

and sucker control again influenced the amount of fruit lost during mechanical harvest (Table 4). As in 1971 the tendency was that ground losses increased as crown width increased. That was true in all cases except the control and the 1.13 kg paraquat/ha treatments. At the 30 cm width the 1.13 kg paraquat gave least ground loss although it was not different from the 0.56 kg paraquat in foam treatment. There was no difference among treatments at the 25 cm width and all treatments except 0.56 kg paraquat sprayed were superior to the control at the 20 cm width.

Comparison of potential yield (data not shown) with harvested yield show why the harvested yield data were not statistically different. Greater crown width favored increased potential yield, but also favored increased ground losses. The effects canceled each other.

#### Berry size

Analysis of berry size data (not shown) indicated that there was no difference among treatments in any of the years.

### Discussion

The highbush blueberry industry became established in Michigan in the post-war years in response to the pioneering efforts of Stanley Johnston<sup>7</sup> and major plantings went in during the years 1945–1955.<sup>1</sup> The plantings at that time were primarily of 'Jersey', and it remains the major cultivar in Michigan to date. Many of these old plantings in recent years have not received adequate pruning which coupled with plentiful rainfall and organic soils resulted in large, unthrifty bushes. Estimates<sup>5</sup> have been given to suggest that 30–40% of the 'Jersey' plantations in the state are in such condition. For an industry with \$8–10 million, depending on the season, this is a major economic concern.

We have been concerned with several questions: 1) was the process

as outlined a feasible means of returning low productive plantations to peak productivity; 2) could width reduction and maintenance reduce ground losses without reducing production; 3) if 2 was affirmative, what was the optimum width and width maintenance treatment.

Table 5 shows that the answer to question 1 was yes. The rapid regrowth and return to productivity of radically pruned bushes made the approach not only feasible, but also economically desirable in cases of reduced productivity and excess vigor. Tables 3 and 4 showed that width reduction reduces ground loss. The reason was based on the nature of the spring-loaded catching mechanism on commercial harvesters. Reduced width of crown results in a narrower opening of these "pans" and thus allowed less ground loss.

The answer to question 3 was not fully satisfied by this study. The data in Table 5 show that narrow crowns increased in yield more slowly, but by 1973 increased ground losses made the 30 cm treatment nearly identical with the 25 cm treatment. Whether the optimum width is 20 cm or less cannot be determined from these data. The data do suggest that bushes with the 20 cm width crown did catch up with the productivity of wider crown bushes while maintaining reduced ground losses. On that basis the 20 cm width would be preferred.

Maintenance of crown width at the initial status was accomplished via chemical means in this study. Based on the data in Table 1 any of the paraquat treatments would be acceptable. The foam application would be preferred because of drift control. We do not suggest that this chemical approach to width maintenance is the best; however, it does work. Other methods such as mechanical maintenance should be evaluated.

#### Literature Cited

1. Phillips, E. A. 1959. Methods of vegetative study. Henry Holt Co., Inc. 107 pp.

## Inheritance of Sex Expression from Crosses of Dioecious Cucumber (*Cucumis sativus* L.)<sup>1</sup>

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**Abstract.** The hybrids and segregating populations obtained by crossing 4 gynoeceious with 4 androeceious lines were analyzed to determine the inheritance of sex expression in dioecious cucumber (*Cucumis sativus* L.). Sex expression of all F<sub>1</sub> hybrids was characterized by plants with a continuous pistillate stage of flowering on the main stem. This included both gynoeceious and predominantly female plants. No reciprocal cross differences were observed in the F<sub>1</sub> and backcross generations. Backcrosses to the gynoeceious parents produced plants with a continuous female stage. Backcrosses to the androeceious parent produced plants with continuous pistillate, monoecious (without a continuous pistillate stage), and androeceious expression in a 2:1:1 ratio, respectively. The F<sub>2</sub> generation segregated 12:3:1 continuous pistillate, monoecious, and androeceious phenotypes, respectively. Two major loci, *a* and *acr*, with epistasis are proposed to control sex expression. The *a* locus permits male (*aa*) as opposed to female (*A* –) flower expression. The *acr* locus conditions the intensity of femaleness.

Kubicki (9) reported that androeceious (all-male) sex 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 was 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 gynoeceious (all-female) F<sub>1</sub> plants from certain gynoeceious x androeceious crosses. This result stimulated interest in the use of an androeceious parent for hybrid seed production. Use of vigorous, androeceious pollinators might be advantageous over current monoecious (11) or hermaphroditic (5, 12) pollinators as used in 3-way hybrid seed production (14).

Our purpose was to determine the inheritance of sex expression in crosses of gynoeceious and androeceious cucumber. The genetic information is essential to explore the feasibility of using androeceious phenotypes as pollinators for hybrid seed production.

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<sup>3</sup> Seed of MSU 1A1, MSU 1A2, and MSU 1A3 was supplied by E. T. Mescherov, All-Union Institute of Plant Industry, Leningrad, USSR. Seed of MSU 2A was supplied by M. Yordanov, Plovdiv, Bulgaria.

## Materials and Methods

In August 1972, 4 gynoecious and 4 androecious lines of cucumbers were planted in the greenhouse to produce  $F_1$  and  $S_1$  seed. The 4 gynoecious inbred parents were: 1) Gyl4, a white spined pickling line developed at Clemson University; 2) MSU 713-5, a black spined pickling line developed at Michigan State University; 3) Tablegreen 68G, a white spined slicer line developed at Cornell University; and 4) MSU 394G, an experimental white spined pickling line developed at Michigan State University. The androecious parents were 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 habit.<sup>3</sup>

A second planting of parental and  $F_1$  seed was made in November 1972 to obtain reciprocal  $F_1$  ( $RF_1$ ), reciprocal backcrosses to each of the parental lines, and  $F_2$  seed. Induction of male flowers in gynoecious and predominantly female (PF) lines for seed production was accomplished with GA4/7 (13). Ethephon (50 ppm) was used for

induction of female flowers for selfing and reciprocal crossing with androecious parent lines (1).

Seed obtained from the various crosses was planted at 2 field locations in the summer of 1973. The  $S_1$ , reciprocal  $F_1$  and backcross, and  $F_2$  generations were planted near East Lansing, MI, June 15 and 26. On July 12, a second planting was made near Sodus, MI. A completely randomized design with 3 replications was used at each location. Seedlings 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.

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 or monogynoecious (PF), some early male flowers followed by a continuous pistillate stage; 3) monoecious, many male with some female flowers, but no continuous female stage; and 4) androecious, only male flowers or some plants with late female flowers formed on third-order laterals.

Homogeneity of replications,  $F_2$  families, reciprocal crosses, pedigrees, and locations were tested by using  $X^2$  contingency tables (18) in order to pool the data.

Table 1. Sex expression of  $S_1$  plants from gynoecious and androecious parental cucumber lines<sup>a</sup>.

Parent	Sex <sup>y</sup>				Total plants
	G	PF	M	A	
Gyl4	93	12	0	0	105
MSU 713-5	126	10	0	0	136
MSU 394G	130	8	0	0	138
TG <sup>x</sup>	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

<sup>a</sup> Each  $S_1$  population consisted of seed from 2 self-pollinated plants; data were homogeneous and pooled.

<sup>y</sup> G = gynoecious; PF = predominantly female; M = monoecious; A = androecious.

<sup>x</sup> TG = Tablegreen 68G.

## Results and Discussion

Sex expression of the parental lines was determined (Table 1). All gynoecious lines exhibited a low percentage of PF plants with most plants gynoecious. All androecious parent lines were true-breeding for androecious expression.

Replicates,  $F_2$  families, and reciprocal crosses were homogeneous ( $p > .05$ ) and thus pooled. Different pedigrees of like generation and location proved heterogeneous and were reported separately. When like 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 on sex expression could be determined.

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

Pedigree	Generation	Sex frequencies <sup>a</sup>				Total no. plants	Genetic relationships			
		G	PF	M	A		Obtained G+PF:M:A	Expected G+PF:M:A	$X^2$	P
Gyl4 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 <sup>x</sup> x MSU 1A1—E.L. <sup>*</sup>		13	27	0	0	40				
Gyl4 x MSU 1A1	$BC_1P_1$	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. <sup>w</sup>		24	1	0	0	25				
Gyl4 x MSU 1A1	$BC_1P_2$	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	32:12:9		2.6224	.28
TG x MSU 1A1—S.		15	22	15	14	66	37:15:14		1.0000	.62
Gyl4 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

<sup>a</sup> G = gynoecious; PF = predominantly female; M = monoecious; A = androecious.

<sup>x</sup> TG = Tablegreen 68G.

<sup>\*</sup> E.L. = East Lansing location.

<sup>w</sup> S. = Sodus location.

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

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

<sup>z</sup> G = gynoecious; PF = predominantly female; M = monoecious; A = androecious.<sup>y</sup> TG = Tablegreen 68G.<sup>\*</sup> E.L. = East Lansing location.<sup>w</sup> S. = Sodus location.

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

Pedigree	Generation	Sex frequencies <sup>z</sup>				Total no. plants	Genetic relationships			
		G	PF	M	A		Obtained G+PF:M:A	Expected G+PF:M:A	X <sup>2</sup>	P
Gyl4 × MSU 1A3	F <sub>1</sub>	23	70	2	0	95				
MSU 713-5 × MSU 1A3		23	140	0	0	163				
MSU 394G × MSU 1A3		20	81	0	0	101				
TG <sup>y</sup> × MSU 1A3—E.L. <sup>*</sup>		37	17	6	0	60				
TG × MSU 1A3—S. <sup>w</sup>		8	14	0	0	22				
Gyl4 × MSU 1A3	BC <sub>1</sub> P <sub>1</sub>	4	7	0	0	11				
MSU 713-5 × MSU 1A3		15	17	0	0	32				
MSU 394G × MSU 1A3		98	64	2	0	164				
TG × MSU 1A3—E.L.		31	0	0	0	31				
TG × MSU 1A3—S.		52	5	0	0	57				
Gyl4 × MSU 1A3	BC <sub>1</sub> P <sub>2</sub>	19	44	41	33	137	63:41:33	2:1:1	1.8174	.42
MSU 713-5 × MSU 1A3		27	60	38	42	167	87:38:42		0.4849	.79
MSU 394G × MSU 1A3		22	45	20	24	111	67:20:24		5.0540	.08
TG × MSU 1A3—E.L.		32	28	31	17	108	60:31:17		4.9630	.09
TG × MSU 1A3—S.		46	32	32	38	148	78:32:38		0.9189	.64
Gyl4 × MSU 1A3	F <sub>2</sub>	132	158	83	30	403	290:83:30	12:3:1	2.3847	.31
MSU 713-5 × MSU 1A3		193	262	116	33	604	455:116:33		0.5769	.75
MSU 394G × MSU 1A3		144	145	58	21	368	289:58:21		2.5123	.29
TG × MSU 1A3—E.L.		188	66	48	20	315	247:48:20		2.5651	.28
TG × MSU 1A3—S.		84	42	30	4	160	126:30:4		3.9000	.15

<sup>z</sup> G = gynoecious; PF = predominantly female; M = monoecious; A = androecious.<sup>y</sup> TG = Tablegreen 68G.<sup>\*</sup> E.L. = East Lansing location.<sup>w</sup> S. = Sodus location.

For all crosses (Tables 2 to 5), the F<sub>1</sub> generation exhibited gynoecious and PF plants with infrequent monoecious segregates (10/1404 = .7%). Hence, the heterozygote resulting from the cross of gynoecious × androecious included gynoecious with a relatively high percent (38 to 100) of PF plants. Therefore, no genetic basis for

differences between these 2 classes was proposed in this study.

In the BC<sub>1</sub>P<sub>1</sub>, 50% P<sub>1</sub> genotypes (homozygotes) and 50% F<sub>1</sub> genotypes (heterozygotes) were expected. Thus depending on the percentage of heterozygotes which were gynoecious, a greater number of gynoecious with a lesser number of PF plants was expected. This

Table 5. Sex expression from the cross of gynoecious  $\times$  androecious (MSU 2A)<sup>z</sup> cucumber.

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

<sup>z</sup> MSU 2A is suggested to be a monoecious genotype but appears androecious under long day, high temperature conditions.

<sup>y</sup> G = gynoecious; PF = predominantly female; M = monoecious; A = androecious.

was true for all BC<sub>1</sub>P<sub>1</sub> populations with the exceptions of Gyl4  $\times$  MSU 1A1 (Table 2). In this cross, the heterozygous F<sub>1</sub> population expressed a low percentage (4%) of gynoecious plants in the F<sub>1</sub>, so the nearly 1:1 gynoecious to PF ratio in the BC<sub>1</sub> is surprising. Other exceptions were Gyl4  $\times$  MSU 1A3 and MSU 713-5  $\times$  MSU 1A3 (Table 4), but the population size may be inadequate.

In the BC<sub>1</sub>P<sub>2</sub>, segregation of monoecious and androecious phenotypes was observed along with gynoecious and PF. The gynoecious and PF phenotypes were combined as a single class (continuous pistillate) since the F<sub>1</sub> populations included both. Moreover, a consistent segregation between the 2 phenotypes was not observed in BC<sub>1</sub>P<sub>2</sub> or F<sub>2</sub>. The monoecious and androecious classes were nearly equal in frequency while the continuous pistillate class was twice as large. Thus the ratio of continuous pistillate to monoecious to androecious was 2:1:1.

Plants in the F<sub>2</sub> population segregated approximately 12:3:1 for continuous pistillate to monoecious to androecious, respectively. The p values ranged from .07 to > .95 for goodness of fit (Tables 2 to 5). Based on the ratios observed in the BC<sub>1</sub>P<sub>2</sub> and F<sub>2</sub> generations, an independently inherited digenic system is proposed. The significant number of androecious segregates in both the BC<sub>1</sub>P<sub>2</sub> and F<sub>2</sub> generations seems to discount a more complex system of inheritance for androecious expression.

A model was developed (Table 6) using the genetic nomenclature as proposed by previous researchers. The 2 loci involved are designated as *a* after Kubicki (9) and *acr* as originally designated by Shifriss (16, 17) and then by Kubicki (6, 7, 8). The female flower allele *A* is dominant to the male flower allele *a*. The *acr* locus controls female intensity with *acr*<sup>F</sup> homozygotes conditioning high female intensity; whereas *acr*<sup>+</sup> homozygotes exhibit a low female intensity. The sex expression of plants heterozygous for *acr* are intermediate between the homozygotes, but tend toward the *acr*<sup>F</sup> homozygote phenotypically (6). The *acr*<sup>F</sup> allele is epistatic to *a*. An *acr*<sup>+</sup> complement results in plants with continuous pistillate stage whereas *acr*<sup>+</sup> homozygotes do not. The difference between gynoecious and PF may be due to the strength of alleles at the *acr* locus (7) and/or modifier genes (7, 8, 16) and/or environment (2, 3, 4, 10, 16, 19). Plants of both monoecious and androecious phenotypes are *acr*<sup>+</sup>*acr*<sup>+</sup>. The difference between monoecious and androecious is that monoecious is *A*— whereas androecious is *aa*. Except for the difference between monoecious and androecious, it is beyond the scope of our data to show that *A*— adds to the femaleness of other sex phenotypes. For example, *aa acr<sup>F</sup> acr<sup>F</sup>* and *A — acr<sup>F</sup> acr<sup>F</sup>* are assumed of equal female intensity for this study and the proposed model.

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

Generation	Ratio	Genotype	Phenotype
Gynoecious Parent (P <sub>1</sub> )	1	<i>AA acr<sup>F</sup>acr<sup>F</sup></i>	Gynoecious
Androecious Parent (P <sub>2</sub> )	1	<i>aa acr<sup>+</sup>acr<sup>+</sup></i>	Androecious
F <sub>1</sub>	1	<i>Aa acr<sup>F</sup>acr<sup>+</sup></i>	Gynoecious/PF <sup>z</sup>
BC <sub>1</sub> P <sub>1</sub>	3/8	<i>A- acr<sup>F</sup>acr<sup>F</sup></i>	Gynoecious
	1/8	<i>aa acr<sup>F</sup>acr<sup>F</sup></i>	Gynoecious
	3/8	<i>A-acr<sup>F</sup>acr<sup>+</sup></i>	Gynoecious/PF
	1/8	<i>aa acr<sup>F</sup>acr<sup>+</sup></i>	Gynoecious/PF
BC <sub>1</sub> P <sub>2</sub>	1/4	<i>Aa acr<sup>F</sup>acr<sup>+</sup></i>	Gynoecious/PF
	1/4	<i>aa acr<sup>F</sup>acr<sup>+</sup></i>	Gynoecious/PF
	1/4	<i>Aa acr<sup>+</sup>acr<sup>+</sup></i>	Monoecious
	1/4	<i>aa acr<sup>+</sup>acr<sup>+</sup></i>	Androecious
F <sub>2</sub>	3/16	<i>A- acr<sup>F</sup>acr<sup>F</sup></i>	Gynoecious
	1/16	<i>aa acr<sup>F</sup>acr<sup>F</sup></i>	Gynoecious
	3/8	<i>A- acr<sup>F</sup>acr<sup>+</sup></i>	Gynoecious/PF
	1/8	<i>aa acr<sup>F</sup>acr<sup>+</sup></i>	Gynoecious/PF
	3/16	<i>A- acr<sup>+</sup>acr<sup>+</sup></i>	Monoecious
	1/16	<i>aa acr<sup>+</sup>acr<sup>+</sup></i>	Androecious

<sup>z</sup> PF = predominantly female.

A major deviation from the proposed genetic model occurred with crosses involving MSU 2A (Table 5). This was resolved by demonstrating the monoecious expression of this line under certain environmental conditions. Greenhouse experiments in the fall of 1973 demonstrated that the androecious expression of MSU 2A was unstable under low temp and/or short day conditions. Only under high temp and long day conditions (as with 1973 field experiments) was MSU 2A stable for androecious expression. Under short day (10 to 11 hr) and/or low night temp (10 to 12°C) conditions, MSU 2A exhibited monoecious expression (15). Generally, stronger femaleness in monoecious lines was observed with short days and low night temp conditions (2, 3, 4, 10, 16, 19) which may explain the monoecious expression of MSU 2A.

For these data (Table 5), MSU 2A does not fit a 2:1:1 BC<sub>1</sub>P<sub>2</sub> or a 12:3:1 F<sub>2</sub> ratio so the androecious and monoecious classes were combined and 1:1 BC<sub>1</sub>P<sub>2</sub> and 3:1 F<sub>2</sub> ratios, typical of monoecious

