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Inheritance of Parthenocarpic Yield in Gynoecious Pickling Cucumber for Once-over Mechanical Harvest by Diallel Analysis of Six Gynoecious Lines[1]

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Abstract. **Six gynoecious inbred lines of cucumber (*Cucumis sativus* L.) were evaluated for parthenocarpic yield by using 2 diallel analysis programs. A complete diallel of F_1 and half-diallel of F_2 generations, including parents, was used to study the genetics of parthenocarpic yield. Highly significant differences for GCA and SCA effects were found for all yield characters, suggesting that both additive and non-additive gene action were important. Reciprocal differences or maternal effects were not significant for any of the yield characters. Diallel analysis suggested that recessive genes were acting in the direction of higher yields. Accordingly, the development of a parthenocarpic hybrid cultivar with high yield potential would require that both parents possess genotypes with high yield potentials. Heritability estimates varied from nearly 0 to 32% for 3 different yield measurements with number of fruits on the main stem most heritable. Significant ratios for heterosis and heterobeltiosis were obtained for all yield measurements. However, only fruit number on the main stem was affected by an inbreeding depression. Breeding improvement programs for parthenocarpy might include recurrent selection for fruit number on the main stem of gynoecious seed parent lines combined with backcrossing of the gene for hermaphroditic expression into gynoecious parthenocarpic lines for pollen parents.**

Mechanical harvest by a once-over destructive system necessitates a uniform set of high fruit numbers for an economic yield of pickling cucumbers. The combination of gynoecious expression with parthenocarpic fruiting for field production of pickling cucumbers has been suggested (2, 6, 7, 22, 23). Parthenocarpic gynoecious pickling cucumbers may produce higher yields than conventional seeded cultivars (2, 6, 23). However, relatively little is known about the inheritance of parthenocarpic yield in gynoecious cucumber cultivars for outdoor production. Originally (12), parthenocarpy was suggested to behave as a recessive trait. However, a more comprehensive study (22) suggested 1 gene with incomplete dominance. Conversely (16, 21), a single recessive gene for parthencarpy was postulated. The inheritance of par-

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thenocarpy was further confused by a report (18) that many incompletely recessive genes conditioned parthenocarpy. Most recently (24), 3 independent, isomeric major genes with additive action, together with non-allelic interaction were suggested as being responsible for parthenocarpy in glasshouse fresh market cucumbers.

Hybrid vigor is well documented in cucumber. Yield of the F_1 generation for seeded fruits was found to exceed the high parent in many cases (4, 8, 10, 13). Inbreeding depression in pickling cucumber was only recently documented for yield of seeded fruits (8). Such information on the yield of parthenocarpic fruits is not well documented. Diallel analysis can be used as a tool to evaluate an array of inbred lines for combining ability (9) and to provide genetic information on that array of lines (11, 14, 15). The objectives of our study were to evaluate a 6-parent diallel of gynoecious cucumbers for parthenocarpic yield by their hybrid performance and to study their inheritance patterns for parthenocarpic yield by diallel analysis. Information about the genetic system for parthenocarpy would assist cucumber breeders in choosing an efficient breeding program for this trait.

Materials and Methods

A complete diallel was constructed from 6 cucumber lines by controlled pollinations under greenhouse conditions. The gynoecious lines were Gy3, Gy14, MSU 92G, MSU 364G, MSU 402G and MSU 921G and were previously described (7). Staminate flowers were produced on gynoecious plants by standard techniques and used 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 obtained by selfing the half-diallel.

The S_1, F_1, and F_2 seeds were planted in the field at the Horticultural Reseach Center near East Lansing, Mich. on July 7, 1977, in a randomized complete block design with 6 replicates. Thus, each block/replicate consisted of 51 single-row plots spaced 1.5 m apart and 7.6 m in length. Plots were over-seeded and seedlings thinned to 30 cm between plants. Standard cultural practices were used with irrigation.

Staminate floral buds were removed daily from the 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. Each plant was harvested individually when the first fruit reached 5 cm in diameter. Individual plants were pulled at the time of harvest, and fruits were counted from the main stem and from the laterals separately. Fruits between 2 and 5 cm diameter were counted; then, all fruits per plant were weighed. All large fruits (>5 cm diameter) were cut to confirm the absence of seed and presumed parthenocarpic fruit-set. Plants with fruit that contained one or more seeds were discarded.

The complete diallel was subjected to an analysis of variance for combining ability. The procedures of Griffing (9) Method 1, Model 1, were utilized. Also, data of both F_1 and F_2 generations were subjected to Jinks-Hayman method for diallel-cross analysis (14). A computer program developed by Lee and Kaltsikes (19) 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 for each block (replicate) and 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-component estimates and standard errors.

Gene action and dominance were interpreted from the Wr/Vr regression of each trait as proposed by Mather and Jinks (20).

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

Vp = variance of the parents = $D + E$
Vr = mean variance of the arrays = $\frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F + (E + \frac{1}{2}(n-1)E')/n$
Vr = The variance of the means of the arrays = $\frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}H_2 - \frac{1}{4}F + (E + \frac{1}{2}(n-2)E')/n$
Wr = mean covariance between the parents and the arrays = $\frac{1}{2}D - \frac{1}{4}F + 1/nE$

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 = $2\,Vp - 4\,\overline{Wr} - 2(n-2)E/n$.
H_1 = component of variation due to the dominance effects of the genes = $Vp - 4\,\overline{Wr} + 4\,\overline{Vr} - (3n-2)E/n$.
$H_2 = H_1\,(1-(u-v)^2)$ = dominance indicated by asymmetry of positive and negative effects of genes = $4\overline{Vr} - 4\overline{Wr} + 2E$, and
E = the expected environmental component of variation.

Results and Discussion

Heterosis and inbreeding depression. The 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. Number of fruits per main stem ranged from 2.7 (921G) to 4.5 (364G) and fruit number on laterals ranged from 0.6 (402G) to 9.7 (364G). Yields as fruit weight per plant 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 on the laterals.

Estimates for heterosis were 54%, 28%, and 22% for fruits on the main stem, on laterals, and for fruit 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 fruit weight/plant, respectively. The 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.

Combining ability. The analysis of variance for the 3 yield characters was conducted on the mean performance of the complete diallel (6x6). The mean squares for GCA and SCA were significant for yield which suggested both additive and non-additive genetic effects were responsible for this variability (Table 2). However, a comparison of the relative magnitudes of 6^2_{GCA} and 6^2_{SCA} effects revealed that GCA was far more important than SCA for all the parthenocarpic yield characters (Table 2).

The magnitudes and directions of GCA and SCA effects were used to judge the average and specific performance of the parents for parthenocarpic yield (Table 3). The estimation of GCA effects (Table 3) from the diallel showed that 364G was the best performer for high fruit number on main stem, whereas 921G com-

Table 1. Parthenocarpic yields 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 fruit weight (g)		
	$\overline{P}$	$\overline{F_1}$	$\overline{F_2}$	$\overline{P}$	$\overline{F_1}$	$\overline{F_2}$	$\overline{P}$	$\overline{F_1}$	$\overline{F_2}$
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	497.7c	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	466.2cd	55.1b	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]Mean separation within columns by Tukey's multiple range test, 5% level.
[y] * and ** are significantly different from zero at the 5 and 1% levels of probability, respectively. Average % heterosis = $(\overline{MF_1}-\overline{MP}/\overline{MP})$ x 100; average % heterosis = $(\overline{MF_1}-\overline{HP}/\overline{HP})$ x 100; and % inbreeding depression = $(\overline{MF_2}-\overline{MF_1}/\overline{MF_1})$ x 100.

Table 2. Analysis of variance (ANOVA) for GCA, SCA and reciprocal cross effects for parthenocarpic yield from a complete diallel (6 x 6) of gynoecious pickling cucumber.

Source	df	Mean squares[z]		
		Main stem	Laterals	Weight
GCA	5	0.50*	53.7**	10722*
SCA	15	0.20*	7.4**	8583*
Reciprocals	15	0.07	1.5	2832
Error[y]	2124	0.07	0.8	1463
6^2_{GCA}: 6^2_{SCA}		16:1	46:1	8:1

[z]* and ** are significant at the 5% and 1% level of probability, respectively, by F test.
[y]The error term was estimated from the variance within plots divided by 60 (number of replications x number of plants per plot).

bined poorly for fruit number on the main stem. The GCA effects for yield of fruit on main stems were not significant for the other parents. For the number of parthenocarpic fruits on the laterals, 4 lines were strong combiners for high fruit counts based on GCA effects. The line, 921G, was the stronger combiner followed by 364G, Gy14, and Gy3. The poorest combiner was 402G followed by 92G. The highest GCA values for fruit weight/plant were exhibited by 364G and 402G, whereas Gy3 and 92G were poor combiners with significant negative values. On the dual yield bases of high overall fruit numbers (main stem plus laterals) (Table 1) and high GCA (Table 3), the parental lines 364G and 921G were judged the better performers.

The SCA effects for parthenocarpic yield were also estimated from the 6-parent diallel (Table 3). Only one of the F_1 crosses dis-

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

Parent	Yield 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./main stem						-0.20	-0.18*
	No./laterals						-3.50	1.96*
	Wt /plant						-73.22	-2.30

Standard error	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.

played significant positive effects for fruit number on the main stem: Gy3 x 921G; whereas two F_1 crosses exhibited significant negative effects for SCA: Gy3 x 364G and 402G x 921G. Four of the 15 F_1 combinations showed significant positive SCA effects for fruit number on laterals. One of the F_1 parents, Gy14, was involved in 3 of the 4 crosses: Gy14 x 364G, Gy14 x 402G and Gy 14 x 921G. However, the highest performer for SCA effects was Gy 3 x 921G. 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, Gy 14 and 402G, accounted for 5 of the crosses. The cross of Gy 3 x 402G had the highest value, 129.5, for SCA effects. Only 2 crosses had significant negative effects for SCA: 92G x 402G and 364G x 402G.

Diallel cross analysis. Diallel analysis (11, 14, 15) provided further information about the nature of the genetic system conditioning parthenocarpic yield in gynoecious cucumber. The complete validity of Jink-Hayman's diallel cross analysis is based on fulfillment of several assumptions, which are often questionably fulfilled (3). 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 to fulfill any of these assumptions limits the analysis to some degree (3, 5). The first 6 assumptions were met. Two general tests (20) were also used to test for fulfillment of the assumptions. The analysis of variance for the quantity (Wr–Vr), where Vr is the array variances and Wr is the parent-offspring covariances, was calculated. This test was conducted for 6 arrays in each of 6 replications for F_1 and F_2 generations. The value of Wr–Vr for lines was constant over arrays with no significance. Thus, all the assumptions were valid and the environmental effects were zero (1, 14, 20). Mather and Jinks (20) 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). In the second test, the regression coefficient of (Wr, Vr) is expected to be significantly different from 0, but not significantly different from 1.0. 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 generation; 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 second test, while the other 2 were partially satisfied for this second general test of assumptions (20). A recent review of diallel analysis (3) cautions researchers to meet the assumptions for independent distribution of genes among parents and for the absence of epistasis in order to properly interpret the findings. Thus, cucumber breeders should be careful in extrapolating our genetic findings from the diallel analysis to their programs.

Mean estimates of genetic variances (D, F, H_1, and H_2) were calculated for both F_1 and F_2 generations (Table 4). 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 both fruit number on laterals and fruit weight per plant which indicated a majority of recessive alleles for these 2 measurements of yield. The value of $D–H_1$ for fruit number on the main stem indicated that additive effects were more important than dominance gene effects.

The average degree of dominance, $(H_1/D)^{1/2}$, was 0.62 and 0.83 for fruit number on the main stem in the F_1 and F_2 generations, respectively (Table 5). The crude estimate for frequency of negative (v) versus positive (u) alleles ($H_2/4H_1$) at loci which exhibit dominance in the parents (5) is expected to be 0.25 if equally distributed among the parents. For our study, the number of fruits on the main stem exhibited a 0.24 ratio indicative of a symmetrical distribution of positive and negative alleles at the 'non-additive' loci of the parental lines; whereas, both fruit number on laterals and fruit wt/plant were estimated as 0.31 and 0.36 respectively (Table 5).

The ratio of K_D/K_R for the F_1 generation (Table 5) indicated that more dominant than recessive alleles were present for fruit number 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 for loci which control these 2 characters. Values of K, which estimate the number of genes or groups of genes that exhibit dominance, were estimated at 1.4, 1.3, and 2.5 for fruit number on the main stem and on the laterals and fruit weight per plant, respectively (Table 5).

The narrow sense heritability ratios were 0.17 and 0.32 for fruit number on the main stem in the F_1 and F_2 (Table 5), respectively. The heritability ratios for fruit number 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.

The Wr/Vr graphs (Fig. 1 to 3) are the regression of Wr (parent-offspring covariances) on Vr (parental array variances) and their limiting parabola in the 6-parent diallel for parthenocarpic yield. The (Wr, Vr) graph provides tests of significance for the presence of dominance ($b \neq 0$) and the average degree of dominance (the sign of a); where b is the slope of the regression line and a is the in-

Table 4. Genetic variance components for parthenocarpic yield of gynoecious pickling cucumber in a field experiment.

Genetic parameter[z]	Yield[y]					
	Fruit number					
	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 by asymmetry of positive and negative effects of genes; F = covariance of dominance and additive effects; E = error (see reference 19).
[y]* and ** are significantly different from zero at the 5% and 1% level of probability, respectively.

Table 5. Heritability parameters for parthenocarpic yield in gynoecious pickling cucumber for outdoor culture.

Genetic components[z]	Yield[y]					
	Fruit no.					
	Main stem		Laterals		Weight (g)	
	F	F	F	F	F	F
$(H/D)^{1/2}$	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

[z]$(H_1/D)^{1/2}$ = average degree of dominance, $H_2/4H_1$ = average frequency of negative vs positive alleles; $K_D/K_R = ((4DH_1)^{1/2} + F)/(4DH_1^{1/2} - F)$ is the ratio of dominant to recessive alleles. Heritability is 1/4D(1/4D – 1/4F + 1/4H_1+ E); $K = h^2/H_2$, an estimate of number of groups of genes exhibiting dominance, where $h^2 = 4(ML1–ML0)^2–4(n–1)E/n^2$, and (ML1–ML0) is the difference between the mean of the parents and the mean of their progeny (see reference 19 and Table 4 footnote).

tercept of b on Wr axis. According to the diallel theory (11, 15), the regression of Wr on Vr is a straight line of unit slope (b is not significantly different from unity, but significantly different from zero). As indicated by Jinks (15) and Hayman (11), 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 the fruit number on the main stem (Fig. 1) revealed that the slope (b = 0.78 ± 0.84) was not significantly different from either 1 or zero. 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. Nevertheless, the array point for 364G indicated a preponderance of recessive genes for this yield trait; whereas, gynoecious lines Gy14, 402G, and 92G expressed high frequencies of dominant genes.

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 (b = 0.98) is indicative of genic interaction which could obscure simpler genic effects. Parent Gy14 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 again that 364G contains a preponderance of recessive genes. Conversely, Gy3 contains a preponderance of dominant genes. The remaining 2 lines (921G and 402G) expressed slightly more dominant genes than recessive, while 92G showed a balance of dominant and recessive genes.

The regression of Wr on Vr for fruit weight per plant (b = 0.43) was not significantly different from either zero or unity which again indicated possible genic interaction (Fig. 3). The negative large value of "D" (Table 5) likely upsets the Wr/Vr regression. However, the 2 lines Gy3 and Gy14 appeared to possess recessive genes responsible for relatively low yields (weight/plant).

Based on combining ability (9) and diallel cross analysis (11,

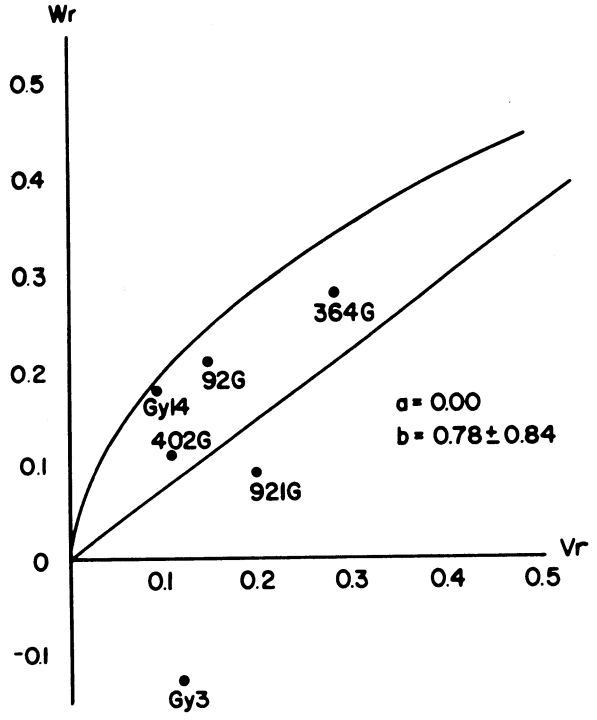

Fig. 1. Wr, Vr regression for fruit no. on main stem of F_1 parental arrays.

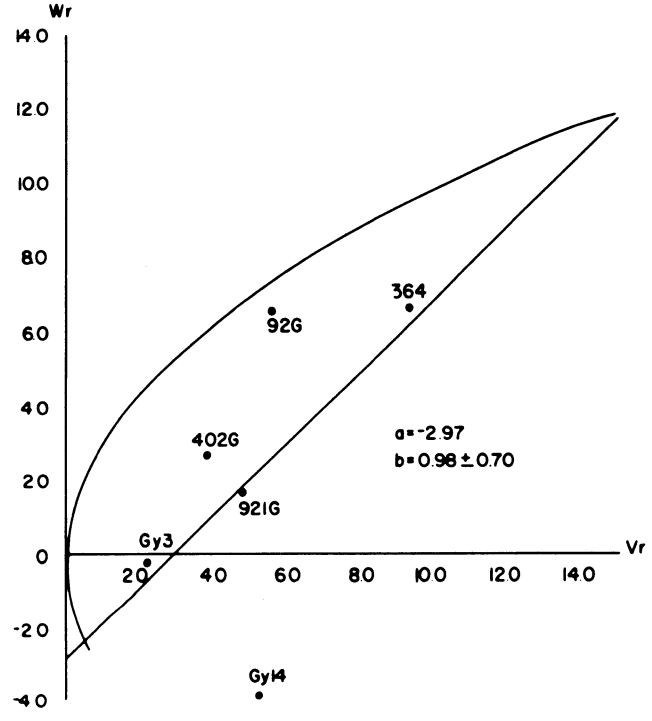

Fig. 2. Wr, Vr regression for fruit no. on laterals of F_1 parental arrays.

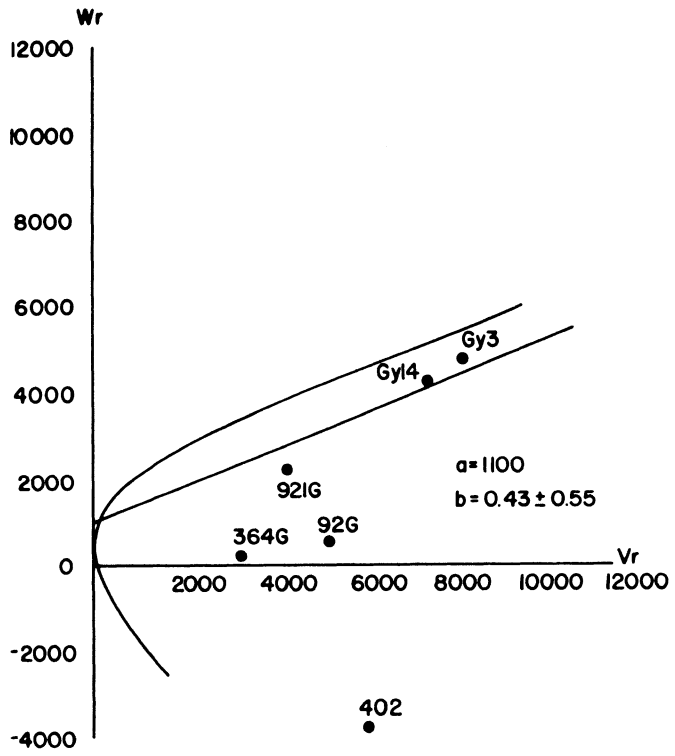

Fig. 3. Wr, Vr regression for yield weight (g)/plant of F_1 parental arrays.

15), the inheritance of parthenocarpic yield was found to be quantitative with a heritability ratio from near 0 to 0.32 depending on the yield trait measured. Parthenocarpic yield was controlled by both additive and non-additive gene effects. A similar conclusion was drawn recently from an investigation of parthenocarpy in glasshouse fresh market cucumbers (24). The presence of high levels of heterosis for parthenocarpic yield together with an inbreeding depression for fruit number on the main stem were not surprising. Heterosis for yield was reported long ago (10) for seeded cucumber. Heterosis was also reported for various other cucumber characters (4, 10, 13, 25). Recently (8), heterosis and inbreeding depression for yield was reported in seeded fruit-set on cucumber. Based on the present study, hybrid vigor also can be utilized to improve the yield of parthenocarpic pickling cucumber. Therefore, gynoecious lines could be improved for parthenocarpy by using a recurrent selection scheme for fruit on the main stem. If gynoecious-hermaphroditic crosses are used for hybrid cultivars, then a backcross program might be used to improve the parthenocarpic yield of the hermaphroditic (pollen) parent because a single gene is responsible for the difference between gynoecious and hermaphroditic expression (17). Superior parent lines and hybrid combinations with high parthenocarpic yields might be developed as hybrid gynoecious cultivars for once-over mechanical harvest.

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