renewal canes/plant would probably be exceeded greatly if plants were layback-pruned earlier in the season and treated with PBA after their second year of growth. Some rose growers do not like layback pruning because of the extra labor required in laying down the plants and their eventual removal. If sufficient renewal canes could be produced by some PBA-layback treatment, then the extended life of the plants might offset the additional labor costs.

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Parthenocarpy in *Cucumis sativus* L. as Affected by Genetic Parthenocarpy, Thermo-photoperiod, and Femaleness[1]

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Abstract. **Parthenocarpic fruiting of genetically parthenocarpic and non-parthenocarpic pickling cucumber lines was determined under different thermo-photoperiods. The genetically parthenocarpic line, MSU 364G, produced both earlier and more fruits under all thermo-photoperiod treatments than the genetically non-parthenocarpic line, Gy 3. This was especially true at high night temperatures (18°C). Thus, maximum selection pressure for yield in genetically parthenocarpic lines might be best exerted under high night temperatures. Conversely, the production or yield of parthenocarpic fruits was greatest under low night tempeartures (12°C). Hybrids involving either of these 2 parental lines and 2 hermaphroditic lines were intermediate for parthenocarpic yield. Yield of parthenocarpic lines was associated with intensity of femaleness, i.e., strong femaleness resulted in earlier fruiting and greater numbers of parthenocarpic fruits. The development of parthenocarpic pickling cucumber cultivars for once-over mechanical harvest seems practical by combining parthenocarpic with gynoecious genotypes.**

The use of parthenocarpy for pickling cucumber production has received increasing attention from researchers because of its apparent yield potential (1, 9, 17). Monoecious parthenocarpic cultivars have been used in glasshouses for many years, especially in Europe (27) and Japan. American plant breeders are now developing gynoecious strains with genetic parthenocarpy (1, 24). The genetic control of parthenocarpy was proposed as due to a single dominant gene expressing incomplete dominance with modifier genes (24).

On the other hand, parthenocarpy can be induced with plant growth regulators (5-8, 10, 22, 28-30). Auxins (10, 13, 14, 18, 20) and auxin transport inhibitors (3, 28, 29) have been particularly effective, but to-date, none have proven acceptable in commercial practice.

Parthenocarpy in cucumber is subject to the effect of various environmental factors (12, 13). In 1928, a comprehensive study of cucumber flowering and fruiting suggested parthenocarpy occurred under low light conditions (35). This was especially true of monoecious cultivars having low ratios of staminate to pistillate flowers (more femaleness). Both late and cool growing season conditions were especially effective in causing parthenocarpic fruiting (13). Nitsch and co-workers (18-20), found that low night temp and short daylength were primary factors enhancing parthenocarpy in monoecious cucumber. They observed that relatively older plants of both squash (*Cucurbita pepo* L.) and cucumber produced more parthenocarpic fruits than young ones. These plants produced pistillate flowers with "super" (larger than normal) ovaries which usually developed parthenocarpically.

The development of gynoecious cucumber lines has enabled the development of hybrid cultivars with predominantly female expression (23). The recent development of hermaphroditic pollen parents permits the production of 100% gynoecious hybrids when crossed with gynoecious seed parents (26). Accordingly, the opportunity exists to combine genetic

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parthenocarpy with gynoecious expression in the development of future cultivars for outdoor production. Theoretically, such cultivars should be higher yielding than conventional ones, especially for once-over mechanical harvest (1, 9).

The interaction of environmental factors with parthenocarpy probably complicates selection for genetic parthenocarpy in a breeding program. Hence, we studied the influence of night temp, photoperiod, and femaleness on parthenocarpic fruiting in genetically parthenocarpic and non-parthenocarpic lines of gynoecious pickling cucumbers.

Materials and Methods

The genotypic and phenotypic descriptions of the lines used are given in Table 1. Two of the 4 gynoecious lines are genetically parthenocarpic and 2 are non-parthenocarpic. The 2 hermaphroditic lines were genetically non-parthenocarpic. All lines have been previously described (1, 2, 23).

Table 1. Genotypes and phenotypes used to study the effect of genetic parthenocarpy, femaleness and environment on parthenocarpy of pickling cucumber.

MSU line	Parthenocarpy[z]		Sex[y]	
	Phenotype	Genotype	Phenotype	Genotype
364G	strong	*PP*	gynoecious	*MM/acr^{F}acr^F*
394G	weak	*PP*	gynoecious	*MM/acr^{F}acr^F*
Gy 3	non	*pp*	gynoecious	*MM/acr^{F}acr^F*
713-5	non	*pp*	gynoecious	*MM/acr^{F}acr^F*
4108H	non	*pp*	hermaphrodite	*mm/acr^{F}acr^F*
7152H	non	*pp*	hermaphrodite	*mm/acr^{F}acr^F*

[z]The genotype is based on Pike and Peterson (24). The degree or intensity of parthenocarpy may be an expression of modifier genes and/or polygenes.

[y]The genotype for sex expression is after Kubicki (16) and Shifriss and Galun (34). The *acr* locus is over-simplified as multiple alleles occur at this locus (16).

Seeds were planted in peat pots and individual seedlings selected for uniformity for transplanting into 20 cm pots. Plants were fertilized weekly by irrigating with a solution containing 1 part fertilizer (20.0% N: 8.9% P: 16.6% K) to 15 parts water, which provided approximately 6 g of fertilizer weekly to each plant. The main stem of each plant was trained vertically on a 2 m bamboo stake. Experiments were conducted from Feb. to April under greenhouse conditions. Day temp was maintained near 28 ± 2°C for all experiments. The naturally occurring daylength is less than 12 hr during this time. The combined effect of night temp and daylength on parthenocarpy was evaluated by the following 4 combinations of night temp with photoperiod.

1. HT-SD; high night temp (18±1°C) with short days (11 hr); natural daylight supplemented with cool white fluorescent light.
2. HT-LD; high night temp with long days (11 hr natural daylight plus supplemental light as above with an additional 5 hr of light from six 60-watt incandescent bulbs).
3. LT-SD; low night temp (12±1°C) with short daylength as above.
4. LT-LD; low night temp with long daylength as above.

Parthenocarpic fruits, normal in shape and size, were harvested when length exceeded 5 cm. Pollination could not have occurred due to the complete absence of pollinating insects during March and April in Michigan and to the use of greenhouses equipped with screened vents.

The rate of ethylene evolution was determined from the apices of 20-day old plants using methods previously reported (4, 31, 33). In experiments using gibberellin, plants were sprayed to run-off with an aqueous solution of 50 ppm $GA_{4/7}$ at the 2-leaf stage (25).

For each temp, a separate greenhouse was used as a whole plot which was split by photoperiod. The photoperiod subplot was then split by the appropriate number of lines with the number of single-plant replications as indicated in the tables. All other experiments were completely randomized with 6 to 8 single-plant replications.

Results

Genetic vs. non-genetic parthenocarpy. The degree or intensity of parthenocarpy might be measured by either the earliness of fruiting or the total number of fruits (27). As expected, the strongest parthenocarpic line, MSU 364G, produced the earliest fruits on the lowest nodes under most growth conditions (Table 2). Fruiting by this line was 7 to 32 days earlier than the weakly parthenocarpic and genetically non-parthenocarpic lines.

Hybrids derived from 3 gynoecious lines crossed with the 2 hermaphroditic pollen parents fruited similarly to the MSU 394G and Gy 3; i.e., a weak expression of parthenocarpy. However, the hybrid involving MSU 364G with MSU 7152H fruited earlier than did most other hybrids. Interestingly, Gy 3 and hybrids with Gy 3, the genetically non-parthenocarpic line, also fruited parthenocarpically under all environmental conditions. However, the 2 hybrids with the strongly parthenocarpic line, MSU 364G, usually produced more fruits although not always significantly more. Yield of parthenocarpic fruits was diluted in the hybrids of genetically parthenocarpic by non-parthenocarpic crosses comparable to the genetically non-parthenocarpic hybrids. Only MSU 364G × 7152H under LT conditions produced yields comparable to the strongly parthenocarpic and gynoecious parent, MSU 364G.

Influence of thermo-photoperiod. Elucidation of the effect of these 2 factors on parthenocarpic fruiting might enable breeders to apply greater selection pressure for early and high yield of parthenocarpic fruits. So the parthenocarpic fruiting of

Table 2. Effect of genetic parthenocarpy and thermo-photoperiod on parthenocarpic fruiting by pickling cucumber.[z]

MSU pedigree	Node no. 1st fruit				No. days to 1st fruit				Total no. fruit/plant			
	HT[y]		LT		HT		LT		HT		LT	
	SD	LD	SD	LD	SD	LD	SD	LD	SD	LD	SD	LD
Genetically parth												
364G (strong)	2.8b	5.3c	4.8d	6.5e	45.2c	44.5d	58.0b	69.0c	14.1a	12.0a	14.0a	11.0a
394G (weak)	17.0a	18.3ab	15.8a	12.8bc	67.3a	76.0ab	79.8a	75.8abc	7.0bc	3.0c	3.5d	9.6ab
Genetically nonparth												
Gy 3	17.0a	17.2ab	9.6c	10.6cd	71.5a	75.4ab	75.8a	80.8ab	5.0c	2.8c	9.0b	9.0abc
F_1 hybrids												
364G × 4108H	17.3a	16.6ab	11.0bc	11.8bc	63.0ab	66.7abc	75.5a	71.7bc	6.8bc	5.8bc	6.8bcd	6.0bc
364G × 7152H	17.5a	16.1ab	9.0c	8.0de	52.5bc	56.0cd	61.5b	58.6d	9.3b	7.1b	13.6a	11.6a
364G × 4108H	19.5a	20.0ab	13.3abc	15.6ab	67.2a	77.5a	73.7a	75.2abc	7.5bc	4.1bc	9.1b	6.5bc
364G × 7152H	19.3a	20.0ab	14.6abc	14.4abc	65.7a	65.8abc	81.0a	73.0abc	6.6bc	3.3c	8.3bc	6.0bc
Gy 3 × 4108H	20.0a	21.5a	12.0abc	17.0a	73.2a	75.0ab	81.7a	82.0a	6.1bc	3.8c	4.5cd	4.5c
Gy 3 × 7152H	13.4a	14.6b	13.2abc	13.0abc	61.2ab	63.3bc	75.3a	75.8abc	5.3bc	5.0bc	8.6bc	6.0bc

[z]Means are averages for 6 plants; mean separation in columns by Duncan's multiple range test, 5% level. Experiment was terminated after 94 days.

[y]HT = 18°C, LT = 12°C, SD = 11 hr, and LD = 16 hr.

the 2 genetically parthenocarpic lines, having different intensities of parthenocarpic expression as reflected by their yields, was compared to a genetically non-parthenocarpic line. For these 3 gynoecious lines, night temp was more important than photoperiod (Table 2). The strongly parthenocarpic line produced the most fruits under all conditions, but especially under the HT treatment. The LT treatment generally delayed fruiting of all lines and hybrids, although fruiting occurred on lower nodes. This was probably caused by the overall reduction in growth rate. Differences in parthenocarpic fruiting were greatest for HT-LD treatments where as much as 4 times or more fruits were produced by stronger than both weaker parthenocarpic and genetically non-parthenocarpic lines. Logically, then, the combination of HT-LD should provide the greatest selection pressure for genetic parthenocarpy. Generally, the temp and photoperiod induced differences in the parthenocarpic expression of these hybrids between gynoecious and hermaphroditic lines which were intermediate, but tended towards the parthenocarpic parent.

Femaleness and parthenocarpy. To further separate genetic parthenocarpy from other factors, the effect of femaleness on parthenocarpic fruiting of genetically non-parthenocarpic lines was determined. We suggest that the intensity of femaleness might be measured by the rate of ethylene evolution, number of staminate flowers induced after GA treatment (21), and phenotypic stability for gynoecious expression under different environmental conditions.

Table 3. Ethylene evolution from the apices of 20-day-old gynoecious and hermaphroditic cucumber plants and their hybrids.

MSU pedigree	Sex phenotype	Ethylene nl•hr^{-1}/apice[z]
Gynoecious		
Gy 3	Gynoecious	0.056c
713-5	Gynoecious	0.057c
Hermaphroditic		
7152H	Hermaphrodite	0.093b
4108H	Hermaphrodite	0.060c
F_1 hybrids		
Gy 3 x 7152H	Gynoecious	0.112a
713-5 x 7152H	Gynoecious	0.086b
Gy 3 x 4108H	Gynoecious	0.132a
713-5 x 4108H	Gynoecious	0.113a

[z]Means are averages for 6 plants; mean separation in column by Student-Newman-Keuls multiple range test, 5% level.

Both of the non-parthenocarpic gynoecious lines (Gy 3 and 713-5) evolved relatively high rates of ethylene (Table 3), which agreed with earlier reports (4, 31, 33). However, the hermaphroditic lines evolved ethylene at rates as high or higher than the gynoecious lines. Furthermore, there was a heterotic effect as all hybrids but one evolved significantly more ethylene than did the parental lines. This high degree of femaleness was further substantiated by the relative difficulty of staminate flower induction by $GA_{4/7}$ treatment. Relatively few staminate flowers were induced on most of the hybrids as compared to the parental gynoecious and hermaphroditic lines (Table 4).

Phenotypic stability for sex expression under various conditions was determined for the hermaphroditic parents (Table 5). The phenotypic stability of gynoecious lines has been reported in several studies (11, 15, 16, 23). In our study, under certain growth conditions, the hermaphroditic lines expressed staminate (HT-LD) or pistillate (LT-SD) flowers in addition to bisexual ones (Table 5). The line, MSU 7152H, produced several (3.5) pistillate flowers under LT-SD, whereas none was observed on MSU 4108H. Hence, MSU 7152H appeared to express more femaleness than MSU 4108H.

The intensity of parthenocarpic fruiting was measured under HT vs. LT regimes (Table 6). As expected, the yield of parthenocarpic fruits was less under HT than LT conditions, although fruiting was considerably delayed with LT. Furthermore, the hybrid plants produced more fruits than their gynoecious parents. Hence, genetically non-parthenocarpic fruiting was enhanced by a strong female intensity as measured by ethylene evolution, GA-induced staminate flowers, and phenotypic stability of gynoecious expression.

Table 4. Effect of $GA_{4/7}$ on the phenotypic stability of sex expression in gynoecious and hermaphroditic cucumbers and their hybrids.[z]

MSU pedigree	GA	No. of nodes with ♂	No. of nodes with ♀	No. of nodes with ☿	No. of flowers ♂	No. of flowers ♀	No. of flowers ☿
Gynoecious							
Gy 3	–	0	9.5a	0	0	19.7a	0
	+	3.5a	5.3b	0	12.8a	12.7b	0
713-5	–	0	8.8a	0	0	18.3a	00
	+	3.7a	5.3b	0	13.2a	10.2b	0
Hermaphroditic							
7152H	–	0	0	9.3a	0	0	40.7a
	+	2.7b	0	6.0b	10.8a	0	23.8b
4108H	–	0.4c	0	10.8a	0.5c	0	37.3a
	+	3.8a	0	3.8b	10.2a	0	19.0b
F_1 hybrids							
Gy 3 x 7152H	–	0	9.0a	0	0	20.2a	0
	+	3.3a	5.2b	0	11.7a	13.2ab	0
713-5 x 7152H	–	0	8.6a	0	0	10.8b	0
	+	0.7bc	7.5a	0	0.3c	11.7b	00
Gy 3 x 4108H	–	0	8.5a	0	0	15.8b	0
	+	0.2c	8.5a	0	0.5c	13.3ab	0
713-5 x 4108H	–	0	8.3a	0	0	12.8b	0
	+	1.5b	5.8b	0	5.2b	12.7b	0

[z]Means represent averages for 6 plants; mean separation in columns by Student-Newman-Keuls multiple range test, 5% level. Experiment terminated after 45 days.

Table 5. Phenotypic stability of sex expression in hermaphroditic lines of cucumber as influenced by temperature and daylength under greenhouse conditions.

MSU pedigree	Environmental condition		Flower sex[z] ♂	Flower sex[z] ♀	Flower sex[z] ☿
4108H	HT	LD	0.4	0	47.9
	HT	LD	0	0	54.5
	LT	LD	0	0	48.8
	LT	SD	0	0	47.2
7152H	HT	LD	0.2	0	48.0
	HT	SD	0	0	47.1
	LT	LD	0	0.67	39.5
	LT	SD	0	3.50	39.7

[z]Means represent averages for 8 plants; all flowers were classified for the first 20 nodes.

Table 6. Effect of night temperature on genetic, non-parthenocarpic fruit development in cucumber.[z]

MSU pedigree	No. of fruit/plant High temp	No. of fruit/plant Low temp	Days to 1st fruit High temp	Days to 1st fruit Low temp
Gy 3	1.6b	3.3c	63.0a	86.0a
713-5	1.7b	4.7bc	70.0a	86.5a
Gy 3 x 7152H	4.0a	9.6a	56.0b	84.2a
713-5 x 7152H	2.5b	6.3b	63.7a	83.0a
Gy 3 x 4108H	2.4b	4.4c	67.0a	86.3a
713-5 x 4108H	3.5b	4.2c	62.3a	87.0a

[z]Means represent averages for 8 plants; mean separation in columns by Student-Newman-Keuls multiple range test, 5% level. Experiment terminated after 100 days; high temp = 18°C and low temp = 12°C.

Discussion

Parthenocarpy is the formation of fruit without fertilization of the ovules (18, 20). As expected, plants of the strongly genetically parthenocarpic line produced some 2 to 4 times more fruits than genetically non-parthenocarpic plants under growth conditions conducive to parthenocarpy (Table 2). The thermo-photoperiod treatment of LT-SD, which enhanced parthenocarpy, concurs with earlier work with monoecious

cultivars (18-20, 35) and gynoecious hybrids (1).

Mescherov and Yuldasheva (17) refer to the "intensity" of parthenocarpy, suggesting either a major gene with polygenes or quantitative inheritance of parthenocarpy. Our data indicate the degree or intensity of parthenocarpy could be measured by both the earliness of fruiting and the total number of parthenocarpic fruits. These 2 criteria could be used by plant breeders to measure the parthenocarpic yield potential of a given plant or breeding line. Hence, selection for high yielding parthenocarpic segregates or lines might be based on early fruiting alone. This would have the further advantage and convenience of selection before profuse vine growth makes individual plant selection difficult.

However, consideration must be given to the cultural practices and particular harvest system for which the parthenocarpic variety is aimed. Besides high yield, the fruiting pattern must be more concentrated for once-over harvest than for multiple harvest systems. Thus, earliness of yield might be compromised somewhat to provide more vine growth to support higher fruit numbers per plant for once-over harvest (1, 9).

Under HT conditions, parthenocarpic fruiting was much reduced in the genetically non-parthenocarpic line, Gy 3, regardless of daylength (Table 2 and 6). However, the best genetically parthenocarpic line produced 12 and 14 fruits per plant respectively, under HT with LD or SD conditions. Seemingly, then, the maximum selection pressure for genetic parthenocarpy in plant breeding programs would be realized under HT-SD conditions.

The association of female intensity with parthenocarpy is not surprising. Tiedjens (35) found that monoecious lines with high female/male ratios of flowers were more parthenocarpic than those with low ratios. Nitsch and co-workers (17-19) proposed a sequence of 4 physiological stages for flowering and fruiting in monoecious cucumber and other cucurbits. They viewed the monoecious cucumber plant as a multiple inflorescence which initiates flowering with strongly male expression, followed by a mixture of male and female flowers, then a continuous female stage which terminates with parthenocarpic fruiting. This final stage represents the ultimate in the feminization process. It is often associated with late season effects including strong femaleness, low temp, and short days (1, 12, 13, 35). We would speculate that genetically gynoecious, parthenocarpic lines represent genetic selection for the fourth and last physiological stage in the flowering and fruiting of cucumber.

Nitsch (18-20) and others (1, 12-14) suggest that high auxin levels in the ovary are most likely responsible for parthenocarpy. Indirect evidence for auxin as the mechanism for parthenocarpy in cucumber comes from exogenous applications of auxin (10, 13, 14, 20) and auxin transport inhibitors (3, 28, 29) which induce parthenocarpy. The effect of photoperiod on parthenocarpy can likewise be explained as an auxin effect. Rudich and co-workers (32) demonstrated that short photoperiods increased auxin activity, which might account for increased parthenocarpy. We have preliminary data (unpublished) which supports the hypothesis that there may be higher endogenous auxin activity in the ovaries of genetically parthenocarpic than non-parthenocarpic lines. However, more definitive studies are required before this hypothesis can be accepted as a possible basis for genetic parthenocarpy.

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