INHERITANCE OF SEX EXPRESSION IN THE DIOECIOUS CUCUMBER (CUCUMIS SATIVUS L)

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JOHN WARNER SCOTT

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ABSTRACT

INHERITANCE OF SEX EXPRESSION IN DIOECIOUS CUCUMBER (*CUCUMIS SATIVUS* L.)

By

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The hybrids and segregating populations of 4 gynoecious lines crossed with 4 androecious lines were analyzed to determine the inheritance of sex expression in dioecious cucumber (*Cucumis sativus* L.). Sex expression of the hybrids was characterized by gynoecious and predominantly female phenotypes. Both phenotypes are characterized by a continuous pistillate stage of flowering on the main stem. No reciprocal cross differences were observed. Backcrosses to the gynoecious parents produced plants with a continuous female stage. Backcrosses to the androecious parent produced plants with a continuous pistillate, monoecious (without a continuous pistillate stage), and androecious phenotypes in a 2:1:1 ratio, respectively. The F_2 generation segregated 12:3:1 continuous pistillate, monoecious, and androecious phenotypes, respectively. Two major loci were proposed to control sex expression in the populations studied. The *a* locus permits male (*aa*) versus female (*A-*)

flower expression. The *acr* locus conditions the intensity of femaleness where Acr^F is epistatic to *aa* and results in a continuous pistillate stage.

Accordingly, gynoecious and predominantly female genotypes are homozygous or heterozygous for acr^F, while monoecious and androecious phenotypes are acr^+ homozygotes. With an acr^+acr^+ genotype *A-* conditions monoecism and *aa* conditions androecism.

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INTRODUCTION

Kubicki (9) reported that androecious (all-male) expression of cucumber (Cucumis sativus L.) was controlled by a single recessive gene a and was also influenced by the acr locus. The influence of the acr locus on sex expression had been reported earlier (16,17). The acr locus is probably analogous to the st locus (4), which in still earlier work was called f (20). Kubicki (9) obtained entirely gynoecious (all-female) F_1 plants from some crosses of gynoecious x androecious. This result stimulated interest in the use of an androecious parent for hybrid seed production. Use of a vigorous, androecious pollinator might be advantageous over current monoecious (11) or proposed hermaphroditic (5,12) pollinators. It might also be useful as a pollinator for 3-way hybrid seed production (14).

The purpose of this study was to determine the inheritance of sex expression in crosses of gynoecious and androecious cucumber. This information is essential to determine the feasibility of using androecious lines as pollinators for hybrid seed production.

MATERIALS AND METHODS

In August 1972 crosses involving 4 gynoecious and 4 androecious lines of cucumbers were planted in the greenhouse to obtain F_1 and S_1 seed. The 4 gynoecious inbred parents were: 1) Gyl4, a white spined pickling line developed by Clemson University; 2) MSU 713-5, a black spined pickling line developed by Michigan State University; 3) Tablegreen 68G, a white spined slicer line developed by Cornell University; and 4) MSU 394G an experimental white spined pickling line developed by Michigan State University. The androecious parents consisted of 3 lines of black spined slicing cucumbers designated MSU 1A1, MSU 1A2, and MSU 1A3. The fourth androecious line, designated MSU 2A, was a white spined slicer line with prolific growth and late flowering.[1]

A second planting of parental and F_1 seed was made in November 1972 to obtain reciprocal F_1 (RF_1), BC_1, reciprocal BC_1 (RBC_1), BC_2, reciprocal BC_2 (RBC_2), and F_2 seed. The sex expression of these F_1 plants under greenhouse conditions was recorded.

Gynoecious parents were sprayed 3x at 4 day intervals with 50 ppm $GA_{4/7}$ beginning at the 1-leaf stage to induce male flowers (13) for selfing and reciprocal crosses. The androecious parents were sprayed with 50 ppm ethephon at

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[1]Seed of MSU 1A1, MSU 1A2, and MSU 1A3 was supplied by Dr. E. T. Mescherov, All-Union Institute of Plant Industry, Leningrad, USSR. Seed of MSU 2A was supplied by Dr. M. Yordanov, Plovdiv, Bulgaria.

the 3-leaf stage to induce female flowers (1) for selfing and reciprocal crosses. To obtain staminate flowers for F_2 and BC seed the gynoecious F_1 plants were sprayed 3x with 50 ppm $GA_{4/7}$, whereas PF F_1 plants were sprayed 2x after classification.

Seed obtained from the various crosses was planted at 2 field locations in the summer of 1973. The S_1, F_1, RF_1, BC_1, RBC_1, BC_2, RBC_2, and F_2 generations were planted near East Lansing, Michigan on June 15 and 26. On July 12, a second planting was made near Sodus, Michigan, approximately 120 miles southwest of East Lansing. A completely randomized design was used at both locations with 3 replications. Plants were thinned to 25 plants per 9.14 meter (30 foot) plot to avoid excessive crowding. Twenty-five plants were desired yet not always attained due to variable plant stands. Plots were fertilized with 22.59 kg (49.8 lb) N, 11.7 kg (25.8 lb) P, and 22.59 kg (49.8 lb) K by using 336 kg/ha (300 lb/acre) 20-20-20 before planting and side-dressed with 8.16 kg (18 lb) N using 56 kg/ha (50 lb) $NH_4\ NO_3$ at the 6-leaf stage.

For East Lansing, daylength ranged from 15 1/4 hr to 13 hrs. Average maximum temperature for East Lansing was 26.0°C (78.8°F), average minimum temperature was 13.83°C (56.9°F), and average mean temperature was 20.5°C (68.9°F). At Sodus, daylength ranged from 15 hr to 13 hrs. Sodus average maximum temperature was 26.6°C (79.9°F), average

minimum temperature was 15.89°C (60.6°F), and the average mean temperature was 21.28°C (70.3°F).

All plants were classified for sex over the entire growing season (June through September) and placed into 4 categories:

1) gynoecious, all female flowers;
2) predominantly female (PF), some early male flowers followed by a continuous pistillage stage;
3) monoecious, many male with some female flowers, but no continuous female stage; and
4) androecious, only male flowers with no female flowers or in some cases with very late female flowers formed on third order laterals.

Each plot was coded for replicate number, F_2 sister (if an F_2), pedigree, generation, and location, together with the frequencies of the observed sex phenotypes. Genetic analysis consisted of testing for homogeneity with X^2 contingency tables (18) in order to pool and simplify the data. Homogeneity was tested in the following order: replicates of same plot and location, F_2 populations of the same pedigree and location, reciprocal crosses within generation within location, plots of the same pedigree (plots derived from sister plants - this includes S_1 plants) and location, pedigrees within generation within location, and location within pedigree within generation.

RESULTS AND DISCUSSION

Replicates within plots and locations, F_2 sisters (3 to 5) within pedigree and location, reciprocal crosses of F_1, BC_1, and BC_2 within location, and sister plots (of the same pedigree, generation, and location) were homogeneous ($p > .05$) and were pooled. Progenies from 2 selfed plants (S_1) for each parental line were homogeneous ($p > .05$) with each other and between locations (Table 1). Pedigrees within generation within location proved heterogeneous and are reported separately. When pedigrees within a generation were compared between locations, most proved to be homogeneous. Location differences were not significant ($p > .05$) within crosses, excluding those involving Tablegreen 68G and a single F_2 population involving MSU 394G x MSU 1A2. Thus all other data are reported with locations pooled (Tables 2 to 5). No definite location effect could be determined for heterogeneous crosses except that locations may have influenced sex expression in different ways.

For all crosses (Tables 2 to 5), the F_1 generation segregated gynoecious and PF plants with exceptional monoecious segregates resulting from 3 crosses. Hence, the heterozygote resulting from the cross of gynoecious x androecious exhibited a low percentage of gynoecious with a relatively high percentage of PF plants. Therefore, no genetic basis for differences between these 2 classes could be proposed.

Table 1. Sex expression of S_1 plants from gynoecious and androecious parent lines of cucumber.

Variety	Sex[z]				Total plants
	G	PF	M	A	
Gy14	93	12	0	0	105
MSU 713-5	126	10	0	0	136
MSU 394G	130	8	0	0	138
TG[y]	75	12	0	0	87
MSU 1A1	0	0	0	63	63
MSU 1A2	0	0	0	72	72
MSU 1A3	0	0	0	68	68
MSU 2A	0	0	0	79	79

[z]G = Gynoecious, PF = Predominantly Female, M = Monoecious, A = Androecious.

[y]TG = Tablegreen 68G

Table 2. Sex expression in the cross of gynoecious x androecious (MSU 1A1) cucumber.

Pedigree	Genera-tion	Sex frequencies[z] G	PF	M	A	Total no. plants	Genetic relationships Obtained G+PF:M:A	Expected G+PF:M:A	X^2	P
Gy14 x MSU 1A1	F_1	4	105	0	0	109				
MSU 713-5 x MSU 1A1		3	22	0	0	25				
MSU 394G x MSU 1A1		20	166	2	0	188				
TG[y] x MSU 1A1 - E.L.[x]		13	27	0	0	40				
Gy14 x MSU 1A1	BC_1	85	92	1	0	178				
MSU 713-5 x MSU 1A1		106	97	1	0	203				
MSU 394G x MSU 1A1		187	156	1	0	344				
TG x MSU 1A1 - E.L.		38	13	20	0	71				
TG x MSU 1A1 - S.[w]		24	1	0	0	25				
Gy14 x MSU 1A1	BC_2	19	65	48	46	178	84:48:46	2:1:1	0.6068	.74
MSU 713-5 x MSU 1A1		17	58	42	30	147	75:42:30		2.0202	.38
MSU 394G x MSU 1A1		39	108	73	54	274	147:73:54		4.0984	.14
TG x MSU 1A1 - E.L.		9	23	12	9	53	32:1:9		2.6224	.28
TG x MSU 1A1 - S.		15	22	15	14	66	37:15:14		1.0000	.62
Gy14 x MSU 1A1	F_2	130	211	83	25	449	341:83:25	12:3:1	0.4037	.82
MSU 713-5 x MSU 1A1		139	267	98	31	535	406:98:31		0.2874	.87
MSU 394G x MSU 1A1		295	383	128	56	862	678:128:56		8.6155	.02
TG x MSU 1A1 - E.L.		263	99	58	26	446	362:58:26		10.2424	.008
TG x MSU 1A1 - S.		49	33	19	7	108	82:19:7		0.0982	>.95

[z] G = Gynoecious; PF = Predominantly Female; M = Monoecious; A = Androecious.

[y] TG = Tablegreen 68G.

[x] E.L. = East Lansing location.

[w] S. = Sodus location.

Table 3. Sex expression in the cross of gynoecious x androecious (MSU 1A2) cucumber.

Pedigree	Generation	Sex frequencies[z] G	PF	M	A	Total no. plants	Genetic relationships: Obtained G+PF:M:A	Expected G+PF:M:A	X^2	P
Gyl4 x MSU 1A2	F_1	9	26	0	0	35				
MSU 713-5 x MSU 1A2		14	118	0	0	132				
MSU 394G x MSU 1A2		46	105	0	0	151				
Gyl4 x MSU 1A2	BC_1	85	51	0	0	136				
MSU 713-5 x MSU 1A2		53	40	1	0	94				
MSU 394G x MSU 1A2		326	184	1	0	511				
TG[y] x MSU 1A2 - E.L.[x]		46	15	18	0	79				
TG x MSU 1A2 - S.[w]		112	27	0	0	139				
Gyl4 x MSU 1A2	BC_2	23	54	47	27	151	77:47:27	2:1:1	5.3576	.08
MSU 713-5 x MSU 1A2		6	20	20	9	55	26:20:9		4.5634	.10
MSU 394G x MSU 1A2		28	60	50	37	175	88:50:37		1.9371	.39
TG x MSU 1A2 - E.L.		0	0	1	0	1				
TG x MSU 1A2 - S.		20	21	20	17	78	41:20:17		0.4359	.81
Gyl4 x MSU 1A2	F_2	157	129	53	19	358	286:53:19	12:3:1	4.6221	.10
MSU 713-5 x MSU 1A2		151	174	82	28	435	325:82:28		0.0312	>.95
MSU 394G x MSU 1A2-E.L.		207	231	64	25	527	438:64:25		18.8010	<.001
MSU 394G x MSU 1A2-S.		105	69	39	14	227	174:39:14		0.3827	.83
TG x MSU 1A2 - E.L.		38	7	6	7	58	45:6:7		5.3687	.07
TG x MSU 1A2 - S.		19	10	17	8	54	29:17:8		14.2397	<.001

[z] G = Gynoecious; PF = Predominantly Female; M = Monoecious; A = Androecious.

[y] TG = Tablegreen 68G.

[x] E.L. = East Lansing location.

[w] S. = Sodus location.

Table 4. Sex expression in the cross of gynoecious x androecious (MSU 1A3) cucumber.

Pedigree	Genera-tion	Sex frequencies[z] G	PF	M	A	Total no. plants	Genetic relationships Obtained G+PF:M:A	Expected G+PF:M:A	X^2	P
Gy14 x MSU 1A3	F_1	23	70	2	0	95				
MSU 713-5 x MSU 1A3		23	140	0	0	163				
MSU 394G x MSU 1A3		20	81	0	0	101				
TG[y] x MSU 1A3 - E.L.[x]		37	17	6	0	60				
TG x MSU 1A3 - S.[w]		8	14	0	0	22				
Gy14 x MSU 1A3	BC_1	4	7	0	0	11				
MSU 713-5 x MSU 1A3		15	17	0	0	32				
MSU 394G x MSU 1A3		98	64	2	0	164				
TG x MSU 1A3 - E.L.		31	0	0	0	31				
TG x MSU 1A3 - S.		52	5	0	0	57				
Gy14 x MSU 1A3	BC_2	19	44	41	33	137	63:41:33	2:1:1	1.8174	.42
MSU 713-5 x MSU 1A3		27	60	38	42	167	87:38:42		0.4849	.79
MSU 394G x MSU 1A3		22	45	20	24	111	67:20:24		5.0540	.08
TG x MSU 1A3 - E.L.		32	28	31	17	108	60:31:17		4.9630	.09
TG x MSU 1A3 - S.		46	32	32	38	148	78:32:38		0.9189	.64
Gy14 x MSU 1A3	F_2	132	158	83	30	403	290:83:30	12:3:1	2.3847	.31
MSU 713-5 x MSU 1A3		193	262	116	33	604	455:116:33		0.5769	.75
MSU 394G x MSU 1A3		144	145	58	21	368	289:58:21		2.5123	.29
TG x MSU 1A3 - E.L.		188	66	48	20	315	247:48:20		2.5651	.28
TG x MSU 1A3 - S.		84	42	30	4	160	126:30:4		3.9000	.15

[z] G = Gynoecious; PF = Predominantly Female; M = Monoecious; A = Androecious.

[y] TG = Tablegreen 68G.

[x] E.L. = East Lansing location.

[w] S. = Sodus location.

Table 5. Sex expression from the cross of gynoecious x androecious (MSU 2A)[z] cucumber.

Pedigree	Generation	Sex frequencies[y] G	PF	M	A	Total no. plants	Genetic relationships Obtained G+PF:M+A	Expected G+PF:M+A	X^2	P
Gyl4 x MSU 2A	F_1	0	18	0	0	18				
MSU 713-5 X MSU 2A		4	84	0	0	88				
MSU 394G x MSU 2A		24	154	0	0	178				
Gyl4 x MSU 2A	BC_1	38	23	0	0	61				
MSU 713-5 X MSU 2A		135	122	0	0	257				
MSU 394G x MSU 2A		396	238	2	1	637				
Gyl4 x MSU 2A	BC_2	10	47	39	7	103	57:46	1:1	1.1748	.28
MSU 713-5 x MSU 2A		29	130	139	25	323	159:164		0.0704	.79
MSU 394G x MSU 2A		32	95	86	12	225	127:98		3.7378	.05
Gyl4 x MSU 2A	F_2	193	204	115	8	520	397:123	3:1	0.5025	.82
MSU 713-5 x MSU 2A		336	512	282	28	1188	848:310		0.7587	.40
MSU 394G x MSU 2A		460	504	326	32	1322	964:385		3.0207	.09

[z]MSU 2A is suggested to be a monoecious genotype but appears androecious under long day, high temperature conditions.

[y]G = Gynoecious; PF = Predominantly Female; M = Monoecious; A = Androecious.

In the backcross to the gynoecious parent (BC_1) 50% $\underline{acr^F acr^F}$ homozygotes and 50% $\underline{acr^F acr^+}$ heterozygotes were expected. Thus depending on the percentage of heterozygotes which are gynoecious, a greater number of gynoecious with a lesser number of PF plants is expected. This is true for all BC_1 populations with the exception of Gyl4 x MSU 1A1 (Table 2). In this cross, the heterozygote expresses a low percentage (4%) of gynoecious plants in the F_1 so the nearly 1:1 gynoecious to PF ratio in the BC_1 is not surprising. Other exceptions are Gyl4 x MSU 1A3 and MSU 713-5 x MSU 1A3 (Table 4), but the small populations may reflect sampling error.

In the backcross to the androecious parent (BC_2), a segregation of monoecious and androecious phenotypes was observed along with gynoecious and PF phenotypes. The gynoecious and PF phenotypes were combined as a single class since the heterozygous F_1 expressed both and a consistent segregation between the 2 wasn't observed in BC_2. The monoecious and androecious classes are nearly equal in frequency with the gynoecious plus PF class containing approximately twice their number. Thus the ratio of gynoecious plus PF to monoecious to androecious is 2:1:1 respectively.

Plants in the F_2 population segregated approximately 12:3:1 for gynoecious plus PF to monoecious to androecious, respectively. The p values ranged from .07 to > .95 for

goodness of fit to this ratio (Tables 2 to 5). Based on the ratios observed in the BC_2 and F_2 generations, an independently inherited digenic system is proposed. The significant number of androecious segregates in both the BC_2 and F_2 generations seems to discount a more complex system of inheritance for androecious expression.

The 2 loci involved are designated as *a* after Kubicki (9) and *acr* as originally designated by Shiffriss (16,17) and then by Kubicki (6,7,9). These designations will be used here to avoid confusion with nomenclature. The *A* allele as the female flower allele is dominant to *a* the male flower allele. The *acr* locus controls female intensity with acr^F homozygotes being of high female intensity while acr^+ homozygotes exhibit a low female intensity. The $acr^F acr^+$ heterozygote is intermediate between the homozygotes, but tends toward the acr^F homozygote phenotypically (6). An acr^F complement exhibits epistasis with *aa*. The proposed model is outlined in Table 6. An acr^F complement results in a continuous pistillate stage, i.e. gynoecious or PF; whereas acr^+ homozygotes do not. The difference between gynoecious and PF may be due to different alleles at the *acr* locus (7) and/or minor modifier genes (7,8,16) and/or environment (2,3,4,10,16,19). In common between monoecious and androecious genotypes is $acr^+ acr^+$. The difference between monoecious and androecious is that monoecious phenotypes require an *A-* genotype whereas

Table 6. Proposed genetic model for sex expression from the cross of gynoecious x androecious cucumber.

Generation	Ratio	Genotype	Phenotype
Gynoecious Parent	1	$\underline{AA}\ \underline{acr^F acr^F}$	Gynoecious
Androecious Parent	1	$\underline{aa}\ \underline{acr^+ acr^+}$	Androecious
F_1	1	$\underline{Aa}\ \underline{acr^F acr^+}$	Gynoecious/PF[z]
BCP_1	3/8	$\underline{A-}\ \underline{acr^F acr^F}$	Gynoecious
	1/8	$\underline{aa}\ \underline{acr^F acr^F}$	Gynoecious
	3/8	$\underline{A-}\ \underline{acr^F acr^+}$	Gynoecious/PF
	1/8	$\underline{aa}\ \underline{acr^F acr^+}$	Gynoecious/PF
BCP_2	1/4	$\underline{Aa}\ \underline{acr^F acr^+}$	Gynoecious/PF
	1/4	$\underline{aa}\ \underline{acr^F acr^+}$	Gynoecious/PF
	1/4	$\underline{Aa}\ \underline{acr^+ acr^+}$	Monoecious
	1/4	$\underline{aa}\ \underline{acr^+ acr^+}$	Androecious
F_2	3/16	$\underline{A-}\ \underline{acr^F acr^F}$	Gynoecious
	1/16	$\underline{aa}\ \underline{acr^F acr^F}$	Gynoecious
	3/8	$\underline{A-}\ \underline{acr^F acr^+}$	Gynoecious/PF
	1/8	$\underline{aa}\ \underline{acr^F acr^+}$	Gynoecious/PF
	3/16	$\underline{A-}\ \underline{acr^+ acr^+}$	Monoecious
	1/16	$\underline{aa}\ \underline{acr^+ acr^+}$	Androecious

[z]PF = Predominantly Female.

androecious phenotypes require aa. Except for the difference between monoecious and androecious, it is beyond the scope of the data to show that A- adds to the femaleness of other sex phenotypes. For example, aa $acr^F acr^F$ and A- acr^F- acr^F are assumed of equal female intensity for this study and the proposed model. The phenotypic difference between these 2 genotypes is likely small.

A major deviation from the proposed genetic model occurs with crosses involving MSU 2A (Table 5). Greenhouse experiments at Michigan State University in the Fall of 1973, demonstrated that the androecious expression of MSU 2A was unstable under low temperature and/or short day conditions. Only under high temperature and long day conditions (as with 1973 field experiments) is MSU 2A stable for androecious expression. Under short day (10 to 11 hr) and/or low night temperature (10 to 12°C) conditions MSU 2A exhibits monoecious expression (15). Environmental influences on sex expression have been observed previously (2,3,4,10,16,19). It is generally accepted that stronger femaleness is observed with short days and low temperature conditions. However, some lines are environmentally stable, such as MSU 713-5 (3) and MSU 1A1 (15). Such a genetic system for sex expression which causes certain varieties to be environmentally sensitive while others are stable has not been reported. Thus, the genotype of unstable MSU 2A might be aa $acr^+ acr^+$ with a gene complement which causes

femaleness under short days and/or cold temperatures or the genotype A- acr^+acr^+ with a gene complement which causes maleness under long day and high temperature conditions. The cross of MSU 2A and MSU 1A1 might provide an answer to this question.

For this data, MSU 2A does not fit a 2:1:1 BC_1 or a 12:3:1 F_2 ratio so the androecious and monoecious classes were combined and 1:1 BCP_2 and 3:1 F_2 ratios, typical of monoecious inheritance (7,16) were tested and found to be acceptable fits (Table 5). This suggested that the genotype of MSU 2A is A- acr^+acr^+ with modifier genes for unstable androecious expression resulting in maleness under long day, high temperature conditions.

Other significant deviations ($p < .05$) from expected F_2 ratios occurred with Tablegreen 68G x MSU 1A1 (East Lansing location), Tablegreen 68G x MSU 1A2 (Sodus location), 394G x MSU 1A2 (East Lansing location) and MSU 394G x MSU 1A1. In the case of Tablegreen 68G x MSU 1A1 (East Lansing), the significant deviations are due to a higher than expected female tendency, that is more gynoecious and PF phenotypes. But, the monoecious and androecious classes are observed to be high in the Tablegreen 68G x 1A2 (Sodus). In the first case, the greater female intensity is not too surprising based on higher percentage of gynoecious segregates in other generations as compared to the other pedigrees. Varying intensities of femaleness among "gynoecious"

varieties has been reported previously (7,8,16). Tablegreen 68G is observed to express a strong female intensity such that it is extremely difficult to induce male flowers after treatment with $GA_{4/7}$ (unpublished data). This study lends no evidence for a genetic basis for such a strong female tendency. Its occurrence could lend support to: 1) multiple alleles at the acr locus (7), in this case having a very strong acr^F expression, or 2) another locus controlling female intensity (8), or 3) it may be due to an accumulation of highly female polygenes (7,8,16), or 4) combinations of the above.

Yet certain Tablegreen 68G crosses segregated monoecious phenotypes in the F_1 and BCP_1 generations which is incongruous with its strong female expression (Tables 2, 3, 4). Also the S_1 segregates the highest percentage of PF's of all the parents (Table 1). These incidences of greater maleness are likely related to the Tablegreen 68G x MSU 1A2 F_2 (Sodus) which expressed a greater than expected frequency of monoecious and androecious segregates. Further work must be done with Tablegreen 68G to explain this apparent disparity.

In the F_2 of MSU 394G x MSU 1A1 and MSU 394G x MSU 1A2 (East Lansing location), the significant deviations result from a higher than expected frequency of gynoecious and PF plants. High female intensity is evident in other crosses with MSU 394G (Tables 2 to 5). The S_1 of MSU 394G

segregated the lowest percentage of PF plants indicating a stronger female tendency than the other gynoecious lines (Table 1). This strong female intensity might be analogous to the high female intensity of Tablegreen 68G. The possibility of a unique environmental effect in the F_2 populations of MSU 394G x 1A2 (East Lansing) and Tablegreen 68G x MSU 1A1 (East Lansing) is apparent since the same crosses at Sodus were consistent with the expected.

Additional experiments would be necessary to determine any modifier genes or multiple acr alleles which might cause the significant deviations in sex expression. If actual numbers of male and female flowers were counted, this would provide quantitative data which might elucidate the modifier genes affecting sex expression.

SUMMARY AND CONCLUSIONS

The inheritance of sex expression in the cross of gynoecious and androecious phenotypes appears to be controlled by 2 major, independently inherited loci; viz., a and acr. A flower sex allele A conditions pistillate flowers and is dominant to a which allows staminate flower development. The sex phenotype is controlled by alleles at a female intensity locus acr. The $acr^F acr^F$ or $acr^F acr^+$ genotypes condition a continuous pistillate stage on the main runner of the plant as opposed to the $acr^+ acr^+$ genotype which is not associated with a continuous pistillate stage. The acr^F allele exhibits epistasis to the a allele (9). The only major genetic difference between monoecious and androecious phenotypes is that androecious phenotypes require aa whereas monoecious require A-. Other modifier genes and environment also influence phenotypic sex expression.

For hybrid seed production an androecious pollinator would be used in the same way as monoecious pollinators (11, 14) in producing highly female F_1 varieties. Hermaphrodites seem more suitable for production of seed of all-gynoecious F_1 (5,12) varieties which are necessary for parthenocarpic cucumber production (12).

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