ABSTRACT

THE INHERITANCE AND RELATED STUDIES
OF THE PARTHENOCARPIC CHARACTER
IN CUCUMBER, *CUCUMIS SATIVUS* L.

by Leonard Maxwell Pike

Parthenocarpy in the cucumber is conditioned by an incompletely dominant gene *P-*. Heterozygous *Pp* plants produce fruits later and generally fewer in number than the homozygous *PP* genotype. Homozygous recessive *pp* plants do not produce parthenocarpic fruits.

All plants in progenies derived from a backcross to the non-parthenocarpic parent were classified as non-parthenocarpic when fruiting was identified by means of trapping pistilate flowers to prevent pollination. The fact that six out of eighteen progenies from plants self-pollinated in this backcross generation segregated typical *PP* plants that were parthenocarpic and multiple-fruiting is evidence for incomplete dominance.

Cage isolation of gynoecious progenies segregating for parthenocarpy is an effective technique for identifying late fruiting heterozygous plants. The difficulty of trapping all pistilate flowers over the entire fruiting period resulted in incorrect classification of heterozygous plants,

especially in progenies segregating for monoecious sex expression with very late pistilate flower production. Homozygous _PP_ plants were identified accurately in the F_2 by selecting for early, multiple fruiting in parthenocarpic plants. Progenies from selfed F_2 plants of this type produced only the parental type of F_3.

Modifying genes may influence fruit numbers since 19 of 54 plants classified as _Pp_ produced three or more late fruits.

The smooth, non-ridged skin of Spotvrije is conditioned by the homozygous recessive _snr_, _snr_.

Gynoecious parthenocarpic plants exhibit earlier fruiting than monoecious and are necessary for field production of seedless fruits.

Parthenocarpic fruits ten inches long and 2 1/2 inches in diameter did not brine satisfactorily unless pricked. Six inch fruits, 1 1/2 inches in diameter, brined as well as seed fruits the same size.

A consumers panel showed no preference between parthenocarpic and seed-type fresh market cucumbers but preferred the products processed from seedless fruits.

It was demonstrated that multiple-fruiting, parthenocarpic varieties suitable for mechanical harvesting can be developed and that seedless cucumbers and processed products will be accepted by consumers.

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INTRODUCTION

The processing cucumber industry in Michigan during 1960-1964 averaged 25,000 acres which yielded 122,000 tons with a farm value of approximately seven million dollars based on 55 dollars per ton. In 1965, 17,000 acres were grown producing 95,000 tons at a value of 93 dollars per ton. In 1966, 21,000 acres yielded 122,000 tons at a value of 91 dollars per ton. Increase in value per ton from 55 dollars to over 90 reflects added cost of labor for harvest resulting from minimum wage law and increased use of domestic labor following termination, on December 31, 1964, of Public Law 78 which provided for importing Mexican laborers.

The acute shortage of labor for harvesting processing cucumbers has cost growers and processors in Michigan more than three million dollars per year in labor costs alone. It has threatened the loss of at least part of the fifty million dollar pickle industry to competing areas where labor problems are not so acute or where mechanical harvesting can be more easily accomplished.

Ideals for plant phenotypes of new varieties suitable for mechanical harvesting have varied among engineers, processors and plant breeders but one fact generally accepted is the need for multiple fruiting by the cucumber plant.

The work reported here was undertaken to determine the inheritance and possible utilization of parthenocarpy in developing cucumber varieties for the new mechanical harvesters. Successful genetic control of this character and its incorporation into acceptable varieties might contribute to achieving the concentrated fruiting and higher yields needed for mechanical harvesting.

REVIEW OF LITERATURE

CHARACTERISTICS OF THE CUCUMBER

I. Qualitative

The cucumber, *Cucumis sativus*, has been used by geneticists for studying inheritance of many fruit and plant characteristics. The advantages of great variability and a relatively short life cycle led many researchers to explore and to report on its characteristics. This review is limited to literature dealing with improvement of quality, yield, or other characteristics pertinent to this study.

The development of any crop variety is generally the result of some demand imposed upon it either by nature or man to alter its genetic construction. Qualitative characters, generally established by the cucumber processing industry and consumer preferences, stimulated investigations by researchers.

Fruit shape was studied very early by Tiedjens (36) who noted that environmental influence was important in developing well-shaped fruits. Spine color, number of spines, wartiness, skin color, skin toughness, and flesh color have been listed as important by processors. Wellington (39) reported that black spines are dominant to white, coarse spines dominant to fine and few spines dominant to numerous spines. Strong (33) later reported that mottled fruit color was dominant to non-mottled, wartiness dominant to non-warty fruits, green flesh dominant to white flesh color and thick, tough skin dominant to thin, tender skin. He noted what appeared to be a linkage between the group of mottled, dull, warty, thick tough skin characters and the group of non-mottled, glossy, non-warty, thin tender skin characters. Younger (41) reported that three-locule fruits were dominant over five-locule fruits.

Bloating, a term applied in the industry to fruits which develop internal cavities during the fermentation process, is of great importance. Bloaters can not be used in any cut product except relish. The inheritance of the bloating tendency has not been reported but is presently being investigated at Michigan State University. The inheritance of a bitter tasting compound was found by Barham (3) to be conditioned by a single dominant gene. Later Andeweg (1) reported a single recessive gene for non-bitter and outlined methods for selecting the non-bitter genotype.

Quality of the cucumber often depends upon its freedom from infection by disease producing organisms. Important contributions have been made to understanding the inheritance of disease resistance and incorporating it into useful varieties. Shifriss, Myers, and Chupp (28) reported that resistance to cucumber mosaic virus was conditioned by multiple genes. A later report by Wasuwat and Walker (38) established that the resistance was conditioned by a single dominant gene with possibly modifying genes. Both Walker (37) and Andeweg (1) found scab resistance to be controlled by a single dominant gene. Barnes and Epps (4), (5), found resistance to anthracnose varied from almost complete dominance to a highly complex type of inheritance. Busch and Walker (8) reported finding a similar type of resistance. The inheritance of downy mildew resistance was reported by Jenkins (16) to be conditioned by a large number of genes. Smith (32) reported that resistance to powdery mildew is multigenic.

II. Plant Characteristics

In some of the first studies concerned with multiple-pick mechanical harvesting, Stout and Ries (34) described problems of vine entanglement and foliage damage. It was demonstrated that a great disadvantage of multiple-pick machines then available was that they could not remove fruits borne within six inches of the base of the plant.

The demand for developing new varieties of cucumbers acceptable for mechanical harvesting led several researchers to investigate plant characteristics. Phenotypes suggested as suitable for mechanical harvesting varied from dwarf vines to indeterminant having either many laterals or no laterals. Hutchins (14) reported in 1940 that determinant plant growth in the cucumber is dominant to indeterminant and that tall plants are dominant to dwarf. Odland and Groff (20) later reported finding what was assumed to be a different determinant since they demonstrated that in their material indeterminant habit was dominant to determinant.

Researchers interested in adapting plants for a multiple-pick harvester investigated vine habits which would permit multiple pickings with the least damage to the vines. Bowers (6) reported a radiation-induced mutation for absence of tendrils. Rowe and Bowers (26) later reported that the tendrilless character is conditioned by a single recessive gene and suggested this character might prevent tangling in multiple harvesting of cucumbers. Burnham (7) investigated the inheritance of branching, sex reversal, and ease of stem separation from the fruit. He demonstrated the branching character was conditioned by a polygenic system, in which a threshold number of heterozygous loci interact with the environment. He reported that five generations of inbreeding failed to fix sex-reversal in which the plant produces several nodes with male flowers and then converts to gynoecious. He observed an almost constant 1:1 segregation for sex reversal and normal monoecious types. The ease of stem separation was shown to be related to the area of stem attachment of the fruit.

III. Development of Cucumber Varieties for Mechanical Harvesting

The rapid change from manual to mechanical harvesting of processing cucumbers created the need for modifying the cucumber plant. Greatest emphasis has been on qualitative characteristics such as fruit color, spine color, length/width ratio, and bloating of the fruit during brining. A cucumber plant acceptable for mechanical harvesting must resist mechanical damage from multiple harvest by machines or for a single destructive harvest it must produce several marketable fruits at one time even at high plant populations. Peterson (21) used gynoecious sex expression from the variety Shogoin (PI 220860) in a backcrossing program to develop MSU 713-5, a gynoecious line of pickling cucumber. This development made possible the use of hybrids in which greater uniformity of maturity could be obtained. Peterson and Anhder (22) discovered that gibberellin A_3 induced staminate flowers on gynoecious plants and proposed a method for maintaining gynoecious lines. The hybrid pickling cucumber Spartan Dawn described by Peterson and deZeeuw (23) was released in 1961. It consistantly out yielded standard monoecious varieties and proved to be acceptable for mechanical harvesting. Many similar hybrids are now being produced with most using MSU 713-5 or derivaties of it as the female parent.

The inheritance of the sex expression in cucumber was reported by Shrifriss (27), who found three groups of genes conditioned the expressions. He listed one major gene for differentiating pistillate flowers, a group of poly-genes which regulate speed of sex conversion, and a major gene (Acr) which accelerates the speed of conversion.

Mitchell (18) hypothesized that sex expression was controlled by levels of endogenous auxins. However, these substances were not identified. Hayashi (15) found that monoecious cucumber seedlings contained greater quantities of gibberellin A_1 or A_3 than gynoecious.

Burnham (7) reported that the multiple fruiting habit of Rhensk Drue was expressed in F_1 between MSU 713-5 and Rhensk Drue.

IV. Cultural Practices Contributing to Mechanical Harvesting

Besides the genetical rearrangement used to increase yields for a once-over harvest, cultural practices have been explored. Cucumbers previously were grown at wide spacings of forty-two to forty-eight inches between rows and one foot or more between plants within the row. The main reasons were that most farm machinery was fitted for those spacings, and irrigation was neither available nor economical. Ries (24) studied the effect of spacing and supplemental fertilizer application and found both early and total yields of pickling cucumbers could be increased by close spacing. Putnam (23) showed the number of fruits per plant was greater at one foot spacing than at six inches and dollar yields were highest using 43,560 plants per acre. Higher populations did not increase dollar yields.

V. Observations Concerning Concentrated Fruit Set

Probably the most limiting factor in the development of varieties suitable for mechanical harvesting is that multiple fruiting does not occur in standard varieties of cucumbers. McCollum (17) and Dearborn (9) reported that a developing fruit exerts an inhibitory effect on further vegetative development in cucumber plants. This has led some investigators to believe that developing embryos produce a growth regulating substance which limits further vegetative growth. Tiedjens (36) noted a difference between varieties in their capacity to mature a number of fruits at the same time. He felt this was due to the time of flowering since in his observations flowers pollinated at the same time developed equally well while later pollinated fruits did not develop once the first fruit began growing. Putnam (24) found from growth measurements of normally developing and arrested fruit that both showed similar growth for the first two days after pollination, but after the third day the arrested fruit showed no further increase in size.

VI. The Parthenocarpic Fruiting Character

It is evident that manipulations of the cucumber phenotype and alterations of cultural practices have not yet solved the problem of obtaining concentrated fruiting. If earlier reports are correct in assuming seed development inhibits subsequent fruit from developing it seems logical that a fruit which produced no seeds would permit a more concentrated fruit production.

Parthenocarpic varieties of cucumbers have been used for many years in European greenhouse production. These varieties have not been used in outdoor production because pollination by insects results in unmarketable seed-fruits which have a depressing effect on subsequent pollinations similar to that of early fruits borne on non-parthenocarpic varieties. Peterson (21) proposed incorporating parthenocarpy into gynoecious lines for greenhouse production. Wellington and Hawthorn (40) studied the character while developing an intermediate length fruit for use in American greenhouses. However, with the small populations used in their breeding work the genetic data was not conclusive. In crosses of White Spine with Telegraph and White Spine with Richard Invincible no seedless fruits were developed on F_1 plants. Upon replanting F_1 seed the following year one plant produced a parthenocarpic fruit. This led to the assumption that the character is incompletely dominant. In a cross of Fiske White Spine and Early Russian, six F_1 plants produced a single parthenocarpic fruit, one plant produced two and twelve plants produced none. In a backcross to Richard Invincible a progeny of six plants had only one that produced a single parthenocarpic fruit. In a cross of Arlington White Spine x Rochford Market the F_1 produced no parthenocarpic fruits but an F_2 plant, selfed because of its shape and color, produced an F_3 progeny in which all plants developed parthenocarpic fruits. The following F_4 generation also produced only plants with parthenocarpic fruiting. Wellington and Hawthorn (40) also noted a difference in the capacity of the European varieties to produce high numbers of fruits.

In a genetic study on the inheritance of the parthenocarpic character in diploid bananas, Dodds and Simmond (10) found the character to be controlled by a dominant gene with additional modifier genes being responsible for the varying degrees of parthenocarpic fruit set.

VII. Physiological Factors Associated with the Parthenocarpic Character

Parthenocarpic fruit development has been studied in several species of plants. Fitting (11) noticed ovary development in orchids occurred in some cases if either foreign or dead pollen was applied to the stigma. He also demonstrated that water and absolute alcohol extracts of pollen induced ovary development. Thimann (35) then demonstrated that pollen extracts caused a curvature of *Avena* coleoptiles. Gustafson (12) studied ovary enlargement after observing that seedless fruit sometimes developed following attempted crosses between species or genera of plants. Seed never developed following these wide crosses but parthenocarpic fruit development occasionally occurred. Chloroform extracts of pollen from *Curcurbita maxima* were found to produce ovary development if applied to cucumbers. Usually the ovaries only doubled in size. In a later study Gustafson (13) demonstrated that ovaries from parthenocarpic varieties of oranges, lemons, and grapes contained much higher auxin levels at the bloom state than did ovaries from seed-developing types. Two to four weeks after pollination the seed types attained auxin levels as high or higher than the parthenocarpic types. He suggested that this relationship should hold true for other species of plants producing parthenocarpic fruits. He also concluded that pollination and developing seeds produced auxin. Gustafson stated that auxin in parthenocarpic varieties was produced either in the ovaries themselves or was transferred into the ovary from the leaves.

Sinnott (29), (30), (31), analyzed the relation between cell development and ovary development in the cucumber and found that cell division occurs up until anthesis.

Further ovary development then proceeds by cell enlargement without appreciable cell division. He also noted that ovary development proceeded at a constant exponential rate, slowing down only as the fruit approached maturity.

Nitsch (19) performed an extensive study of plant hormones in the development of fruits of several species. He observed and reported the following:

1. Previous assumptions that the fruit nourished the ovules were found to be false.
2. It is apparent that chemical stimuli for ovary development comes from: a. vegetative parts of the plant; b. the pollen and/or pollen tubes; c. the ovules.
3. Auxins influence the transformation from a vegatative to reproductive phase.
4. In gherkin ovaries growth proceeded so smoothly and quickly that no differences could be detected in ovary growth before and after pollination, but in slower developing ovaries of orchids two growth peaks were observed, one following pollination and a second as ovules began to develop.
5. Since such low levels of auxin are present in pollen, possibly a hormone in pollen converts tryptophane to auxin in the ovary.
6. Both pollen and ovary tissue produced auxin when incubated in the presence of tryptophane.

7. The developing seeds promoted growth of ovaries as evidenced by the observation that growth stopped if the ovules were removed or destroyed before a certain stage of development had been reached.
8. Plants which produced parthenocarpic fruits probably have genes for increased auxin production.
9. Indole-3-acetic acid was ineffective in producing parthenocarpic fruits. Possible reasons are that it was rapidly destroyed during application, or by plant enzymes, or that IAA is not the fruit setting hormone.

EXPERIMENTAL

INHERITANCE AND RELATED STUDIES OF THE PARTHENOCARPIC CHARACTER 1965

Materials and Methods

During the summer of 1964, an inbred gynoecious pickling cucumber MSU 713-205 was crossed to the European, parthenocarpic variety, Spotvrije. Twelve F_1 plants, grown in the greenhouse during the fall of 1964 were vigorous, predominantly female, and did not produce parthenocarpic fruits by the time they had grown to the height of approximately four feet. From this observation it was concluded that parthenocarpic is not dominant to non-parthenocarpic fruiting or that the inheritance of parthenocarpy in varieties used by Wellington and Hawthorn (40) differed genetically from that of the variety Spotvrije.

A genetic study was outlined to determine the inheritance of the parthenocarpic character. Crosses were made between MSU 713-205 and Spotvrije and the F_1 was selfed and backcrossed to both parents. Spotvrije was also crossed to gynoecious lines MSU 713-5, MSU 153, MSU C-29-63 and MSU C-14-64 to be observed in the summer of 1965.

Seed was planted in peat pots in the spring of 1965 and transplanted to the field in the first true leaf stage. A spacing of four feet between rows and two feet between plants within the row was used.

The population for observation included 24 plants of each parent, MSU 713-205 and Spotvrije, 48 F_1 plants, 104 of the F_2, 89 of the backcross to MSU 713-205, and 91 of the backcross to Spotvrije. Twenty-four plants of each F_1 in which Spotvrije was crossed with MSU 713-5, MSU 153, MSU C-29-63, and MSU C-14-64 were observed for parthenocarpic fruiting.

In order to test the plants for the parthenocarpic fruiting character, all female flowers were trapped the day previous to blooming using Top Clip No. 2 paper clips to prevent pollination.

It soon became evident that trapping all pistilate flowers in these large populations would be very difficult so a goal of ten trapped flowers per plant was established.

Data were recorded when as many plants as possible had ten female flowers trapped. Because of extreme maleness some plants did not produce ten pistilate flowers during the period of trapping. In these cases all pistilate flowers on the plant were trapped through July 21. Trapping was discontinued at this time because of excessive vine growth.

Records were taken on sex expression, fruit type, number of parthenocarpic fruits, date of flowering, and skin type. Sex expressions were classified as monoecious, predominantly female, and gynoecious. Fruit types were divided into three classes: short, medium and long. Parthenocarpy was classified on the basis of development of one or more fruits without pollination. Date of flowering was recorded when the first pistilate flower reached anthesis. Skin type was classified as smooth or rough.

The phenotypic expressions of sex, fruit type and skin type were evaluated as follows:

1. Sex types

    a. Gynoecious (G) - plants producing no staminate flowers.

    b. Predominantly female (PF) - plants producing staminate flowers in the first to fifth nodes and producing only pistilate flowers thereafter.

    c. Monoecious (M) - plants producing predominantly staminate flowers with only occasional pistilate flowers.

2. Fruit types

    a. Short - an approximate classification of pickle type fruits resembling MSU 713-205.

    b. Medium - an approximate classification given to fruits with lengths generally intermediate between those of MSU 713-205 and Spotvrije.

    c. Long - an approximate classification given to fruits which were of the general length of Spotvrije.

3. Skin types

    a. Rough skin - fruits with rough or ridged skin typical of MSU 713-205 and American processing varieties.

b. Smooth skin - fruits with the non-rigid skin of Spotvrije.

Sex expressions, fruit types, date of flowering, and skin types were recorded to detect any linkage with parthenocarpic fruiting.

Results and Discussion

Inheritance of the Parthenocarpic Character

Observations made in 1965 indicated that parthenocarpy was not conditioned by a single dominant gene. None of the F_1 plants produced any parthenocarpic fruits during the period of trapping. In the F_2 population only 23 plants produced parthenocarpic fruits where 78 plants were expected if expression is due to a single dominant gene. Only five plants were classified as parthenocarpic in the backcross to MSU 713-205 while 44 were expected and 49 were classified as parthenocarpic in the backcross to Spotvrije where 91 were expected.

The data in Table 1 show that genetic ratios were a good fit for a single recessive gene controlling the parthenocarpic character except for the backcross to MSU 713-205. The five out of 89 plants in the backcross to MSU 713-205, which produced at least one parthenocarpic fruit, disproved the single recessive gene theory since homozygous recessives for parthenocarpy could not occur in the backcross to non-parthenocarpic. The ratios observed in 1965 will be discussed in more detail along with the data secured in 1966. However, these data suggested something other than single gene action with complete dominance. The results could only be explained on the basis of incomplete dominance and the failure to properly identify the phenotype of heterozygotes in the F_1, F_2, and backcross populations.

Relation of Sex, Fruit Type, Skin Type, and Flowering Date to Parthenocarpic Fruiting

It was not possible to observe a relation between fruit length and parthenocarpy in the F_2 population since only three plants out of 104 were classified as having short fruit and none were recorded as short in the backcross to Spotvrije. No relationships were observed in the backcross to MSU 713-205 since all fruits had the rough skin and only five plants were classified as parthenocarpic.

Sex expression and skin types segregated as expected in both the parthenocarpic and non-parthenocarpic portions of the populations indicating that no linkages existed between these characteristics and parthenocarpy.

Relation of Sex Expression and Earliness

The relation of sex expression and earliness of flowering is shown in Tables 2, 3, and 4.

Table 1. Segregation for parthenocarpic fruiting in cucumber progenies in 1965. A test for a single recessive hypothesis.

Pedigree	Number Classified	Fruiting Habit				P	X^2
		Observed		Expected			
		Parth.	Non-Parth.	Parth.	Non-Parth.		
MSU 713-205 (non-parth.)	24	0	24	0	24	--	--
Spotvrije (Parth.)	24	24	0	24	0	--	--
(205 x Spot.) F_1	48	0	48	0	48	--	0.00
(205 x Spot.) F_2	104	23	81	26	78	.49	.47
205 (205 x Spot.)	89	5	84	0	89	--	∞
(205 x Spot.) Spot.	91	49	42	45.5	45.5	.47	.54

Table 2. The relationship between sex expression and earliness of female flowering as observed in F_2 generation of the cross MSU 713-205 and Spotvrige.

Anthesis of First Pistilate Flowers in the F_2 Population			
Sex Expression	Range of Flowering	Average Date	Total Plants
Gynoecious	6-30 → 7-13	7-5	29
Predominantly Female	6-30 → 7-14	7-6	33
Monoecious	7-1 → 7-21	7-11	42

Table 3. The relation between sex expression and earliness of female flowering as observed in the backcross to MSU 713-205.

Anthesis of First Pistilate Flowers in the BC_1 to MSU 713-205			
Sex Expression	Range of Flowering	Average Date	Total Plants
Gynoecious	6-30 → 7-10	7-2	58
Predominantly Female	7-1 → 7-15	7-4	31
Monoecious	-[a]	-	0

[a]There were no monoecious segregates in the backcross to MSU 713-205.

Table 4. The relation between sex expression and earliness of female flowering as observed in the backcross to Spotvrije.

Sex Expression	Anthesis of First Pistilate Flowers in the BC_1 to Spotvrije. Range of Flowering	Average Date	Total Plants
Gynoecious	-[a]	-	0
Predominantly Female	7-1 → 7-8	7-5	12
Monoecious	7-10 → 7-21[b]	-[c]	79

[a]There were no gynoecious segregates in the backcross to Spotvrije.

[b]July 21 was the latest date recorded for anthesis of the first pistilate flower due to excessive vine growth and labor required for trapping in the study.

[c]No average can be shown since a few plants were so extremely male that female flowers were not produced until some time after July 21.

The observations of sex expression and earliness of the first pistilate flower established the following points:

1. Gynoecious or predominantly female cucumber plants have the potential for developing fruit earlier than monoecious plants.

2. The earliness associated with the gynoecious and predominantly female plants indicated that an earlier crop of greenhouse grown parthenocarpic fruits could be obtained in a gynoecious variety. There is a potential increased number of fruit because of the greater number of pistilate flowers.

3. In addition to earliness in gynoecious plants, cucumber greenhouses would not have to be screened if the parthenocarpic variety was also gynoecious. If insect pollinations occur the resulting seed-fruits are deformed in the area of seed development and are unmarketable.

Another fact of great importance is that gynoecious parthenocarpic varieties could be produced under isolated field conditions since, without a source of pollen, there would be no production of seed fruits.

Inheritance of Skin Types

The two distinctly different skin types of MSU 713-205 and Spotvrije were studied in addition to the parthenocarpic character and are shown in Figures 1 and 2. It was observed that the ridged skin associated with MSU 713-205, was independent of spine color, fruit length or shape. It was also independent of uniform green and mottled fruit. The skin of Spotvrije was smooth with no ridges or warts. Table 5 illustrates the inheritance of this character.

The data illustrates a good fit if the skin type of the European variety, Spotvrije is assumed to be controlled by a single homozygous recessive gene snr, snr (smooth non-ridged).

Multiple Fruiting on Parthenocarpic Plants

It was observed that some plants in the segregating populations developed several large parthenocarpic fruit while others developed only one fruit. Data summarized in

Figure 1. A parthenocarpic fruiting plant with rough skin.

Figure 2. A parthenocarpic fruiting plant with smooth skin.

Table 5. The inheritance of smooth skin type in cucumber. A test for a single homozygous recessive gene.

Pedigree	Rough Skin		Smooth Skin		Total Plants	X^2	P
	Obser.	Exp.	Obser.	Exp.			
MSU 713-205	24	24	0	0	24	--	--
Spotvrije	0	0	24	24	24	--	--
(205 x Spot.) F_1	24	24	0	0	48	.00	--
(205 x Spot.) F_2	73	78	30	26	104	.94	.36
205 (205 x Spot.) BC_1	89	89	0	0	89	.00	--
(205 x Spot.) Spot. BC_1	46	44.5	45	44.5	91	.06	.82

Table 6 show that no direct relationship exists between the sex expression and number of parthenocarpic fruits. The gynoecious parthenocarpic segregates, in the F_2 of MSU 713-205 x Spotvrije, developed one to six fruits per plant. These fruits developed from approximately ten trapped pistilate flowers. The average of two fruits per plant is not considered significant since only six plants segregated as parthenocarpic, gynoecious types.

Predominantly female plants also developed from one to six fruits per plant with an average of 3.1. Monoecious plants developed one to five fruits per plant with an average of 2.6.

The backcross to Spotvrije produced no gynoecious segregates. Predominantly female plants developed one to eight fruits per plant averaging 4.2. Monoecious segregates ranged from one to four and averaged 2.3 fruits per plant.

This indicates that there is no direct relation between sex expression and the number of fruits developed at one time.

Fruit number appears to be controlled by a gene or group of genes. Predominantly female plants in the backcross to Spotvrije averaged higher fruit numbers than gynoecious or predominantly female plants in the F_2 population. Presumably, Spotvrije has been selected for high total numbers of fruit borne over a long season but

Table 6. The relation between sex expression and fruit numbers in parthenocarpic cucumbers.

Pedigree	Number of Fruits on Parthenocarpic Plants								
	Gynoecious			Predominantly Female			Monoecious		
	Number Plants	Range[a]	$\overline{X}$	Number Plants	Range	$\overline{X}$	Number Plants	Range	$\overline{X}$
(205 x Spot.) F_2	6	1-6	2.0	10	1-6	3.1	7	1-5	2.6
(205 x Spot.) Spot.	-	-	-	12	1-8	4.2	36	1-4	2.3
Spot.	-	-	-	-	-	-	-	1-3[b]	-

[a]Range indicates the variation between lowest and highest number of fruits produced on different plants.

[b]Counts were not recorded but general observations were that only one to three fruits were developing at one time on the extremely male plants.

concentrated fruiting is not characteristic of this variety because of extreme maleness. This could also be the reason for low fruit numbers on monoecious plants from the backcross to Spotvrije, some of which were extremely male. Data from the 1966 study will further verify this observation.

INHERITANCE STUDIES OF THE PARTHENOCARPIC CHARACTER 1966

Materials and Methods

In 1965 it was found that in this material parthenocarpic fruiting is not conditioned by either a single dominant or a single recessive gene. Several problems had developed which made a detailed study very difficult. They may be listed as:

1. High labor requirements made it difficult to trap all the large populations grown in 1965.
2. The attempt to trap ten pistilate flowers on each plant failed in cases where extremely male plants produced only a few pistilate flowers during the period of trapping.
3. The development of parthenocarpic fruit on the three predominantly female and two gynoecious plants in the backcross to MSU 713-205 indicated that the fruit might have developed on other plants if trapping of all pistilate flowers had been achieved.

A need for revisions in techniques for identifying parthenocarpic segregates was evident. Extremes in sex expressions introduced a variable which made detailed studies difficult because of wide range in numbers and rate of pistilate flower development.

From several parthenocarpic lines in the breeding program at Michigan State University, a homozygous parthenocarpic F_3 line segregating for gynoecious sex expression was selected for further study. Gynoecious segregates were propagated by cuttings so that all crosses would have an identical genetic constitution on the side of the parthenocarpic parent.

One of three vegetatively-propagated gynoecious plants (no. 3182-1) produced three well-developed parthenocarpic fruits on the main stem early in the development of the plant. It was selected for genetic study and increased by additional cuttings.

A cross was made between MSU 713-205 and 3182-1 and the F_1 was selfed and backcrossed to MSU 713-205 and a 3182-1 plant propagated by a cutting from the one used in the original cross.

In the spring of 1966, 22 F_1 plants, 135 F_2, 54 of the backcross to 3182-1, and 52 of the backcross to MSU 713-205 were planted in the field in rows four feet apart with two feet between plants. Plans were to hand trap pistilate flowers to identify fruiting habit since these gynoecious populations could be more easily trapped than those in previous experiments where there were many monoecious plants.

To investigate the possibility of using isolation from sources of pollen to identify parthenocarpic plants in gynoecious lines a second outdoor planting of the same material was protected under a 12 x 80 foot screen cage, Figures 3 and 4. An isolation or cage for gynoecious material would allow the breeder to observe and select in populations exhibiting the wide range of fruit numbers observed in 1965.

Five F_2 lines from F_1 plants selected in 1965 as early multiple-fruiting were also observed in outdoor plantings to determine segregation for earliness and multiple-fruiting.

Eighteen progenies from selfed plants of the backcross to MSU 713-205 were planted to determine if parthenocarpic plants could be recovered in progenies of plants which had produced no parthenocarpic fruit.

Pistilate flowers of F_1, F_2 and backcross progenies between MSU 713-205 and 3182-1 were trapped over a period of time that seemed sufficient for all plants to develop fruits. The plants were vigorous, indeterminant, branching and all were gynoecious. Some plants exhibited early development of parthenocarpic fruit while others were difficult to classify because ovaries of the latest flowers trapped were beginning to grow slowly. It was impossible to make a definite classification of parthenocarpic or non-parthenocarpic since it was not known if those ovaries

Figure 3

Figure 4

A 12' x 80' screen cage used for protecting parth-
enocarpic cucumber plants from insect pollination.

would develop completely or if still later ovaries might develop. The excessive growth of the plants made it difficult to continue trapping all pistilate flowers, so attention was directed toward the same progenies being grown under screen isolation.

It was found that the same behavior was occurring in the cage and in the outside plots. Since all plants were gynoecious and were protected from insects carrying cucumber pollen, a decision was made to wait for several weeks until the plants had time enough to more completely develop before recording data. Detailed observations were made in September, after the plants had attained most of their vegetative growth with large fruits which in some cases were turning to a color associated with normal maturity. Each plant was pulled and stripped of its leaves and laid out for observation with fruits remaining attached. The nodes at which fruit were borne were recorded for both the main stem and laterals in order to establish precise classes.

An example illustrating the recording procedures is shown in Table 7.

Results and Discussion

The data were first divided into parthenocarpic and non-parthenocarpic classes then analyzed for node number at which the first fruit developed and for total number

Table 7. Example of method used to record data on parthenocarpic fruiting in cucumbers.

Plant Number	Sex	Fruiting Node(s)	Number of Fruit Large	Small	Total
6633-3	G	L1, 2 = 0[a]	2[b]	0[c]	2
		L3 - 4 = 1			
		L4 - 3 = 1			
		L5, 6, 7, = 0			
		M = 0			

[a]L1, 2 = 0 signified that laterals at nodes 1 and 2 produced no fruit.

L3 - 4 = 1 signified that the lateral at node 3 produced a fruit on node 4 of that lateral.

L4 - 3 = 1 signified that the lateral at node 4 produced a fruit on node 3 of that lateral.

L5, 6, 7 = 0 signified that there were laterals at nodes 5, 6, and 7 but that no fruit was produced on them.

M = 0 signified that no fruits were produced on the main stem.

[b]Fruits which were fully developed were classified as large fruit.

[c]Fruits which were small but definitely growing were classified as small fruit.

of normal fruits. This procedure provided a way for the data to be analyzed to distinguish between early fruiting, late fruiting, and non-parthenocarpic fruit development.

Plants in the F_2 and backcross to 3182-1 were classified as homozygous <u>PP</u> if they produced three or more parthenocarpic fruits with the first developing within five nodes. Plants which produced no fruits by September 15 were classified homozygous recessive pp and those yielding less than three fruits or later than at node five were classified as heterozygous Pp. Data on inheritance of parthenocarpy from the cross MSU 713-205 x 3182-1 are summarized in Table 8. Diagrams representing typical plants of the three genotypes are illustrated in Figures 5, 6 and 7.

The analysis demonstrated that parthenocarpy in the cucumber material used is conditioned by an incompletely dominant gene P-, with early fruiting on homozygous PP plants, late fruiting on the heterozygous Pp and non-parthenocarpic fruiting on the homozygous recessive pp. It seems, however, that a gene or group of genes associated with the parthenocarpic character modifies earliness and fruiting numbers. Table 9 shows plants in the backcross to non-parthenocarpic had the widest range and highest average for the first fruiting nodes in the Pp. The modifying mechanism is demonstrated further by five plants in F_2 and three in backcross to parthenocarpic which produced three or more fruits with the first fruit at node six to eight. These plant types classified as Pp were borderline cases and partially account for the one to six range of fruit numbers in the table. To accurately determine the genotypes of such plants an F_3 test

Table 8. Segregation for parthenocarpy in the cucumber. A test for a single incompletely dominant gene.

Pedigree	Genotype	Early Parth.[a] PP		Late Parth.[b] Pp		Non-parth.[c] pp		X^2	P
		Obser.	Exp.	Obser.	Exp.	Obser.	Exp.		
(205 x 3182-1) F_1	pp x PP	0	0	4	4	0	0	0	-
(205 x 3182-1) F_2	Pp x Pp	13	9.25	15	18.5	9	9.25	2.24	.31
205 (205 x 3182-1)	pp x Pp	0	0	16	16.5	17	16.5	.04	.97
3182-1 (205 x 3182-1)	PP x Pp	19	20	21	20	0	0	.10	.95

[a] A classification given to plants producing the first of three or more fruits within five nodes from plant base.

[b] A classification given to plants producing fruits later than five nodes from plant base.

[c] A classification given to plants which produced no parthenocarpic fruits.

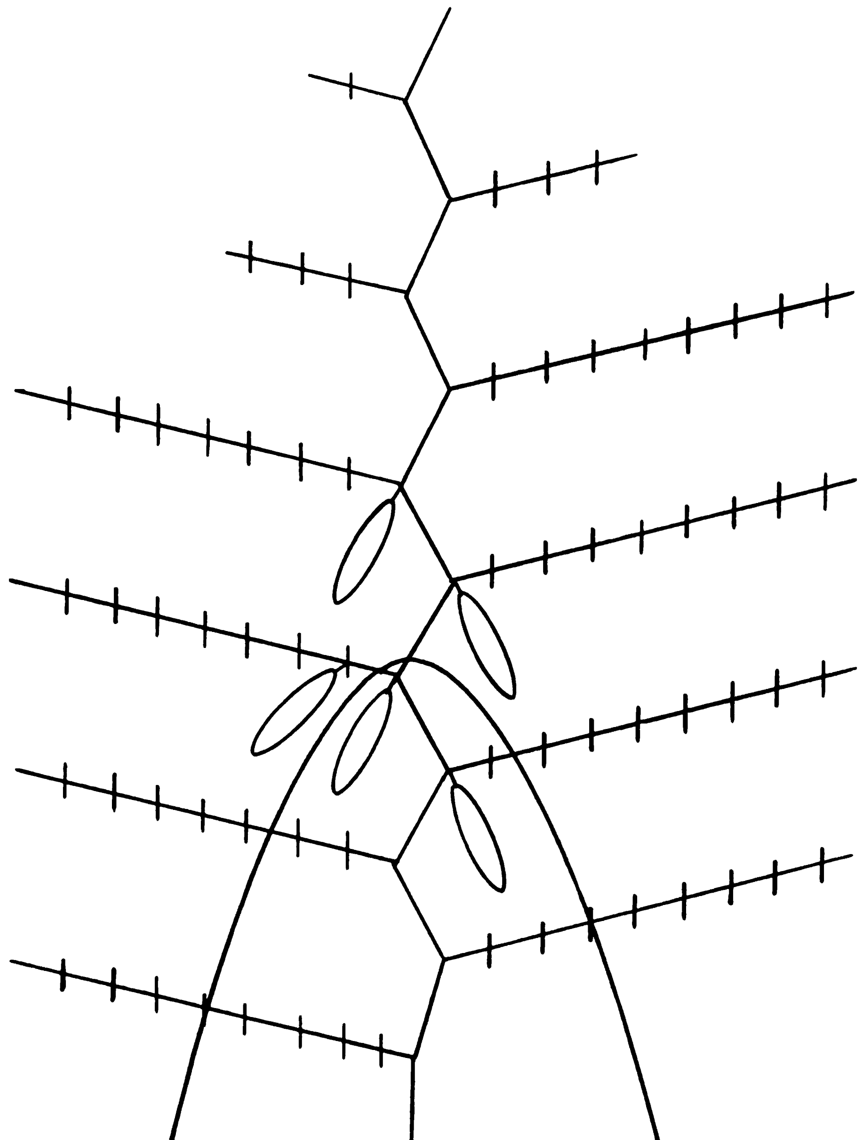

Figure 5. Parthenocarpic fruiting habit of a typical plant classified as homozygous dominant PP showing fruit production within five nodes.

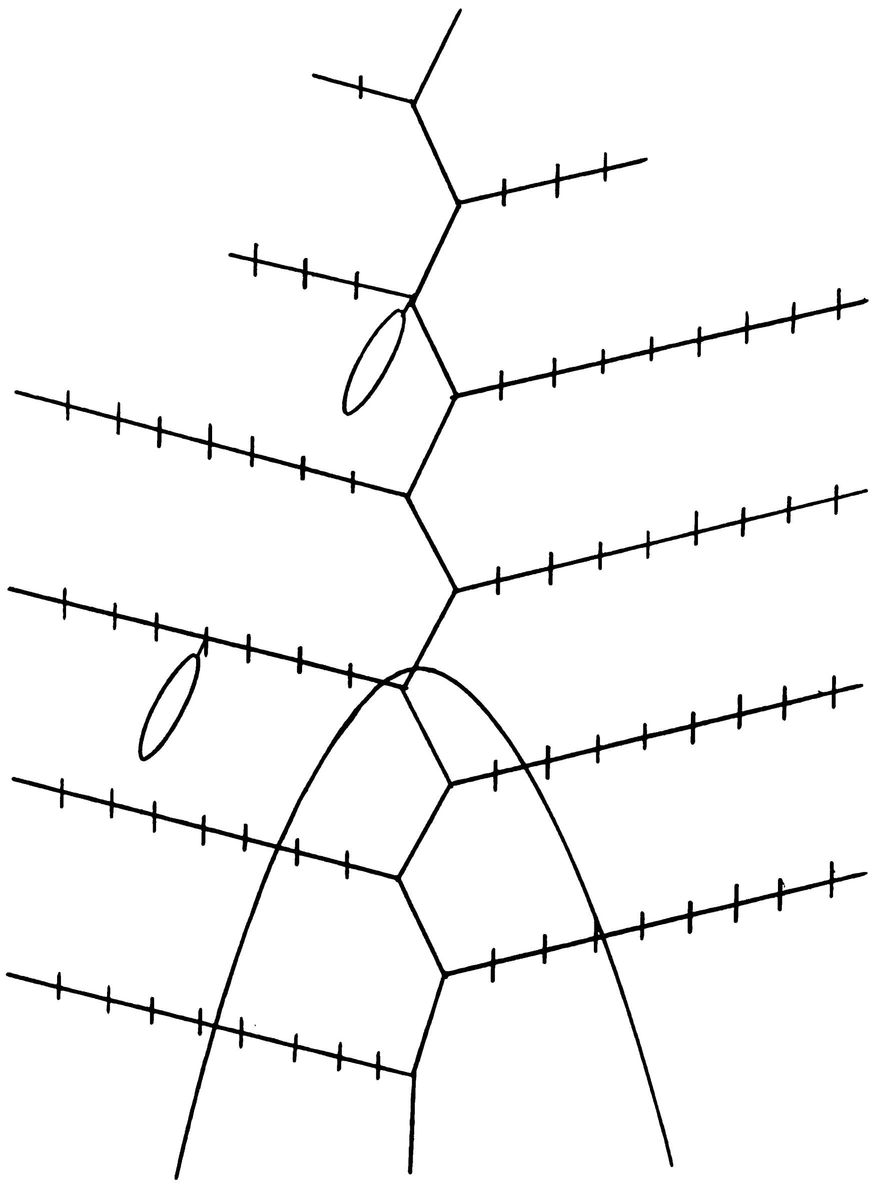

Figure 6. Parthenocarpic fruit production on a typical plant classified as heterozygous Pp showing fruit production later than five nodes.

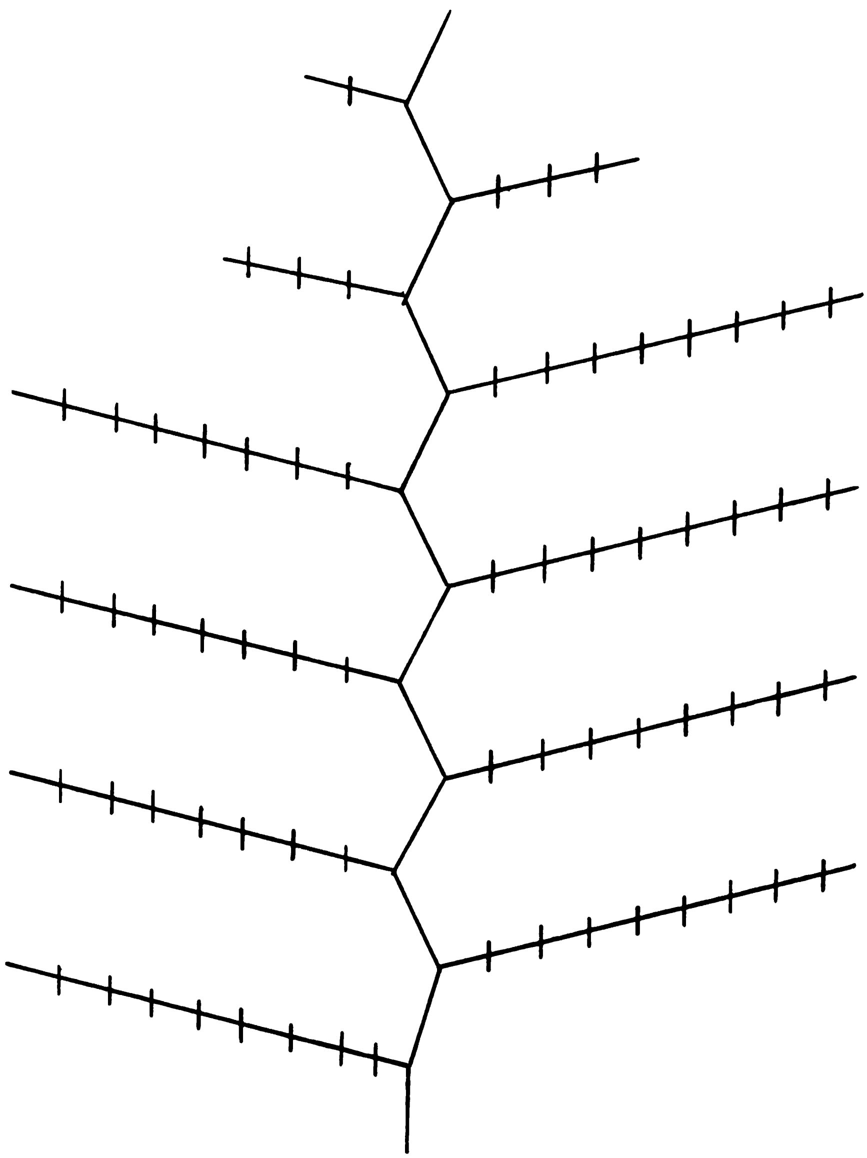

Figure 7. A typical non-parthenocarpic plant classified as homozygous recessive pp.

Table 9. Number of fruits and range of nodes at which parthenocarpic fruits were borne in cucumber.

	Range of 1st Fruiting Node		Average 1st Node		Range of Fruit No.		Average No. Fruits	
	PP	Pp	PP	Pp	PP	Pp	PP	Pp
(MSU 713-205 x 3182-1) F_1	-	5-12	-	8	-	1-4	-	2.0
(MSU 713-205 x 3182-1) F_2	3-5	5-11	4	8	3-9	1-6	5.1	3.0
3182-1 (205 x 3182-1)	2-5	4-14	4	8	3-7	1-6	4.6	2.4
205 (205 x 3182-1)	-	6-25	-	12	-	1-6	-	2.6

is needed. Nineteen of 54 plants classified as Pp, but not considered borderline cases, finally produced three or more late fruits. This indicates that possibly after a stimulus for ovary growth occurs modifiers may influence fruit numbers.

Classification of Progenies from Backcross to MSU 713-205 Selfed

Plants from the backcross, 205 (205 x 3182-1), selected for selfing in 1965 were predominantly female. These progenies segregated gynoecious, predominantly female, and monoecious plants in the 1966 plants. Trapping of all pistilate flowers was again not possible. However, it was found that six of the 18 lines tested segregated plants which produced early parthenocarpic fruits. This demonstrated that early parthenocarpic fruiting plants could be obtained from at least one-third and probably one-half of the progenies from plants in the backcross to a non-parthenocarpic parent.

The data from the 1966 study explained why parthenocarpic segregates were recovered in progenies of six out of 18 of these backcross plants, all of which had been classified as non-parthenocarpic in 1965. One-half of these plants in the backcross to MSU 713-205, incorrectly classified by the trapping technique, were heterozygous Pp and one-half homozygous recessive pp. The homozygous PP segregates from selfed Pp were identified by their early fruiting even though trapping had to be discontinued long before the plant completely developed. An even better fit might have been achieved if the plants had been under screen and observed for a longer period of time.

Observations from F_3 Progenies

Five F_3 lines from F_2 plants selected as early, multiple-fruiting, parthenocarpic were classified and are shown in Table 10.

Line 6601 was obtained by selfing a gibberellin-induced gynoecious F_2 plant. The resulting twelve F_3 plants were gynoecious and all were early and multiple-fruiting.

Line 6602, 6603, 6604 and 6605 were from selfed predominantly female F_2 plants also selected as early and multiple-fruiting. Those four lines segregated monoecious, predominantly female, and gynoecious plants in the F_3. Four plants in line 6602 and two plants in 6603 were extremely male and were not classified as either parthenocarpic or non-parthenocarpic. However, since a total of 30 gynoecious, 12 predominantly female, and 9 monoecious plants were observed and classified as early, multiple-fruiting, the F_3 lines were considered homozygous for the parthenocarpic character. The early, multiple-fruiting, parthenocarpic plants produced progenies which were all early, multiple-fruiting except where late fruiting and

Table 10. Results in the F_3 generation from F_2 plants selected for early multiple fruiting.

Parent Plant	Sex Exp.[a]	Line No.	Sex Exp.	Parth.	Non-parth.	Extreme Maleness[b]
5610-20	G	6601	G	12	0	-
5610-66	PF	6602	Seg.	8	0	4
5610-104	PF	6603	Seg.	9	0	2
5610-21	PF	6604	Seg.	12	0	-
5610-32	PF	6605	Seg.	11	0	-

[a]G designates gynoecious plants and PF predominantly female.

[b]The six plants listed under extreme maleness produced no pistilate flowers during the period of study or produced only one or two which were not trapped and had to be removed.

low fruit numbers were associated with extreme male sex expression.

COMMERCIAL ACCEPTABILITY OF PARTHENOCARPY IN FRESH AND PROCESSED CUCUMBERS

Parthenocarpic cucumbers have been grown and accepted in European countries for many years. All production of such varieties is under glass where screening and other precautions are taken to prevent pollination by insects. Obviously the production of parthenocarpic varieties in the open was impossible because of insect pollination and the resulting development of seed-bearing fruits. This problem was partially solved by the development of a large number of true gynoecious lines beginning with MSU 713-5 (21). A combination of gynoecious sex expression and parthenocarpic fruiting should make it possible to produce such varieties out-of-doors by providing adequate isolation from sources of cucumber pollen. Once it was demonstrated that this combination could be achieved, it was necessary to learn if they might be acceptable for fresh market or for processed products.

Consumer Acceptance of the Parthenocarpic Cucumber

Materials and Methods

During the summer of 1966 fruits of Spartan Dawn, and parthenocarpic fruits from experimental lines were processed at the Michigan State food science laboratories. Three types of cucumber products were processed. A 1/4 inch cross-cut slice known as bread and butter, a 1/8 inch slice known as hamburger slices and longitudinal spears were processed in clear glass jars.

The fresh fruits used in the test consisted of parthenocarpic fruits from breeding lines at Michigan State and seed type slicers purchased locally.

During the fall of 1966 both the processed cucumbers and fresh fruits were rated by a consumers preference panel at Wayne State University in Detroit, Michigan. The participants, in the standard panel used regularly by the Department of Agriculture Economics at Michigan State University, had been selected to simulate a uniform sample of consumers in the Detroit area (17).

The samples used were marked only by code and participants were asked to check their preference and to indicate if samples were either acceptable or not acceptable. Two sessions of the consumers panel were held comprising a total of 160 participants. Figure 8, 9, and 10 show the products as exhibited at the consumers preference panel and Figure 11 illustrates the form used in the test.

Results and Discussion

The afternoon session of 70 consumers preferred the products processed from parthenocarpic fruits over

Figure 8. Cross-cut sections from parthenocarpic fruits are on left and those from Spartan Dawn are on right.

Figure 9. Spears made from parthenocarpic fruits are shown on right and spears from Spartan Dawn on left.

Figure 10. Parthenocarpic fruits are shown at top and locally purchased seed type slicers are below.

PICKLES

MICHIGAN STATE UNIVERSITY

		Preference	Acceptable	Not Acceptable
I.	%	__________	__________	______________
	()	__________	__________	______________
II.	&	__________	__________	______________
	*	__________	__________	______________
III.	#	__________	__________	______________
	%	__________	__________	______________
IV.	()	__________	__________	______________
	&	__________	__________	______________

Name:___________________ Comments: ______________________

Figure 11. The form used by the consumers preference panel in Detroit, Michigan.

those from normal seed fruits in a ratio of more than two to one. In the fresh market samples no preference was shown for either type.

The evening session preferred the processed seedless cucumbers three to one over the normal seed type cucumber products and again accepted equally the fresh fruits.

Table 11 summarizes the data and provides important information for both breeders and processors. It was domonstrated that the public would accept a parthenocarpic fresh market variety and if given a choice, actually preferred the products processed from seedless fruits.

Preliminary Brining Observations on the Parthenocarpic Cucumber

Many questions have evolved from the study on the parthenocarpic cucumber. There is no field production of such cucumbers and no previous investigations have been made on related problems such as brining and processing. The fruits are practically solid wall tissue in most cases with very small areas representing the normal seed bearing tissues. The fruit structure suggests that possibly bloating and carpel separation would not occur to the same extent as in typical seed types. It also led to the question of salt penetration through the thick wall tissue.

Table 11. Acceptance of parthenocarpic fresh cucumber and processed products by a consumers preference panel at Detroit, Michigan, 1966.

	Preferred	Acceptable	Non-Acceptable	Preference
Parthenocarpic B. & B. Slices[a]	105	146	14	2.44 : 1
Spartan Dawn B. & B. Slices	43	130	30	---
Parthenocarpic Hamburg. Slices	110	141	19	2.82 : 1
Spartan Dawn Hamburg. Slices	39	117	43	---
Parthenocarpic Dill Sticks	111	152	8	2.52 : 1
Spartan Dawn Dill Sticks	44	142	18	---
Parthenocarpic Slicer	77	147	13	1 : 1
Seed Type Slicer[b]	75	156	4	---

[a] B. & B. indicates bread and butter style slices.

[b] Locally purchased seed type slicers.

Methods and Materials

Preliminary tests were made to determine brining quality of parthenocarpic fruits. A replicated study was not possible because only early generation parthenocarpic lines were available in 1966. However, plants were selected which exhibited multiple-fruiting and as many fruits as could be obtained from single plants were brined in commercial tanks.

Fruits were harvested from individual plants exhibiting the following characteristics:

1. Twelve fruits 10 to 12 inches long and 2 1/2 inches in diameter from similar F_3 plants were divided into two classes with one group being pricked and the other group being brined without pricking.

2. Fruits 6 inches long with a diameter of 1 1/2 inches representing pickle size cucumbers, were harvested at two stages of development. One stage was mature fruit with skins beginning to turn yellow. The other group consisted of young fruits not turning yellow but of generally the same size.

One-half of the 10 inch fruits tested were pricked to the center 10 times from each of four sides with small diameter needles. The remaining 10 inch fruits were brined without being pricked.

The 6 inch fruits were divided into old fruits which were turning yellow and young green fruits. Mature parthenocarpic fruits were brined because they remained firm for approximately two weeks on the vine after reaching full size and seemed to remain useable as fresh cucumbers longer than seed type fruits. The black rather than white spined fruits were used in order to more precisely select for advanced maturity.

The fruits were placed into the brine at Dailey Pickle Company at Saginaw, Michigan, in late August and removed in December. The large fruits were observed before and after cutting.

Results and Discussion

It was found that the 10 inch fruits which were not pricked had become soft inside and the skin was deteriorating on some of the fruits. The softness seemed to be due to decay or tissue breakdown resulting from respiration which had not stopped early in the brining process. Either of these may result from slow penetration of the brine through the skin or thick wall or a combination of both.

The pickled fruits were firm and generally free of cavities after fermentation, suggesting that pricking might hasten penetration of brine and prevent the defects observed in unpricked samples. Despite the small number of fruits brined these preliminary observations suggest that pricking may be essential for successful brining of the typical thick-walled parthenocarpic varieites.

The sample of less mature 6 inch fruits remained firm and did not bloat. Mature, 6 inch fruits remained firm but exhibited some bloating.

The observations of brined fruits indicated that fruits of the sizes normally used for processing should brine in an immature stage equally as well as seed type fruits of the same size. Figures 12, 13, 14, and 15 show the brined parthenocarpic fruits.

More work on processing quality both for fresh pack and fermentation is needed. Parthenocarpic cucumber fruits are unique and little is known about the problems which might arise in processing if they should become generally available.

Figure 12. The pricked 10 inch parthenocarpic fruits are shown on left and non-pricked on right illustrating condition after brining.

Figure 13. Interior condition of pricked 10 inch parthenocarpic fruits are shown on left and non-pricked on right illustrating condition after brining.

Figure 14. The firm condition of mature 6 inch parthenocarpic fruits after brining.

Figure 15. The firm non-bloated condition of immature 6 inch parthenocarpic fruits after brining.

SUMMARY

Parthenocarpy in the cucumber is conditioned by an incompletely dominant gene _P-_. Heterozygous _Pp_ plants produce fruits later and generally fewer in number than the homozygous _PP_ genotype. Homozygous recessive _pp_ plants do not produce parthenocarpic fruits.

All plants in progenies derived from a backcross to the non-parthenocarpic parent were classified as non-parthenocarpic when fruiting was identified by means of trapping pistilate flowers to prevent pollination. The fact that six out of eighteen progenies from plants self-pollinated in this backcross generation segregated typical _PP_ plants that were parthenocarpic and multiple-fruiting is evidence for incomplete dominance.

Cage isolation of gynoecious progenies segregating for parthenocarpy is an effective technique for identifying late fruiting heterozygous plants. The difficulty of trapping all pistilate flowers over the entire fruiting period resulted in incorrect classification of heterozygous plants, especially in progenies segregating for monoecious sex expression with very late pistilate flower production. Homozygous _PP_ plants were identified accurately in the F_2 by

selecting for early, multiple fruiting in parthenocarpic plants. Progenies from selfed F_2 plants of this type produced only the parental type of F_3.

Modifying genes may influence fruit numbers since 19 of 54 plants classified as Pp produced three or more late fruits.

The smooth, non-ridged skin of Spotvrije is conditioned by the homozygous recessive snr, snr.

Gynoecious parthenocarpic plants exhibit earlier fruiting than monoecious and are necessary for field production of seedless fruits.

Parthenocarpic fruits ten inches long and 2 1/2 inches in diameter did not brine satisfactorily unless pricked. Six inch fruits, 1 1/2 inches in diameter, brined as well as seed fruits the same size.

A consumers panel showed no preference between parthenocarpic and seed-type fresh market cucumbers but preferred the products processed from seedless fruits.

It was demonstrated that multiple-fruiting, parthenocarpic varieties suitable for mechanical harvesting can be developed and that seedless cucumbers and processed products will be accepted by consumers.

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