic variances:

Source of Variation	d.f.	MS	EMS
Replications	R-1	MS_R	
Males	M-1	MS_m	$6^2_e + r6^2_{mf} + rf6^2_m$
Females	F-1	MS_f	$6^2_e + r6^2_{mf} + rm6^2_f$
Males x Females	(M-1) (F-1)	MS_{mf}	$6^2_e + r6^2_{mf}$
Error	(R-1) (Mf-1)	MS_E	6^2_e

where; 6^2_e = environmental variance, 6^2_m = variance of male effects, 6^2_f = variance of female effects, and 6^2_{mf} = variance due to interaction of male and female effects. The model description and the assumptions involved were reported previously (4,5,12).

The GCA's effects for the hermaphroditic male lines and the gynoecious female lines were estimated by subtracting the mean of all hybrids from the mean of each male line and female line in the hybrid combinations. The SCA's effects were obtained by summing the mean for a particular hybrid with the grand mean of all hybrids; then, subtracting the grand means for both the male and female line for that particular hybrid. The GCA:SCA ratios were estimated by $(6^2_m+6^2_f)/6^2_{mf}$.

The degree of dominance, $\bar{a}$, was estimated by the square root of $2\ 6^2_{mf}/6^2_m$; and the maternal effects as $(6^2_f-6^2_m)/2$. Narrow-sense heritability ratios were computed by multiplying 6^2_m or 6^2_f by 4, then dividing by 6^2_p which equals $(6^2_m+6^2_f+6^2_{mf}+6^2_e)$. Genetic and phenotypic associations between characters were estimated from both variance and covariance components (16,35). Genetic (rGij) and phenotypic (rPij) associations for character pairs, i and j, were estimated from:

$$rGij = (6_{mij} + 6_{fij}) \,/\, (6^2_{mi} + 6^2_{fi})^{\frac{1}{2}} (6^2_{mj} + 6^2_{fj})^{\frac{1}{2}}, \text{ and}$$

$$rPij = (6_{P(fs)ij}) \,/\, (6^2_{P(fs)i} \cdot 6^2_{P\,(fs)j})^{\frac{1}{2}} \quad ,$$

respectively. The numerators were estimated by covariance analysis and denominators from the analysis of variance.

RESULTS

The analysis of variance for the F_1 (GxH) hybrids revealed significant differences among the genotypes for most characters measured except yield from the second harvest (Table 1). Data were further analyzed using a two-way classification model with interaction. Since there were no significant interactions between replications with either male or female parent, the genotypic variation was partitioned into the variance due to the additive effects (GCA) of male and female parents and non-additive effects (SCA) by the interaction of male x female (Table 1).

The GCA's for the males (hermaphroditic parents) were significant for all characters except yield in the second harvest. The same was observed for the GCA's of the females (gynoecious lines) with the additional exception that flowering time was not significant. The SCA's were only significant for gynoecious expression.

By observation, the mean performance of GCA of the female lines in the hybrids was generally superior to that of the respective female parent (Table 2). Heterosis was expressed for earlier flowering (8 days) on earlier nodes (0.7 nodes) with earlier harvesting (7 days) and a higher gynoecious expression (10%), with more yield in the second harvest (no. fruit/plant or wt/plant) in contrast to the female parents. Yields

Table 1. ANOVA for yield and certain associated components for 20 gynoecious by hermaphrodite crosses of parthenocarpic gynoecious pickling cucumbers grown in the summer of 1978.[z/]

Factor	d.f.	Flowering time	Node no. 1st pistillate flower	Harvest-time	Gynoecious expression	Yield per plant			
						Harvest 1		Harvest 2	
						Fruit No.	Weight (g)	Fruit No.	Weight (g)
Replication	4	81.2**	2.26**	188.23**	11.00	1.65*	37812**	15.79**	190876**
Male	4	19.9**	0.65**	41.28**	98.5**	2.64**	25959*	1.75	34097
Female	3	4.55	0.90**	77.51**	211.67**	3.56**	53139**	1.72	55198
Male x female	12	4.21	0.14	10.45	89.17**	0.44	8440	2.84	26118
Error	76	2.16	0.14	10.01	14.68	0.57	8244	1.81	25702

[z/] * and ** are significant at the 5 and 1% level, respectively.

Table 2. Means of gynoecious F_1 (GxH) parthenocarpic hybrids in pickling cucumber with one parent in common and the mean of the common gynoecious seed parent.

MSU parent	Flowering time (days)		Node of 1st pistillate fl.		Harvest-time (days)		Gynoecious (%)		Yield per plant: Harvest 1[x] Fruit No.		Harvest 1[x] Weight (g)		Harvest 2[y] Fruit No.		Harvest 2[y] Weight (g)	
	F_1	P	F_1	P	F_1	P	F_1	P	F_1	P	F_1	P	F_1	P	F_1	P
Females[z]																
Gy14	37.8a	47.8a	2.1a	2.5a	58.1ab	68.6	99.2b	100b	1.2a	1.3a	124.9a	148.8a	3.6a	3.0a	362.8a	233.7a
921G	37.8a	46.3a	2.1ab	4.2b	60.1b	69.2	100.0b	100b	1.8b	2.0a	152.0ab	181.4a	3.3a	2.6a	263.5a	201.2a
364G	37.8a	45.3a	2.5b	2.5a	57.1ab	64.1	98.8b	100b	1.9b	1.0a	200.0bc	97.6a	3.0a	1.8a	345.3a	160.9a
402G	38.6a	44.2a	2.3ab	2.4a	55.8a	59.2	93.6a	50a	2.0b	2.2a	226.9c	268.9a	3.2a	1.1a	360.6a	113.0a
Mean	37.7	45.9	2.2	2.9	57.8	65.3	97.9	87.5	1.7	1.6	176.1	170.4	3.3	2.1a	333.0	177.2
Males[z]																
661H	38.1ab	--[w]	2.2ab	-	57.4a	-	99.5a	-	1.2a	-	145.7a	-	3.0a	-	288.2a	-
669H	36.8a	-	2.2ab	-	57.2a	-	99.0a	-	1.5ab	-	160.3a	-	3.3a	-	374.9a	-
319H	37.2ab	-	2.3ab	-	59.2a	-	95.5a	-	2.1b	-	207.1a	-	3.5a	-	375.5a	-
581H	39.3b	-	2.5b	-	59.6a	-	95.5a	-	1.8ab	-	145.2a	-	3.6a	-	297.9a	-
532H	37.2ab	-	2.1a	-	56.2a	-	100.0a	-	1.9ab	-	221.9a	-	3.0a	-	328.8a	-
Mean	37.7	-	2.2	-	57.8	-	97.9	-	1.7		176.1	-	3.3	-	333.0	-

[z] Mean separation within columns by Tukey's Multiple Range Test, 5% level.

[x,y] Harvest 1 and 2, respectively.

[w] Hermaphroditic pollen parents were omitted from the field because of bisexual flowering and resultant seeded, non-parthenocarpic fruit production.

for the first harvest were equivalent between female parents and their hybrids. Comparisons could not be made with the male lines and their respective hybrids since the male parents are bisexual which precludes parthenocarpic fruiting. A multiple comparison among female and male lines in hybrids (Table 2) revealed that 402G and 319H were the best two parent lines, respectively, for fruit no. per plant at the first harvest although not significant from several other lines.

The relative effects of GCA and SCA were obtained for all characters (Tables 3,4,5,6). The earliest flowering was observed for 669H and 364G among the male and female lines, respectively. They were considered to exhibit high GCA for early flowering; whereas, the male line, 581H, and the female line, 921G, showed low GCA for early flowering. Hybrid combinations of Gy14 x 581H, 921G x 669H, and 402G x 661H showed high SCA for early flowering. Notably, none of the parents involved in the first and third cross showed high GCA indicating that the early flowering of these hybrids resulted largely from SCA. The hybrid of 402G x 581H was the latest in flowering time (+1.62 days) as estimated by specific effects.

For nodal position of the first-pistillate flower, the female parent, Gy14, and male parent, 532H, showed high GCA for early pistillate flowers. The female line, 364G, and the male line, 581H, were the only parents with the first-pistillate flower appearing relatively late as explained by GCA effects. The hybrids of 921G x 669H, 402G x 661H, and 364G x 532H displayed high SCA for this same trait.

Table 3. Estimates of combining ability effects for flowering time and node position of first pistillate flower from 20 F_1 (GxH) hybrids of parthenocarpic gynoecious pickling cucumber in the summer of 1978.

MSU parents	SPECIFIC EFFECTS (SCA)				General effects of males (GCA)
		Females			
	Gy14	921G	364G	402G	
Males		Flowering time			
661H	+0.57	+0.30	+0.21	-1.10	+ 0.38
669H	+0.50	-0.97	+0.10	+0.37	- 0.89
319H	+0.16	-0.31	+0.96	-0.81	- 0.53
581H	-1.15	+0.24	-0.73	+1.62	+ 1.58
532H	-0.08	+0.73	-0.56	-0.11	- 0.53
General effects of females (SCA)	+0.12	+0.73	+0.10	+0.39	-
	Node number of the first-pistillate flower				
661H	+0.01	+0.02	+0.06	-0.20	0
669H	-0.02	-0.30	+0.05	+0.10	0
319H	+0.01	-0.02	+0.14	-0.14	+ 0.10
581H	-0.10	+0.10	-0.04	+0.20	+ 0.30
532H	-0.09	-0.10	-0.20	+0.11	- 0.10
General effects of females (GCA)	-0.20	-0.10	+0.30	+0.20	-

Table 4. Estimates of relative GCA and SCA effects for harvesting time and gynoecious expression based on 20 F_1 (GxH) partheno-carpic hybrids of pickling cucumbers grown in the summer of 1978.

MSU parents	SPECIFIC EFFECTS (SCA)				General effects of males (GCA)
			Females		
	Gy14	921G	364G	402G	
Males		Harvesting time			
661H	-0.42	+0.82	+0.70	-1.70	- 0.50
669H	+0.78	-1.38	-0.30	+0.90	- 0.70
319H	-1.57	-0.13	-1.33	-0.85	+ 1.25
581H	-0.22	-1.22	-1.90	-0.90	+ 1.70
532H	+1.43	-0.53	-1.05	+0.15	- 1.75
General effects of females (GCA)	+0.22	+2.18	-0.30	-2.10	-
		% Gynoecious plants			
661H	-0.80	-2.00	-0.40	+2.80	+ 1.60
669H	-0.30	-1.10	-3.90	+5.30	+ 1.10
319H	+3.20	+2.40	+3.60	-9.20	- 2.40
581H	-0.80	+2.40	+1.60	-3.20	- 2.40
532H	-1.30	-2.10	-0.90	+4.30	+ 2.10
General effects of females (GCA)	+1.30	+2.10	+0.90	-4.30	-

Table 5. Estimates of relative GCA and SCA effects for yield (first harvest) based on 20 F_1 parthenocarpic hybrids of pickling cucumbers grown in the summer of 1978.

MSU parents	SPECIFIC EFFECTS (SCA)				General effects of males (GCA)
			Females		
	Gy14	921G	364G	402G	
Males		Fruit number/plant			
661H	-0.05	-0.72	-0.61	-0.21	0.00
669H	-0.50	-0.65	-0.36	-0.46	+ 0.28
319H	-0.57	-0.46	-0.73	-0.22	+ 0.93
581H	-0.46	+0.06	+0.55	-1.05	+ 0.57
532H	-0.49	-0.72	-0.25	-0.54	+ 0.70
General effects of females (GCA)	-0.06	+0.60	+0.67	+0.78	-
		Fruit weight (g)/plant			
661H	+ 6.60	- 4.89	-30.62	+28.88	-30.33
669H	-15.78	+22.85	+ 9.55	+29.39	-15.75
319H	+ 1.80	+ 3.65	+32.94	-38.42	+31.02
581H	+39.76	+50.03	-17.57	-72.26	-30.85
532H	-32.17	-25.98	+ 5.83	+52.46	+45.93
General effects of females (GCA)	-51.17	-24.04	+24.38	+50.83	-

Table 6. Estimates of the relative GCA and SCA effects for yield (second harvest) based on 20 F_1 hybrids of parthenocarpic pickling cucumbers grown in the summer of 1978.

MSU parents	SPECIFIC EFFECTS (SCA)				General effects of males (GCA)
	Females				
	Gy14	921G	364G	402G	
Males	Fruit number/plant				
661H	-0.80	-0.34	+0.47	+0.68	- 0.28
669H	+0.31	-0.70	+0.12	+0.26	- 0.01
319H	-0.75	-0.09	+0.08	+0.76	+ 0.24
581H	+0.79	+0.51	-0.72	-0.60	- 0.36
532H	+0.30	+0.62	+0.04	-1.10	- 0.30
General effects of females (GCA)	+0.37	0.00	-0.24	-0.11	
	Fruit weight (g)/plant				
661H	-45.02	-1.20	+37.68	-8.52	-44.85
669H	+64.02	-145.57	+41.01	+58.55	-41.82
319H	-27.00	-21.09	+ 6.05	+42.02	-42.46
581H	-39.52	+56.60	-56.97	-39.15	-35.18
532H	-13.53	+111.27	-27.79	-69.94	- 4.24
General effects of females (GCA)	+29.76	-69.51	-12.25	+27.51	-

For harvesting time, only 402G showed high GCA effects with respect to early parthenocarpic fruit-set among the female lines. Conversely, the female line, 921G, demonstrated high GCA effects for late parthenocarpic fruiting. No outstanding values were observed for either GCA effects among the male lines or for SCA effects among their hybrids for days to first harvest.

The best combiners among the female and male lines in respect to gynoecious expression were 921G and 532H, respectively. The female line, 402G, was generally a poor combiner for gynoecious expression. High SCA were exhibited by 402G x 669H and 402G x 532H for gynoecious expression; whereas, low SCA was demonstrated by 402G when crossed with either 319H or 581H and by 364G x 669H. The high percent gynoecious expression of Gy14 x 319H and 364G x 319H can be explained by their high SCA.

The best GCA effects for yield (no. of fruit/plant in the first harvest) was noted for the male parent, 319H, and for the female parent, 402G. The SCA obtained among all the hybrids was quite low.

For yield as weight (g/plant) in the first harvest, the greatest GCA effects was exhibited by 532H and 402G for male and female lines, respectively. The highest value for SCA effects was obtained from the hybrid of the above two parents.

Outstanding values for GCA effects for yield (no. of fruit or weight) in the second harvest were not evident for either male or female parents. A high SCA effect was observed for the 921G x 532H hybrid for yield as g/plant, but neither parent showed a high value for GCA effects.

The variance components of the F_1 hybrids from 100 plots (5 replications x 20 populations) for all characters were used to calculate the ratios of GCA:SCA (Table 7). They were 2:1, 47:1, 9:1, 68:1 and 4:1 for flowering time, harvesting time, fruit no./plant in first harvest, g/plant in first harvest, and g/plant in second harvest, respectively. A high ratio also was found for nodal position of the first-pistillate flower. Thus, additive genetic effects were greater than the non-additive effects. The additive genetic effects were less than the non-additive effects as estimated for femaleness expression (0.4:1) and fruit no. in second harvest (0.5:1) as estimated by GCA:SCA ratios.

Differences existed between 6^2_m and 6^2_f for characters such as flowering-time, harvesting-time, gynoecious expression, and yield (Table 7). The degree of dominance was equal or less than unity for all characters depending on the character except for over-dominance for gynoecious expression (7.5). Narrow-sense heritability estimates for half-sibs (male or female parents) were relatively high for most characters (Table 7). Differences in heritability ratios between males and females for all characters were detected for half-sibs estimates.

Table 7. Estimates of combining ability and heritability of parthenocarpic yield from gynoecious x hermaphroditic crosses of cucumber from 1978 field trials.

Components	Flowering time	Node 1st pistillate flower	Harvest time	Gynoecious %	Yield/plant			
					Harvest 1		Harvest 2	
					Fruit No.	Fruit Weight	Fruit No.	Fruit Weight
Male (GCA) 6^2m	± 0.78 - 0.58	± 0.026 - 0.019	± 1.54 - 1.20	± 0.47 - 3.30	± 0.11 - 0.08	± 875.9 - 766.2	-0.055 ±0.073	± 398.9 - 1101.1
Female (GCA) 6^2f	± 0.01 - 0.13	± 0.030 - 0.023	± 2.68 - 1.96	± 4.90 - 5.50	± 0.12 - 0.09	±1787.9 -1350.4	-0.045 ±0.060	1163.2 ± 1451.1
MxF (SCA) 6^2mf	0.39 ± 0.32	± 0.000 - 0.011	± 0.09 - 0.85	±14.89 -15.11	± 0.02 - 0.04	± 39.2 - 690.3	0.206 ±0.220	783.4 ± 2139.1
Maternal effect 6^2mat	-0.38	0.002	0.57	2.19	0.01	456.0	0.005	382.2
Error	2.16	0.140	10.01	14.68	0.57	8244.7	1.810	25702.1
Ratio GCA:SCA	2.05:1	-	47:1	0.36:1	9.4:1	68:1	0.48:1	4.1:1
Degree of dominance	0.99	0.003	0.34	7.56	0.67	0.30	-	0.6
h^2_n male	± 0.93 - 0.69	± 0.53 - 0.38	± 0.43 - 0.33	0.05 ± 0.37	0.53 ± 0.38	± 0.32 - 0.27	± 0.00 - 0.15	0.1 ± 0.1
h^2_n female	± 0.02 - 0.15	± 0.61 - 0.46	± 0.75 - 0.54	0.56 ± 0.62	0.60 ± 0.43	0.65 ± 0.49	0.00 ± 0.12	0.2 ± 0.2

Table 8. Phenotypic and genetic correlations for yield and associated characters from 20 F_1 (GxH) parthenocarpic hybrids of pickling cucumbers grown in summer 1978.

Characters[z] No.		Flowering time (1)	Node 1st flower (2)	Harvest time (3)	% Gynoecious (4)	Average Yield/Plant			
						Harvest 1		Harvest 2	
						Fruit No. (5)	Fruit Weight (6)	Fruit No. (7)	Fruit Weight (8)
Flowering	(1)	-	+0.72	+0.30	-0.12	-0.45	-0.16	-0.19	-0.16
Node	(2)	+0.58	-	+0.21	-0.24	-0.02	-0.02	-0.15	-0.03
Harvest time	(3)	-0.13	-0.05	-	-0.02	+0.14	+0.07	-0.05	-0.21
% Gynoecious	(4)	-0.95	-0.68	+0.21	-	-0.15	-0.03	-0.12	-0.08
Fruit No.	(5)	-0.02	+0.47	+0.04	-0.88	-	+0.65	+0.03	+0.10
Fruit Weight	(6)	-0.16	+0.79	-0.75	-1.20[y]	+0.87	-	+0.03	+0.16
Fruit No.	(7)	-0.51	-0.13	-0.61	-0.00	+0.54	+0.79	-	+0.53
Fruit Weight	(8)	-0.57	-0.13	-1.05[y]	-0.71	+0.01	+0.59	+1.1[y]	-

[z] Phenotypic correlation above diagonal; genetic correlation below diagonal.

[y] Values are assumed to approximate unity.

Genetic and phenotypic correlations were estimated for all pairs of characters (Table 8). The phenotypic correlation coefficients were high between flowering time and nodal position of first-pistillate flower (+0.72), harvest-time (+0.30) and yield as fruit no. per plant in first harvest (-0.45). Positive and high correlations were detected between nodal position of first-pistillate flower with harvest-time (+0.21). High associations were found for yield measurements of fruit number with weight/plant (r=+0.65 and 0.53) in the first and second harvest, respectively.

The genetic correlation coefficient for flowering time and nodal no. of first-pistillate flower was 0.58; whereas, flowering time and percent gynoecious plants was -0.95. High positive genetic correlations for nodal no. of first-pistillate flower and yield parameters in the first harvest (+0.47 and +0.79) were apparent. Conversely, negative genetic correlations were calculated for position of first-pistillate flower with gynoecious expression (-0.68) and between gynoecious expression and the yield parameters. As expected, a high positive genetic association was found between fruit no. and fruit weight for each harvest.

DISCUSSION

The presence of seeded fruits on cucumber vines inhibits vegetative growth and further fruiting as opposed to parthenocarpic or seedless fruitation (6,36). Moreover, seed development has a dual effect on the development of fruit tissue, since the development of the seeds will be at the expense of fruit tissue (6). Development of parthenocarpic hybrid cvs. for out-of-doors production should markedly increase yield potentials by maximizing fruit number and weight for once-over mechanical harvesting. However, neither the heritability nor combining ability of cucumbers for parthenocarpic fruit yields has been reported; although the genetics of parthenocarpy *per se* has been (13,15,19,25,26,27). The present study was based on selected female (gynoecious) and male hermaphroditic lines evaluated in two previous experiments, a diallel cross and a 17-parent top cross for female and male parents, respectively (7,8).

The relative effects of GCA and SCA were important for most of the associated traits and total yield *per se*. But variances for GCA were greater than those for SCA except for gynoecious expression. The SCA for sex expression was some 3X as important as GCA (Table 7), which suggested a strong contribution by non-additive genes. Genes conditioning SCA have the greatest effect when the lines have been subjected to previous testing and selection for that trait (30).

Because our parental lines had been previously selected, the SCA for yield was expected to be more important than GCA, but the converse was true. However, the selected or elite lines used in this investigation could lack genetic diversity; hence, display relatively low SCA. High SCA might be obtained by testing large numbers of genetically diverse inbred lines. The significant differences for GCA among the female lines (combined with larger variances of 6^2_f) for characters such as harvest time, gynoecious expression, and yield indicate that the female lines were responsible for majority of the additive gene effects for the aforementioned characters; whereas, the 6^2_m of male lines was only responsible for majority of the additive genetic variation for flowering time. Accordingly, genetic improvement could be achieved by further selection among the female or male lines depending on the trait. Caution should be used in generalizing this information to other cucumber populations because the genetic variance components of this population (6^2_m,6^2_f,6^2_{mf}) could be overestimated due to linkage disequilibrium and/or epistasis (12,28). The model and the material used did not permit estimation of the variance component for epistasis; therefore, estimation of additive and especially non-additive components of genetic variance could be biased (16).

The unequal values of 6^2_m and 6^2_f could be explained by maternal effects (cytoplasmic inheritance) or linkage disequilibrium (4,5,28). Reciprocal crosses would be the best estimate of maternal effects especially for characters that showed differences in magnitude between 6^2_m and 6^2_f.

The high degree of dominance estimated for flowering time (0.99) indicated complete dominance for the gene(s) that controls this trait. This was similar to a previous report (21). Moreover, they reported that the number of genes that controlled flowering time ranged from 1.1 to 1.9 which is similar to an earlier report (33). The high degree of dominance for gynoecious expression (7.56) could be explained by over-dominance. This huge value for degree of dominance could be biased by both linkage disequilibrium and epistasis (5,12,28). This is probable because sex expression is under the control of moderately few genes with dominance and epistatic effects (18,29,32).

High narrow-sense heritability ratios among the parents and a high ratio of GCA:SCA suggested that most of the variation was genetic and additive for nodal position of the first-pistillate flower, harvest-time, and yield of first harvest. Thus, genetic progress could be made to improve yield (fruit no.) by selection among the high-performance parents. Further improvement could be achieved by testing this parent for GCA and SCA in hybrid combinations. Low heritability estimates among female lines for flowering time and among male lines for gynoecious expression were due to small additive genetic variances in these two cases. Conversely, the small heritability estimates which were negative and positive for yield characters in the second harvesting could result from environmental effects, especially since this harvest was made relatively late in the season

when environmentally induced parthenocarpy might be prevalent.

Phenotypic correlations among characters were in agreement for sign and magnitude with previous reports (14,21,34,37). High genetic correlations among certain characters indicated significant genetic associations between these characters (Table 8). Genetic correlations suggest genetic linkage and/or pleiotropy (22,28). The presence of negative correlations between certain characters; e.g., flowering time and gynoecious expression, node no. of first-pistillate flower and gynoecious expression, and gynoecious expression and yield, could be due to pleiotropy and selection. Robinson and Comstock (28) stated that pleiotropy is a source of negative genetic association between characters. The high negative correlations between gynoecious expression and various yield characters and high positive correlations between yield of second harvest with gynoecious expression could be due to the small values of 6^2_m and/or 6^2_f. Independent genetic associations between characters or negative correlations might be the result of environmental effects and/or interactions. This might be especially true when different characters develop sequentially to a final product, e.g., flowering to yield of fruits which occurs over time and is subject to many environmental influences (9,10). The advantage of a genetic correlation between flowering time and nodal position of the first-pistillate flower and between the latter and yield in the first harvest could be used as a guide for selection of line(s) expected to produce high yields of early crops of parthenocarpic fruits.

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