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thesis entitled

THE GENETICS OF SEX EXPRESSION AND FRUIT
SHAPE, STAMINATE FLOWER INDUCTION, AND F_1 HYBRID
FEASIBILITY OF A GYNOECIOUS MUSKMELON

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ABSTRACT

THE GENETICS OF SEX EXPRESSION AND FRUIT SHAPE, STAMINATE FLOWER INDUCTION, AND F_1 HYBRID FEASIBILITY OF A GYNOECIOUS MUSKMELON

By

Phillip Ray Rowe

Genetics of Sex Expression

The gynoeceous sex expression was controlled by modifying genes in addition to the major genotype, A-gg. The recombination of modifiers conditioning gynoeceous sex expression, after crossing with monoecious, andromonoecious and hermaphroditic sex types, resulted in mostly gynomonoecious plants for the A-gg genotype in the segregating F_2 , BCP_1 and BCP_2 populations. The gynomonoecious plants had $3/4$, $1/2$ and $1/4$ ovary perfect flowers and staminate flowers with rudimentary stigmas in combinations or singly depending upon the modifier complement. Different modifiers were apparently responsible for the different partial ovary perfect flower types observed. Heterozygosity for the major gene A did not affect the expression of the modifiers. Reciprocal crosses showed that the maternal parent did not influence the gynoeceous sex expression.

Inheritance of Fruit Shape

The oblong fruit shape of the gynoecious line was dominant to the round fruit shape of several andromonoecious varieties. Single genes for round fruit shape dominant to the fruit shape of the gynoecious line were found in the andromonoecious Japanese hybrid, Sweetie, and the monoecious line, Morden Monoecious.

Staminate Flower Induction

Chemical spray treatments and environmental manipulations did not induce staminate flowers. Grafting of gynoecious scions onto various cucurbit rootstocks demonstrated differential induction. Pumpkin stocks resulted in the highest number of staminate flowers. The induced flowers were not true staminate flowers, but were mostly staminate flowers with rudimentary stigmas. Different pumpkin stock sizes and scion sizes and ages did not affect the number of staminate flowers induced. Alleviation of the effect of the pumpkin roots by using pumpkin interstocks demonstrated that the induction stimulus was from the foliage of the pumpkin. Staminate flowers were not induced on gynoecious cucumber by grafting onto pumpkin, which suggested that different stimuli are responsible for staminate flower induction in gynoecious sex types of these two different species of the genus Cucumis.

F₁ Hybrid Feasibility of the
Gynoecious Muskmelon

Gynoecious sex expression deserves considerable attention for use in the production of hybrid seed. A gynoecious line was developed with the more desirable round fruit shape which is necessary for production of round-fruited hybrids. Grafting onto pumpkin rootstocks induced adequate staminate flowers for increasing gynoecious seed. It is estimated that one hand pollination to increase the gynoecious parent, with subsequent hybrid seed production by bee pollinations, would produce as much hybrid seed as 5,000 hand pollinations with the present method of making hybrids.

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HYBRID FEASIBILITY OF A GYNOECIOUS
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INTRODUCTION

Michigan has an average annual production of approximately 3,000 acres of muskmelons (36). Hybrid varieties constitute an estimated 90% of this acreage. Hybrid seed is approximately \$100.00 per pound as compared to \$4.00 for open-pollinated varieties. This represents an investment of \$50.00 per acre in seed for the hybrid melon grower.

Hybrid seed is expensive because of the laborious process involved in producing it. Most commercial muskmelons are andromonoecious and to be cross-pollinated must be emasculated, hand pollinated and trapped to prevent pollen contamination. Furthermore, Mann (31) reported that hand pollinations were only 60% as successful as bee pollinations, and the resultant fruit were smaller and contained fewer seeds. Whitaker and Pryor (59) made field hand pollinations and obtained only 24-40% fruit set.

Efforts to improve fruit set have had limited success. Burrell and Whitaker (9) and Whitaker and Pryor (59) found that an increase in fruit set following hand pollinations could be obtained by application of one per cent indoleacetic acid or 4-chlorophenoxyacetic acid to the ovary at the time of pollination, but fruit set by these methods

had fewer seed. Wolf and Hartman (62) increased fruit set of hand pollinations by pruning the fruit and plants. Jones (27) recently facilitated successful hand pollinations by applying benzyladenine to the ovaries at the time of pollination.

Munger (34) recognized the superiority of F_1 hybrids as compared to inbred lines in 1942. He suggested a labor saving procedure of making hybrids in the afternoon by pollinating immediately after emasculation with male flowers picked in the morning and kept in a cool, moist place.

The cost of hybrid muskmelon seed could be lowered if a suitable bee-pollinated seed parent could be developed. Use of the gynoecious sex character is limited by lack of sufficient genetic information, undesirable oblong fruit shape and absence of a chemical treatment that will induce staminate flowers for inbreeding and increasing seed.

This study was conducted to determine the genetics of the gynoecious sex type, to ascertain the genetics of fruit shape, to develop a round-fruited gynoecious plant and to determine the effects of chemical treatments, environmental fluctuations and grafting on staminate flower induction.

LITERATURE REVIEW

Superiority of Hybrids

Since Munger's (34) observation that hybrid muskmelons were superior to varieties, much work has been done to substantiate the desirability of hybrids. The early workers Rosa (46) and Scott (52) were unable to find hybrid vigor in crosses between inbred muskmelon lines. Munger (34) reported a 30% increase in yield and greater uniformity in hybrids as compared to the parental strains. Bohn and Davis (3) obtained results that indicated apparent heterosis for earliness which could be controlled in F_1 hybrids by selecting parental lines for factors affecting fruit maturity. Foster (17) made an extensive study comparing selected inbred lines with their F_1 hybrids. He reported as much as twice the yield from hybrids as compared to the higher yielding inbred parent. Evidence of heterosis was further substantiated by a group of hybrids with a common parent which outyielded the diverse commercial parents by 84%. Quality factors such as net density, blossom end thickness, flesh firmness and cavity dryness tended to be improved in the hybrids as compared with the commercial parents. Fruit shape and soluble solids of the hybrids were intermediate between those of the parents.

Methods of Hybridizing

The wide acceptance of commercial hybrid muskmelons prompted investigations into methods of eliminating the tedious and expensive hand emasculations and pollinations. Bohn and Whitaker (6) and Bohn and Principe (4) discovered genetic male steriles as mutants in normally fertile lines. In both cases the sterility was controlled by a single recessive gene. These have the disadvantage of roguing one-half the seed parent plants in the field. Attempts to find linkages of the sterility genes with seedling markers, and thus facilitate thinning of fertile segregates prior to transplanting the male sterile plants to the field, have been unsuccessful (5).

Foster (18) grew parental stocks in various patterns in the field to determine the best arrangement to obtain maximum natural cross pollination. Using a glabrous recessive marker (16) as the seed parent, he was able to distinguish the hybrid plants in the seedling stage. Although certain planting arrangements yielded a higher percentage of hybrids than others, none resulted in more than 40% hybrids. In later work (19), he was able to obtain 75% hybrids in open-pollinated populations by using monoecious lines segregating 1 male sterile: 1 male fertile, and planted in close proximity to the pollen parent.

Sex Types in Muskmelon

The use of a genetically controlled gynoecious sex type as the seed parent has revolutionized cucumber hybrid seed production. Peterson (38) described a gynoecious cucumber line that made production of hybrid cucumbers economically feasible.

The major sex types in muskmelon are distinctly different and simply inherited. Rosa (47) reported that monoecious is dominant to andromonoecious by a single factor. Foster and Bond (20) reported an androecious mutant that is controlled by a single recessive gene. The mutation was not in the sex expression, but was for absence of lateral branches on which pistillate and perfect flowers occur on monoecious and andromonoecious plants respectively. Poole and Grimball (42) crossed a hermaphrodite from China with a monoecious, and from the F_2 and backcross data proposed a two gene explanation of sex expression in muskmelon: AG is monoecious, Ag is gynomonoecious, aG is andromonoecious, and ag is hermaphroditic.

The gynomonoecious plants in Poole and Grimball's observations had mostly pistillate flowers with a few perfect flowers. They had some gynoecious plants in segregating populations, but hypothesized that the gynoecious sex type was not a true genetic type. The gynoecious plants were defined as transitory phenotypes

caused by environmental influences on the gynomonoecious genotypes AAGg and Aagg. They concluded that there might be additional genes affecting sex expression, but that two major pairs of genes delineated the four primary sex classes.

Peterson (39) proposed that gynoecious muskmelons could be used in hybrid seed production. Kubicki (29) subsequently investigated the possibility of using gynoecious plants for seed parents in hybrids, and suggested that the gynoecious seed could be increased by bee-pollinating a field of isolated gynoecious plants with a hermaphroditic sister line. The resultant gynoecious F_1 could then be used as the seed parent in commercial hybrid seed production. Both Peterson (39) and Kubicki (29) reported that crosses of gynoecious with andromonoecious and monoecious types yielded 100% monoecious hybrids.

Fruit Shapes Associated with Sex Types

Monoecious plants are better suited than andromonoecious plants for making hand pollinations for hybrid seed production since monoecious plants do not require emasculation. Monoecious sex types have not been used as seed parents in hand-pollinated commercial hybrids because, with few exceptions, imperfect pistillate flowers produce oblong fruit. In the Midwest, oblong fruit are not as acceptable to the consumer as round fruit. Rosa (47) observed this pattern of correlated sex-fruit shape

inheritance and suggested that this phenomenon might not be the result of linkage, but of pleiotropic action of the gene determining sex expression. Kubicki (28) reported that pistillate flowers and fruits of monoecious varieties were elongated, whereas the hermaphroditic flowers and fruits of andromonoecious varieties were round. He hypothesized linkage of genes determining fruit shape and sex on the basis of an F_2 ratio of three oblong-fruited, monoecious plants to one round-fruited, andromonoecious plant. Wall (57) suggested that fruit shape was regulated by a single gene with incomplete dominance plus minor modifying genes linked in coupling phase with the gene for determination of sex expression. In a related genus, Poole and Grimball (43) have determined that in water-melons genes for plant sex habit and fruit shape were linked with a crossover value ranging from .14 to .35 in several segregating populations.

Chemical Effects on Sex Expression

The lack of staminate flowers on gynoecious plants creates a problem in obtaining true breeding lines by self pollinations. Wittwer and Bukovac (60) treated monoecious cucumbers with gibberellin A_3 and increased the number of staminate flowers. Subsequently, Peterson and Anhder (40) induced staminate flowers on gynoecious cucumbers by spraying with gibberellin A_3 . Pike and Peterson (41) sprayed gynoecious cucumbers with gibberellin A_4A_7 and

induced staminate flowers with much lower concentrations than with A_3 . Peterson (39) and Kubicki (29) were unable to induce staminate flowers on gynoecious muskmelon by treating with gibberellin A_3 .

Gibberellin has been used on other plants to alter sex expression. Shifriss (53) increased the female tendency of monoecious castor beans by spraying with gibberellin A_3 . This response is directly opposite that of monoecious cucumbers.

Auxins, growth retardants and kinins influence sex expression of many plants. Choudhury and Phatak (10) obtained pistillate flowers on earlier nodes of monoecious cucumbers by treating with maleic hydrazide, naphthaleneacetic acid, indoleacetic acid and 2,4-dichlorophenoxyacetic acid. The production of staminate flowers on squash was inhibited by maleic hydrazide, and the ratio of staminate to pistillate flowers in cucumber and squash was reduced with naphthalene acetic acid and 2,3,5-triiodobenzoic acid by Wittwer and Hillyer (61). Abdel-Gawad and Ketellapper (1) inhibited appearance of pistillate flowers with N^6 -benzyladenine and suppressed staminate flowers with 2-chloroethyltrimethylammonium chloride on squash. A report by Prasad and Tyagi (44) showed an increased number of pistillate flowers on bitter gourds sprayed with maleic hydrazide. Working with grapes, Negi and Olmo (35) changed male clusters to hermaphroditic by applying

a synthetic kinin, SD8339. Andromonoecious muskmelons were treated with N,N-dimethylaminosuccinamic acid by Halevy and Rudich (23) with a resultant shift towards femaleness.

A new area of research of chemical influence on sex expression is the effect of ethylene evolving chemicals. McMurray and Miller (32) reported a very pronounced change in the sex of monoecious cucumber plants sprayed with 2-chloroethanephosphonic acid. The treated plants had numerous continuous pistillate nodes and upon prolonged treatment approached the gynoecious sex type.

Grafting Effects on Flowering and Sex Expression

Grafting onto different rootstocks has been effective in changing flowering habits of certain scions. Zeevaart (63) showed that a flowering stimulus can be transferred from stock to scion by using long day and short day plants. Graft combinations between flowering (donor) and non-flowering (receptor) plants were performed and grown under non-inducing daylength for the receptors. He demonstrated that several plants which remain vegetative under certain light regimes can be easily flowered in non-inductive daylengths by grafting onto flowering specimens of the same or related species. This suggested that one or more factors were transmitted from donors to receptors. Floral stimuli appeared identical in short day and long day plants because donors of one reaction

type could cause flower formation in receptors of the other only if they were induced themselves.

Habermann and Wallace (22) showed that there was a flowering stimulus transferred from day neutral sunflower stocks to scions. Scions flowered after very limited vegetative growth when grafted onto flowering plants as compared to when grafted on non-flowering plants. Curtis (12) and Curtis and Hornsey (13) induced flowering on unvernallized scions of bolting resistant sugarbeets by grafting onto stocks that bolted readily.

Graft induced sterility changes are less common than graft induced flowering responses. Frankel (21) obtained transmission of cytoplasmic male sterility into fertile petunia scions by grafting onto sterile stocks. Subsequently, Corbett and Edwardson (11) transmitted the sterility factor by grafting from petunia through stems of tobacco plants to petunia with no effect of the factor on the tobacco interstock. Negative results were obtained by Sand (48) in attempts to transmit cytoplasmic male sterility in tobacco by grafting. He concluded that transmission of cytoplasmic male sterility through a graft union with fertile plants is not a general phenomenon.

The induced sex reversal of staminate hop stocks by grafted pistillate scions reported by Limberk (30), prompted Mockaitis and Kivilaan (33) to graft gynoeocious muskmelon onto andromonoecious muskmelon and monoecious

pumpkin. They found that grafting on these rootstocks temporarily induced staminate flowers on the gynoeceious scion.

Environmental Effects on Sex Expression

Sex expression of many plants is altered by environmental conditions. Schaffner (49) reported that hemp plants of known sex produced flowers of the opposite sex in winter greenhouses, but had no sex reversion when grown outside in the summer. He (50, 51) subsequently found that Humulus, Plantago, Arisaema, Thalictrum, Myrica, and Morus also exhibited sex reversions when the photoperiod was changed. Tiedjens (56) observed an increase in the proportion of pistillate flowers in cucumber as a result of short day treatment. Nitsch, et al. (37) showed that short days promoted pistillate flowers in gherkin and squash, while long days favored male expression. Conversely, Thompson (54) promoted female sex expression in spinach with long days. Brantley and Warren (7) stated that long days increased the proportion of perfect flowers in andromonoecious muskmelon.

High temperatures shifted monoecious plants and some pistillate plants toward maleness in experiments with spinach by Janick and Stevenson (26). Bukovac and Wittwer (8) found low temperatures accelerated appearance of pistillate flowers in cucumbers. Heslop-Harrison (25)

stated that, in general, low temperatures promoted pistillate and inhibited staminate flowers.

Nitrogen Effects on Sex Expression

Nitrogen levels have been shown to modify sex expression. Hall (24), working with gherkin, and Tiedjens (56), using cucumbers, demonstrated that in these monoecious cucurbits high levels of nitrogen appeared to promote female sex expression, whereas low levels favored male expression. Tibeau (55) and Thompson (54) found that hemp and spinach responded similarly to nitrogen levels. Brantley and Warren (7) reported that medium and high levels of nitrogen increased the total number of flowers and the proportion of perfect flowers in andromonoecious muskmelon.

MATERIALS AND METHODS

Cultural and Planting Procedures

All the field plants were germinated in 2-1/4 inch peat pots in the greenhouse and transplanted at approximately the two true leaf stage. Black plastic mulch was used and Amiben at two pounds per acre was sprayed between rows of plastic prior to transplanting. Recommended rates of commercial fertilizer were disked under before laying the plastic. Insects were controlled with Dieldrin sprays and the plants remained relatively free of powdery mildew, so fungicides were not applied.

To facilitate analysis of large populations at the proper stage of development, the field plantings were made in increments beginning the first week of June. Single plants were hand planted approximately five feet apart in the row.

Genetic Study

Parental Material and Crosses

A gynoeious line selected by Dr. C. E. Peterson was derived from an F_2 gynoeious segregate of the cross monoecious X hermaphrodite. This line was used in crosses to determine the genetics of gynoeious sex expression.

An F₇ single plant was selected and increased by rooting cuttings and inducing staminate flowers for pollinations by grafting onto pumpkin. A progeny test of this seed (henceforth referred to as Gyn 1) showed that it was homozygous for the gynoecious character. Of fifty-four field plants, only two plants produced a perfect (actually 3/4 ovary perfect) flower as the plants approached senescence. Gynoecious plants characteristically produce a few perfect flowers during senescence. Figure 1 illustrates the gynoecious as compared with monoecious sex type.

Crosses were made in the greenhouse between Gyn 1 and monoecious, andromonoecious and hermaphroditic sex types to study the genetics of gynoecious sex expression. The variety Morden Monoecious (45) was used as the monoecious parent, Hale's Best Jumbo as the andromonoecious parent, and a hermaphrodite from Poland (29) as the hermaphroditic parent. F₁'s, F₂'s, BCl's and selected F₃ populations were grown in the field and classified for sex expression.

Progeny Tests of Different Gynomonoecious F₂'s

Gynomonoecious plants have mostly pistillate flowers and a few perfect flowers. The perfect flowers are not normal perfects, but differ by having various ovary sizes. These variable ovary sized perfect flowers are arbitrarily classified as: (1) 3/4 ovary perfect, (2) 1/2 ovary perfect, (3) 1/4 ovary perfect and (4) male with rudimentary stigma.

Figure 1. Monoecious plant (left) with both pistillate and staminate flowers and gynoeceious plant with pistillate flowers only.



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Hereafter, these partial ovary perfect flowers will be referred to by these designations. Gynomonoecious plants may exhibit these perfect flowers either singly or in any combination. Similar types of perfect flowers occur on the main runners of hermaphroditic plants. Figure 2 illustrates the different ovary sizes of perfect flowers on gynomonoecious and hermaphroditic plants. Figure 3 shows the difference between staminate flowers with rudimentary stigmas and normal staminate flowers. Partial ovary pistillate flowers have never been observed.

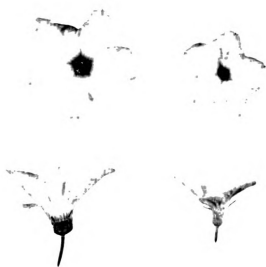
Three F_3 populations from F_2 gynomonoecious plants with different partial ovary perfect flowers were grown to determine the segregation patterns and stability of the different forms. The following three F_2 phenotypes were selected from the cross of Gyn 1 X Hale's Best: (1) predominantly female with a few males with rudimentary stigmas, (2) predominantly female with a few $3/4$, $1/2$ and $1/4$ ovary perfects and a few males with rudimentary stigmas, and (3) predominantly female with a few $3/4$ ovary perfects.

Progeny Test of a Deviant Andromonoecious F_2

A few monoecious and andromonoecious segregates of the cross, Gyn 1 X Hale's Best F_2 , were found which possessed partial ovary perfects. An F_2 andromonoecious plant which deviated from normal by having a few perfect flowers in the axils of main runners, a few $1/2$ ovary

Figure 2. Illustration of the range of ovary sizes on the partial ovary perfect flowers that occur on both gynomonoecious and hermaphroditic plants.

Figure 3. Staminate flower with rudimentary stigma (left) and normal staminate flower.



perfects and a few males with rudimentary stigmas was selected and self-pollinated to observe the F_3 population.

Progeny Test of a Gynomonoecious Segregate

In a seed increase of 300 plants of Gyn 1, a few plants showed perfect flowers before the plants began senescence. A plant with two $1/4$ ovary perfects was self-pollinated to determine if there were genetic differences between this plant and its gynoecious sister plants.

Genetic Differences Between Hermaphroditic Strains

Hermaphroditic sex types have normal perfect flowers on laterals and partial ovary perfect flowers on main runners. The hermaphrodite from Poland produced only $3/4$ ovary perfects on the main runners. Whereas, hermaphrodites segregated in this study from crosses between gynoecious and andromonoecious produced $1/2$ and $1/4$ ovary perfects and often staminate flowers with rudimentary stigmas, as well as $3/4$ ovary perfects on the main runners. Gyn 1 was crossed with the two different hermaphrodites to observe differences in the F_1 populations.

Effect of Selection Pressure on Gynoecious Segregates

The effectiveness of selection pressure for recovering a homozygous gynoecious plant following an outcross to a

different sex type was tested. A gynoeocious segregate A was found in the progeny of a selfed monoecious plant derived from the cross (Gyn 1 X Delicious 51) X Delicious 51. Cuttings were made from this plant, self pollinations were made and the progenies were grown. From this population a gynoeocious B segregate was selected, propagated and selfed. Progenies of gynoeocious A and B were grown simultaneously and compared for relative gynoeociousness.

Classification of Sex Expressions

Because of the diversity of sex types in segregating populations, a classification sheet was devised to record the sex expression of individual plants. Sex readings were made when the main runners were from four to six feet long and prior to fruit set. Gynoeocious segregates were left until the plant growth ceased to allow maximum time for perfect flowers to develop. All plants were pulled at the time of reading.

Fruit Shape Study

A serious objection to the gynoeocious muskmelon is the dominant oblong fruit shape. Crosses were made between fifteen diverse commercial varieties and Gyn 1 in an attempt to find a round-fruited F_1 hybrid. The andromonoecious varieties used were: Bellgarde, DeConinck Bender, Delicious 51, Florida Honey Dew, Golden Perfection, Granite State, Hale's Best Jumbo, Harvest Queen, Hearts of

Gold, Iroquois, Nectarmelon, PMR 45, Seminole, Sungold Casaba, and the Japanese hybrid Sweetie. Ten plants of each were grown.

In a collection of breeding lines, it was noticed that Morden Monoecious (45) differed from other monoecious types by having round instead of oblong fruits. F_1 's, backcrosses and F_2 populations of crosses between Gyn 1 and Morden Monoecious were grown to determine the genetics of this round fruit character. Morden Monoecious was also crossed with Monoecious Iroquois, an oblong-fruited type developed by Dr. Henry Munger at Cornell University.

Round and oblong fruit shapes of individual plants were recorded by visually observing two to four mature fruit per plant. Previous attempts to decipher fruit shape at anthesis were not as reliable as mature fruit readings.

Staminate Flower Induction Studies

Chemical Treatments

The failure of gibberellin A_3 to induce staminate flowers in gynoeocious muskmelon (29, 39) prompted investigations to find a chemical that would induce staminate flowers. An array of chemicals including growth retardants, auxins, kinins, gibberellins, a morphactin, and an ethylene releasing growth regulator were sprayed on field seedlings at the two true leaf stage. Three applications were made at five day intervals.

The concentrations applied were those which had been shown to induce responses on other species of plants and which changed the normal growth pattern, but did not severely stunt or kill the growing point of the plant. Concentrations were based on reports found in the literature for the various chemicals.

Growth retardant sprays were: (1) N-dimethylamino-succinamic acid (B-nine), (2) 2-chlorethyltrimethylammonium chloride (CCC), and (3) maleic hydrazide (MH). Each was sprayed at 10^{-3} molar. MH was dissolved in hot water, and B-nine and CCC were readily soluble in water at room temperature.

The auxin treatments consisted of: (1) indoleacetic acid (IAA), (2) indolebutyric acid (IBA), (3) 2,4-dichlorophenoxyacetic acid (2,4-D), (4) alpha-naphthaleneacetic acid (NAA), (5) beta-naphthoxyacetic acid (NOAA), and (6) 2,3,5-triiodobenzoic acid (TIBA). The 2,4-D and TIBA treatments were 10^{-5} molar, and the others were 5×10^{-4} molar. All of the chemicals with the exception of TIBA were brought into solution with 50 ml methanol and diluted to 500 ml with water. A commercial formulation of TIBA already in solution was used.

Kinetin and N^6 -benzyladenine (BA) were sprayed at 5×10^{-4} molar concentrations. Each was dissolved in 25 ml dilute hydrochloric acid and diluted to 500 ml with water. A commercial solution of synthetic kinin, SD8339,

from Shell Development Company was diluted with water and applied at 5×10^{-4} molar.

A pure acid form of gibberellin A_4A_7 , from Amdal Company, was dissolved in 50 ml methanol, diluted to 500 ml with water, and applied at 3×10^{-5} and 3×10^{-4} molar. Morphactin IT3456, from Vero Beach Laboratories, Inc., was similarly brought into solution and sprayed at 10^{-4} molar. The ethylene evolving compound, Ethrel, from Amchem Products, Inc., was diluted with water and applied at 10^{-3} molar.

Distilled water was used to dilute all the chemicals to the proper concentrations. Tween 80 at .05% was added as a wetting agent to all the formulations and control sprays. The two control treatments consisted of plants sprayed with (1) 50 ml methanol in 450 ml of water, and (2) 25 ml dilute hydrochloric acid in 475 ml water. The experimental design was a randomized complete block with 15 single plant replications of each treatment.

Environmental Fluctuations

Environmental treatments of abnormal cold, heat and daylength were applied to Gyn 1 seedlings to observe the effect of environmental extremes on staminate flower induction.

Cold treatment durations were one to eight days at 40F. Seedlings at the two true leaf stage were placed in a cold chamber with a 14 hour daylength and removed for field planting after one, two, three and four days.

Additional plants were removed from the cold after four days, allowed to revive for three days, and then placed back in the 40F room. These plants were removed at one, two, three and four day intervals and transplanted to the field. Control plants received no cold treatment. Fifteen single plant replications of each treatment were observed in a randomized complete block experimental design.

Combination heat and daylength deviations were tested using growth chambers and greenhouse conditions. Seedlings at the two true leaf stage received treatments consisting of: (1) continuous light, continuous 85F, (2) continuous light, 85F for twelve hours, 60F for twelve hours, (3) twelve hour daylength, continuous 85F and (4) twelve hour daylength, 85F day and 60F night. The continuous 85F treatments were removed from the growth chambers at one week intervals for one month. Subsequently, these plants had 85F days and 60F nights. The continuous light treatments were continued until senescence. Growth chamber and greenhouse lighting consisted of standard cool white inflorescent and interspersed incandescent bulbs. Light intensity in growth chambers was 1000 footcandles. No short day treatments were included since under greenhouse conditions of short days, muskmelon plants tend to remain vegetative. A split-split-plot design with 6 blocks was used. Daylength was the main plot, temperature was the sub-plot and time was the sub-sub-plot.

Graft Studies

Grafting procedure.--The grafting technique used was a modification of that reported by Mockaitis and Kivilaan (33). Their procedure was preferred over the method described by Denna (14). Grafts were made on the internodes between the second and third true leaves of the stocks as soon as the internodes were sufficiently elongated to facilitate adequate incision. The apical buds above the third leaves of the stocks were removed at the time the grafts were made, and lateral buds that developed in the axils of the leaves below the graft union were also removed. Gyn 1 seedlings were tongue grafted onto the stock plants by making approximately 1/2 inch downward incisions halfway through the stems of the stocks and similar upward incisions on the scions, except for opposite direction incisions used for studying girdling effects. Graft unions were held together with Sealtex latex bandage, an elastic material that adheres only to itself and decays as the stems expand. The apical buds of the scions extended approximately one-half inch above the graft union and a three inch stem cut below the incision of the scions was placed in a vial of water for ten days. After the graft unions became established, the stems of the scions below the graft union were removed. Figure 4 illustrates the grafting technique.

Figure 4. Grafting technique.



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Effects of different cucurbit rootstocks.--Grafts were made on several members of the Cucurbitaceae family to determine the effect of different stocks on staminate flower induction of gynoecious scions. The following cucurbits were used as stocks in a field experiment: (1) watermelon (Citrullus vulgaris) cultivar Klondike, (2) squash (Cucurbita moschata) cultivar Butternut, (3) pumpkin (Cucurbita pepo) cultivar Small Sugar, (4) Cucurbita ficifolia, (5, 6) gynoecious and monoecious cucumbers (Cucumis sativus) cultivars MSU713-5 and SMR15 respectively, and (7, 8) andromonoecious and hermaphroditic muskmelons (Cucumis melo var. reticulatus) cultivars PMR45 and MSU breeding line 67-6 respectively. Controls were ungrafted Gyn 1, Gyn 1 grafted onto Gyn 1, and Gyn 1 grafted onto Gyn 1 in a manner requiring plant sap to reverse its flow before going through the graft union. The latter was accomplished by making incisions for tongue grafts upward on the stock and downward on the scion before making the graft union. This was done to induce severe girdling to determine if girdling along affected staminate flower induction. Ten individual plant replications of each of the treatments were transplanted to the field and the number of staminate flowers were recorded. A randomized complete block design was used.

Effects of stock size and scion age and size.--Grafts were made on Small Sugar pumpkin (Cucurbita pepo)

stocks after two, four, six, and eight true leaves. To test the possible effect of age, both seedlings and lateral branches from older flowering plants were used as scions. Scion sizes above the graft union were apical buds, one expanded true leaf, and two expanded true leaves. Ungrafted Gyn 1 and Gyn 1 grafted onto Gyn 1 after the second true leaf were the controls. All plants were grown in eight inch clay pots and the number of staminate flowers recorded until senescence. A split-split-plot design with 4 blocks was used. Stock size was the main plot, scion size was the sub-plot and scion age was the sub-sub-plot.

Origin of stimulus for inducing staminate flowers.--

Studies were conducted to determine whether the staminate flower induction stimulus from pumpkin stocks is derived from the roots or the foliage. de Stigter (15) reported that muskmelon grafts on Cucurbita ficifolia stocks were successful only when leaves were left on the stock. Defoliation of the stock resulted in a rapid collapse of the sieve tubes.

A pumpkin interstock was used to circumvent the effects of pumpkin roots on induction. Seedling pumpkin scions were grafted onto Gyn 1 stocks with two true leaves. Upon establishment of the graft union, Gyn 1 scions were subsequently grafted after the fourth leaf of the pumpkin interstock. Staminate flowers induced with pumpkin interstocks were compared with Gyn 1 scions grafted on pumpkin

stocks with two true leaves. Ungrafted Gyn 1 and Gyn 1 scions on Gyn 1 stocks were grown as controls. Eight single plant replications of each treatment were grown in the greenhouse. Node number and total number of staminate flowers were recorded. A randomized complete block design was used.

Gynoecious cucumber response to pumpkin rootstock.--

The report that gibberellin A₃ was very effective in inducing staminate flowers on gynoecious cucumbers (40), but had no effect when applied to gynoecious muskmelons (29, 39), suggested that different stimuli are responsible for the staminate flower induction of these two closely related species of the same genus. Gynoecious cucumber, MSU713-5, was grafted onto pumpkin to determine if the treatment successful in inducing staminate flowers in muskmelon would be effective in cucumbers. Both gynoecious muskmelon and cucumber were grafted after two true leaves to observe their response on a common stock. Ungrafted plants of both gynoecious cucumber and muskmelon were grown as controls. Eight single plant replications were observed in the greenhouse for staminate flower induction. The experimental design was a randomized complete block.

RESULTS AND DISCUSSION

Genetic Study

The abbreviations used in the tables for the major sex types and deviations were as follows:

Mo = monoecious

Mo' = monoecious except for one pistillate flower
in axil of main runner

Mo" = monoecious except for a few pistillate
flowers in axils of main runners

An = andromonoecious

An' = andromonoecious except for one perfect
flower in axil of main runner

An" = andromonoecious except for a few perfect
flowers in axils of main runners

Gy = gynoeceious

F = gynomonoecious types

P = normal perfect flowers

$3/4$ = $3/4$ ovary perfect flowers

$1/2$ = $1/2$ ovary perfect flowers

$1/4$ = $1/4$ ovary perfect flowers

RS = staminate flowers with rudimentary stigmas

NM = normal staminate flowers

He = hermaphrodite

Mo, An, Gy and He were the major sex classes. The other symbols depicted deviations from the major sex forms.

The gynomonoecious plants were classified to show relative numbers of perfect flowers: P designated predominantly female; M, many females; F, few females. The P, M and F gynomonoecious plants had increasing numbers of perfect flowers, respectively. The numbers of various deviant flowers on each individual plant were indicated by: 1 or 2; F, a few (approximately 3-10); M, many (more than 10).

F₁ Populations

Heterozygosity for the major genes A and G did not affect the sex expression. Tables 1, 2 and 3 illustrate sex expression of the F₁ populations of gynoecious (AAgg) crossed with the three other major sex types. Morden Monoecious (AAGG), Hale's Best (aaGG), and Polish Hermaphrodite (aagg) are monoecious, andromonoecious, and hermaphroditic respectively. In crosses with Gyn 1, the respective F₁ genotypes were AAGg, AaGg, and Aagg. The F₁ phenotypes verified the complete dominance of genes A and G.

The deviants from the monoecious and gynoecious F₁'s were hypothesized to be due to heterozygosity for modifier genes in the gynoecious parent. The difficulty encountered in attempts to obtain a homozygous gynoecious line by successive inbreeding (39) suggested that although the major genes were homozygous, this might not be true for the modifier genes. Also, the non-gynoecious parents could lack homozygosity for the modifying genes since no selection pressure had been applied for the modifying factors.

Table 1. Frequency distribution of the F_1 population from the cross, Gyn 1 X Morden Monoecious, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
85	X														
1	X									1					
1	X												1		
2		X													
1			X												
90															

Expected: All monoecious.

Table 2. Frequency distribution of the F_1 population from the cross, Gyn 1 X Hale's Best, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
86	X														
6	X									1					
1	X									2					
1	X										1				
1			X							1					
95															

Expected: All monoecious.

Table 3. Frequency distribution of the F_1 population from the cross, Gyn 1 X Polish Hermaphrodite, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
27							X								
9								P		1					
5								P		2					
1								P		1	1				
2								P		F	1				
4								P			1				
48															

Expected: All gynoeious.

F₂ Populations

Evidence of the effect of modifying genes on sex expression was noted in the F₂ populations. Table 4 shows the F₂ population of the cross Gyn 1 X Morden Monoecious. The major genes for sex expression segregated independently. The difficulty in recovering gynoeceous types in the F₂ was noted as only three of an expected 46 plants of the AAgg genotype were gynoeceous. The different gynomonoecious segregates suggested multiple modifying genes influencing sex expression. The different deviant monoecious types also suggested modifying genes for sex expression. The hypothesis is advanced that the gynoeceous sex expression is controlled by several modifiers in an infrequent combination with the A-gg genotype. Other combinations of these modifiers result in gynomonoecious types. Disruption of the modifier combination by crossing gynoeceous with another major sex type initiates random assortment in the F₂, and the various gynomonoecious sex forms exhibited are the result of different recombinations of the modifying genes. The predominantly female class of gynomonoecious plants apparently possessed a different complement of the modifying genes than the many female class.

The F₂ population of Gyn 1 X Hale's Best is shown in Table 5. The observed ratio of 108:38:28:12 was in agreement with the expected 9:3:3:1 ratio. The presence

Table 4. Frequency distribution of the F₂ population from the cross, Gyn 1 X Morden Monoecious, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
125	X														
1	X									1					
1	X									F				F	
1	X									1		1		F	
2	X											F			
3	X											F		F	
9	X											F		F	
3	X													M	
5			X												
1			X							F					
1			X							F		F		M	
2			X								F			F	
1			X								F	F		M	
1			X									F			
2			X									F		F	
1			X									F		M	
162	3		X											F	
3							X								
2							P			1					
1							P			F					
1							P			F	F			F	
3							P			F		F		F	
1							P			F	F			F	
1							P				F				
2							P				F			F	
1							P					F			
2							P					1		1	
6							P					F		F	
1							P					F		F	F
7							P							F	
2							M		F			F		M	
2							M		F			F		F	
2							M			F		F		M	
2							M			F		F		F	
1							M			F		F		M	F
1							M				F			F	F
3							M					F		M	
46	2						M							M	F
208															

Expected: 156 Mo: 52 Gy., $\chi^2 = .914$, $P = .25-.50$ (for segregation of major genes only).

Table 5. Frequency distribution of the F₂ population from the cross, Gyn 1 X Hale's Best, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
90	X														
1	X									F	F	F	F		
1	X										1				
1	X										1	1			
1	X										1		F		
2	X											F	F		
3	X												1		
5	X												F		
2		X													
1			X									F	F		
108	1		X									F	M		
25				X											
3				X						1					
3				X						F				F	
1				X						1	1		M		
1				X						F	F	F	F		
1				X							1				
1				X							F	F	F		
1				X								1			
1				X								1	1		
38	1			X									F		
1							X								
1								P		1					
1								P		F					
1								P		F	F	F			
1								M		F	F	F			
1								M		F	F	F	F		
1								F		F	F	F			
10								F		F	F	F	F	F	
1								F		F	F	F	F	F	
7								F		F	F	F	F	F	
1								F		F	F	F	F	F	
28	2							F		F	F	F	M	F	
3								F	F	F	F	F			X
2								F	F	F	F	F	F		X
1								F	F	F	F	F	M		X
12	6							F	F	F	F	F	F	F	X
186															

Expected: 99 Mo: 33 An: 33 Gy: 11 He., $\chi^2 = 2.452$,
 $P = .25-.50$ (for segregation of major genes only).

of only one gynoeceious plant and deviations for partial ovary types in all four major sex classes supported the hypothesis of multiple modifying genes. The predominance of gynomonoecious plants in the few females class indicated a difference between Hale's Best and Morden Monoecious for the modifying genes that affect sex expression.

Table 6 shows the F_2 population of Gyn 1 crossed with the double recessive, aagg, Polish Hermaphrodite. The major gene segregation of 164:60 gynoeceious and gynomonoecious to hermaphroditic plants was in agreement with the expected 3:1 ratio. The relatively few males with rudimentary stigmas, compared to the other F_2 's (Tables 4, 5), suggested that this hermaphroditic line from Poland and Gyn 1 had similar modifying genes. The abundance (89/164) of gynoeceious plants also suggested that the genetic makeup of the two parents was similar. The occurrence of three hermaphrodites with pistillate flowers was probably due to recombinations of modifier genes.

Backcrosses to Gynoeceious Parent and Cytoplasmic Differences

The backcrosses of the F_1 's to the Gyn 1 parent further supported the hypothesis of modifiers. Gynoeceious plants were few in the backcross populations. Table 7 shows the various gynomonoecious types that were postulated to be characteristic of different recombinations of the

Table 6. Frequency distribution of the F_2 population from the cross, Gyn 1 X Polish Hermaphrodite, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
89							X								
18							P			1					
5							P			2					
12							P			F					
11							P			F	F				
6							P			F	F	F			
1							P				1				
1							P				F				
8							P				F	F			
2							P					F			
6							M			F	F				
1							M			F	F	F			
2							F			F	F	F			
1							F			F	F	F	F		
164	1						F				F	F	F		
44										F	M				X
2							1			F	M				X
1							2			F	M				X
7										F	M	F			X
3										F	M	M			X
2										F	F	F	F		X
60	1									F	M	M	F		X
224															

Expected: 168 Gy: 56 He., $\chi^2 = .381$, $P = .50-.75$ (for segregation of major genes only).

Table 7. Frequency distribution of the backcross population from the cross, Gyn 1 X (Gyn 1 X Morden Monoecious F_1), for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
53	X														
3	X									1					
2	X									1				F	
7	X													F	
3		X													
1		X									1				
1			X							F		F		F	
1			X									F		F	
1			X									F		F	
73	1		X											F	
3							X								
2								P		1					
7								P		F					
1								P		1		1			
1								P		F		F			
6								P		F			F		
9								P		F		F	F		
2								P		F		F	F	F	
3								P		F		F	F	F	
1								P				1			
1								P				2			
3								P				F		F	
3								P				F	F		
1								P				F		F	
1								P						1	
2								P						F	
1								M		F		F		F	
1								M		F		F		F	
12								M		F		F		F	
3								M				F		F	
1								M				F		F	
1								F		F		F		F	
4								F		F		F		F	
1								F				F		M	
71	1							F				F		M	

144

Expected: 72 Mo: 72 Gy., $\chi^2 = .028$, $P = .75-.90$ (for segregation of major genes only).

modifiers in the AAgg genotype. The observed ratio of 73:71 monoecious to gynoecious and gynomonoecious types was very near the expected 1:1 ratio. Again, the pre-dominance of monoecious plants without partial ovary perfections indicated the variant types were infrequent recombinations of modifier genes with the double dominant phenotype (A-G-).

The results of the backcross (Gyn 1 X Hale's Best F₁) X Gyn 1 shown in Table 8 were similar to the results shown in Table 7. The many different gynomonoecious types supported argument for modifying genes, with the different partial ovary types being representative of different recombinations of modifiers. The ratio of 64:72 monoecious to gynoecious and gynomonoecious segregates was close to the expected 1:1.

A test was made for cytoplasmic differences on the expression of the modifiers. The small differences between the reciprocal backcrosses in Tables 8 and 9 were attributed to different recombinations of the modifiers. The maternal parent did not influence either the modifiers or the major genes for sex expression.

Table 10 again illustrated the genetic similarity of the Gyn 1 and Polish Hermaphrodite parents with regard to the modifier genes for gynoecious sex expression. The number of gynoecious plants (77/141) recovered in this backcross was much higher than in the backcrosses

Table 8. Frequency distribution of the backcross population from the cross, Gyn 1 X (Gyn 1 X Hale's Best F₁), for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo"	An	An'	An"	Gy	F	P	3/4	1/2	1/4	RS	NM	He
48	X														
3	X								F						
1	X							F	F	F					
1	X							F					F		
2	X									1					
1	X									F			F		
1	X									1		1	F		
2	X											1			
2	X												1		
2	X												F		
64	1		X						F				1		
9						X									
4						P			1						
7						P			F						
4						P			F	F					
1						P			F			F			
8						P			F	F		F			
1						P			F				F		
2						P			F	F			F		
3						P			F			F			
3						P			1						
1						P			2						
1						P			F						
3						P			1		1				
4						P			F		F				
3						P			F		F		F		
2						P			1		2				
1						P					F				
1						P					F		F		
4						P							F		
1						P							F		
1						M		M	F	F		F	F	F	
4						M		M	F	F		F	F	F	
1						M		M	F	F		F	F	F	
1						M		M	F	F		F	F	F	
1						F		F	M	F	F	F	F	F	
72	1					F		F	1	F	F	F	M	F	

136

Expected: 68 Mo: 68 Gy., $\chi^2 = .470$, $P = .50-.75$ (for segregation of major genes only).

Table 9. Frequency distribution of the backcross population from the cross, (Hale's Best X Gyn 1 F₁) X Gyn 1, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
37	X														
3	X									1					
1	X									1		1			
2	X									F	F	F			
2	X									1				1	
1	X									F	F	F		F	
1	X										1				
1	X										F	F		F	
2	X											1			
2	X											F		F	
6	X													1	
4	X													F	
1		X										1			
5			X												
2			X							F	F	F		F	
1			X									1			
1			X									F			
1			X											F	
75	2		X											F	
1						X									
1							P			1					
3							P			F					
4							P			F	F				
8							P			F	F	F			
2							P			F	F	F		F	
1							P			F		F		F	F
1							P			F	F	F		F	F
2							P				2				
1							P				1	1			
1							P				F	F		F	
1							P					1			
3							P					F			
1							P					F		F	
11							M			F	F	F			
1							M			M	F	F			
8							M			F	F	F		F	
1							F			F	F	F		F	
13							F			F	F	F		F	
67	3						F			F	F	F		F	F
142															

Expected: 71 Mo: 71 Gy., $\chi^2 = .450$, $P = .50-.75$ (for segregation of major genes only).

Table 10. Frequency distribution of the backcross population from the cross, Gyn 1 X (Gyn 1 X Polish Hermaphrodite F_1) for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
77							X								
22								P		1					
5								P		2					
8								P		F					
1								P		1	1				
9								P		F	F				
1								P		1		1			
3								P		F	F	F			
4								P			1				
2								P			1	1			
4								P			F	F			
2								M		F	F				
3								M		F	F	F			
141															

Expected: All Gy.

involving monoecious and andromonoecious parents. Furthermore, the occurrence of 22 gynomonoecious plants with only one $3/4$ ovary perfect flower added to the hypothesis of similarity for modifiers. All the backcross plants were gynoecious and gynomonoecious as expected.

Backcrosses to Non-gynoecious Parents

The backcross to Morden Monoecious (Table 11) produced all monoecious progeny as expected, but the four deviant plants indicated an infrequent recombination of the modifiers. The backcross to Hale's Best (Table 12) had similar variant types. The ratio of 69:65 monoecious to andromonoecious types was close to the expected 1:1 ratio. The few deviant plants in these two backcross populations again indicated modifiers that recombined in a manner to be expressed in monoecious and andromonoecious plants.

The predominance of gynoecious plants in Table 13 supported the previous findings (Tables 3, 6, 10) that the Polish Hermaphrodite differed very little from the Gyn 1 parent for the modifiers. The nine hermaphroditic plants that differed from the majority of the hermaphrodites were attributed to different recombinations of modifier genes. The 65:69 ratio deviated only slightly from the expected 1:1 ratio of gynoecious and gynomonoecious to hermaphroditic plants.

Table 11. Frequency distribution of the backcross population from the cross, (Gyn 1 X Morden Monoecious F₁) X Morden Monoecious, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo"	An	An'	An"	Gy	F	P	3/4	1/2	1/4	RS	NM	He
126	X														
1	X												1		
2		X													
1			X										1		
130															

Expected: All Mo.

Table 12. Frequency distribution of the backcross population from the cross, (Gyn 1 X Hale's Best F₁) X Hale's Best, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo"	An	An'	An"	Gy	F	P	3/4	1/2	1/4	RS	NM	He
65	X														
1	X									1					
2		X													
69	1		X												
59				X											
1				X						2					
3				X							1				
65	2				X										
134															

Expected: 67 Mo: 67 An., $x^2 = .120$, $P = .75-.90$ (for segregation of major genes only).

Table 13. Frequency distribution of the backcross population from the cross, (Gyn 1 X Polish Hermaphrodite F_1) X Polish Hermaphrodite, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo''	An	An'	An''	Gy	F	P	3/4	1/2	1/4	RS	NM	He
52							X								
3							P		1						
1							P		2						
2							P		F						
1							P		F		F				
3							P		F		F		F		
1							P				2				
1							P				F				
65	1						P				F		F		
60								F	M						X
2							1	F	M						X
69	7							F	M		F				X
134															

Expected: 67 Gy: 67 He., $\chi^2 = .120$, $P = .75-.90$ (for segregation of major genes only).

Progeny Tests of Different
Gynomonoecious F₂'s

Table 14 illustrates the segregation pattern of the F₃ population derived from an F₂ gynomonoecious plant that had a few male flowers with rudimentary stigmas. The large number (15/54) of F₃ plants that were a replica of the F₂ parent, and the large number that approximated the F₂ parent, suggested that different ovary sizes of the perfect flowers were heritable. Otherwise, an entire array of ovary sizes would have occurred on the perfect flowers. The few F₃ plants with 3/4 and 1/2 ovary perfect flowers were attributed to a low frequency of the modifiers responsible for these ovary sizes in the parent. The many and few female classes of gynomonoecious plants supported the hypothesis of many modifiers and certain recombinations of the modifiers reduced the femaleness of the plants. The few gynoeceous segregates suggested that this type of F₂ gynomonoecious plant would not be very efficient for recovering gynoeceous plants in a breeding program.

The F₃ population of an F₂ gynomonoecious plant that had a few 3/4, 1/2 and 1/4 ovary perfects and a few males with rudimentary stigmas is shown in Table 15. The lack of a predominance of any particular partial ovary type, in contrast to the preceding F₃ population, suggested that the genotypes of these two F₂ plants were different. This also indicated that the different ovary sizes of the perfect flowers were heritable, with different

Table 14. Frequency distribution of the F₃ population from a selfed F₂ gynomonoecious plant with the phenotype, predominantly female with a few males with rudimentary stigmas, for sex expression as influenced by the modifier genes.

No.	Mo	Mo'	Mo"	An	An'	An"	Gy	F	P	3/4	1/2	1/4	RS	NM	He
3							X								
1								P		F					
1								P		F			F		
1								P			F				
4								P			F		F		
1								P			F	F	F		
1								P			F	F	M		
3								P				F			
7								P				F	F		
1								P				F	M		
1								P				F	F	F	
15								P					F		
1								P					M		
1								P					M	F	
1								M		F			M		
2								M				F	M		
1								M				F	F	F	
5								M					M	F	
2								F				F	M	F	
1								F					M		
<u>1</u>								F					M	F	

[illegible]

recombinations of the modifiers resulting in different gynomonoecious types. The small number of gynoecious segregates also limits the usefulness of this F_2 gynomonoecious type for recovering gynoecious plants in a breeding program.

Table 16 illustrates the F_3 population from an F_2 gynomonoecious plant with a few $3/4$ ovary perfects. The low frequency of gynomonoecious plants with only $1/4$ ovary perfects and males with rudimentary stigmas, and the relative abundance of gynoecious plants (17/51) and gynomonoecious plants with $3/4$ and $1/2$ ovary perfects, indicated a different combination of modifier genes in this F_2 plant relative to the two previous F_2 's (Tables 14, 15). Based on these data, most efficient recovery of gynoecious plants from gynomonoecious segregates in a breeding program would be from gynomonoecious plants with a few $3/4$ ovary perfects only.

Progeny Test of a Deviant Andromonoecious F_2

Table 17 shows the segregation pattern of an F_3 population from an F_2 andromonoecious deviant that had a few perfect flowers in axils of the main runners, a few $1/2$ ovary perfects and a few males with rudimentary stigmas. The abundance of normal andromonoecious segregates (29/46) supported the earlier postulation that an infrequent recombination of modifiers resulted

[illegible]

[illegible][illegible]

in partial ovary perfects on andromonoecious plants. The perfect flowers in axils of main runners were attributed to a different infrequent recombination of modifiers.

Progeny Test of a Gynomonoecious Segregate

The progeny test of a Gyn 1 plant that had two $1/4$ ovary perfect flowers before senescence indicated that this plant differed genetically from the Gyn 1 plants. Of 64 plants grown from this selfed gynomonoecious segregate, none was gynoeceous. The number of perfect flowers on the gynomonoecious progeny ranged from 1 to 23 with a mean of 8. The perfect flowers were mostly either $1/4$ ovary perfects or males with rudimentary stigmas. The gynoeceous sister plants grown for comparison were typically gynoeceous.

Genetic Differences Between Hermaphroditic Strains

The breeding behavior of two different hermaphroditic parents are shown in Table 18. The Polish Hermaphrodite parent had partial ovary perfects of the $3/4$ ovary type only, whereas the MSU 1 Hermaphrodite had $3/4$, $1/2$ and $1/4$ ovary perfects and males with rudimentary stigmas. The abundance ($27/48$) of F_1 gynoeceous progeny from the cross, Gyn 1 X Polish Hermaphrodite, and the absence of F_1 gynoeceous progeny in the cross with MSU 1 Hermaphrodite,

Table 18. Breeding behavior of two different hermaphroditic parents, as related to sex expression in the F₁ generation, when used as pollen parents to increase the gynoeious line.

No.	Gy	F	3/4	1/2	1/4	RS
A. Gyn 1 X Polish Hermaphrodite						
27	X					
9		P	1			
5		P	2			
1		P	1	1		
2		P	F	1		
4		P		1		
<u>48</u>						
B. Gyn 1 X MSU 1 Hermaphrodite						
8		P	1			
24		P	F			
3		P	1	1		
1		P	F	1		
4		P	F	F		
1		P	F	F	F	
2		P		1		
1		P		F		
<u>1</u>		P			F	
45						

demonstrated a difference in the modifiers in these two hermaphrodites for gynoeceious sex expression.

Use of Genotype, Aagg,
as Hybrid Parent

Hermaphrodites with only $3/4$ ovary perfects would make the better pollinator if hermaphroditic sister lines were used to increase gynoeceious lines for hybrid seed production. The partial ovary perfects on the gynomonoeceious recombinants in both F_1 's (Table 18A, B) appeared after the plants were of sufficient size to have set fruit. Thus these perfect flowers would have little effect as pollen contamination if the F_1 of gynoeceious X hermaphrodite were used as the female parent in bee-pollinated hybrid seed production. This method of increasing the gynoeceious seed parent may be of value. However, the development of sister hermaphroditic lines would require a more elaborate breeding program than the development of gynoeceious lines alone.

A limitation of the Aagg genotype as a hybrid seed parent in a three-way cross with an andromonoecious, aaGG, pollen parent might be non-uniformity of fruit. One-half of the hybrid plants would be andromonoecious, aaGg, and one-half would be monoecious, AaGg. The blossom end scar on fruits from the perfect flowers of andromonoecious plants often is large and rough; whereas, the scar on monoecious fruit is small and smooth. However, if a

monoecious pollen parent were used, all the hybrid plants would be monoecious, AAGg and AaGg, and the fruit scars would be uniform.

Effect of Selection Pressure
on Gynoecious Segregates

Genetic traits controlled by modifying genes are difficult to reconstitute after hybridizing with diverse parents. Selection within large segregating populations followed by intensive inbreeding is necessary to obtain the desired phenotype. The difficulty in reconstituting the gynoecious character after out-crossing to an andromonoecious plant is shown in Table 19. Table 19A depicts the segregation behavior of a self-one gynoecious segregate selected from the progeny of a selfed monoecious plant derived from the cross, (Gyn 1 X Delicious 51) X Delicious 51. Table 19B shows the segregation behavior after a generation of selfing a gynoecious plant selected from the progeny of Table 19A.

There were approximately 50% gynomonoecious plants following both one and two generations of inbreeding. From a breeding standpoint, several generations of inbreeding gynoecious segregates are apparently required to attain a homozygous gynoecious line. Selection of several gynoecious segregates within a line and perpetuation of the selections with the highest percentage of gynoecious progeny should reduce the generations of inbreeding.

Table 19. Effects of selection pressure and inbreeding on stabilization of gynoeceious sex expression after one and two generations of selfing.

No.	Gy	F	3/4	1/2	1/4	RS	NM
A. Self one of gynoeceious segregate							
23	X						
4		P	1				
1		P	F	F	F		
5		P		1			
3		P		F	F		
2		P		F	F	F	
2		P		F	F	F	F
2		P			1		
1		P			F		
1		P			F	F	
3		P			F	F	F
1		P				F	F
48							
B. Self two of gynoeceious segregate							
27	X						
1		P	1				
3		P	1	1			
1		P	F	F	F		
5		P		1			
1		P		2	1		
1		P		F	F		
1		P		1	1	1	
1		P		F	F	F	
1		P			2		
1		P			F		
1		P			F	F	
1		P			F		F
1		P				F	F
2		P				F	
48							

The difficulty in establishing a homozygous gynoe-cious line would not prohibit its use in hybrid seed production. Perfect flowers on gynomonoecious plants usually occur on terminal ends of runners after the plants have set fruit. In view of the thousands of staminate flowers on a pollen parent, the few perfect flowers on gynomonoecious segregates probably would result in fewer inbreds in the hybrid seed than are now evident in hand-pollinated hybrids.

Fruit Shape Study

The F_1 fruits of Gyn 1 crossed with fourteen round-fruited andromonoecious varieties were all oblong. Apparently the genes for fruit shape in these varieties were similar. Three round-fruited recombinants were found among ten F_1 plants of a cross between Gyn 1 and the andromonoecious Japanese hybrid, Sweetie. Open-pollinated seed from one of the round-fruited monoecious plants was saved. A genetic study was made of fruit shape using a homozygous monoecious round-fruited selection (hereafter referred to as RF Mon) from progeny of the open-pollinated seed. Crosses were made with Gyn 1 to determine the inheritance (Table 20) of this dominant round-fruited trait. The genetic data indicated the round fruit character from Sweetie was controlled by a single dominant gene. A round-fruited gynoe-cious line has been developed using this dominant gene from Sweetie.

Table 20. Inheritance of fruit shape in the family of Gyn 1 X RF Mon.

Cross	Observed		Expected*	
	Round	Oblong	Round	Oblong
RF Mon	20		20	
Gyn 1		20		20
Gyn 1 X RF Mon F ₁	20		20	
Gyn 1 X RF Mon F ₂	44	12	42	14
Gyn 1 X RF Mon F ₁ BC to RF Mon	24		24	
Gyn 1 X RF Mon F ₁ BC to Gyn 1	43	45	44	44

* All P Values greater than 0.500.

Table 21. Inheritance of fruit shape in the family of Gyn 1 X Morden Monoecious, and the F₁ fruit shape in the hybrid of Morden Monoecious with the oblong monoecious line, Monoecious Iroquois.

Cross	Observed		Expected*	
	Round	Oblong	Round	Oblong
MM	15		15	
Gyn 1		15		15
Gyn 1 X MM F ₁	47		47	
Gyn 1 X MM F ₂	64	20	63	21
Gyn 1 X MM F ₁ BC to MM	44		44	
Gyn 1 X MM F ₁ BC to Gyn 1	51	49	50	50
Monoecious Iroquois X MM F ₁	32		32	

* All P Values greater than 0.750.

Table 21 shows the segregation behavior in crosses made with Gyn 1 to determine the inheritance of fruit shape in the round-fruited Morden Monoecious. The genetic factor for round fruit shape was attributed to a single dominant gene (Figure 5). The round-fruited hybrid of Morden Monoecious crossed with the oblong-fruited monoecious type, Monoecious Iroquois, indicated Morden Monoecious as a parent for developing round-fruited monoecious lines in breeding programs.

There are reports of fruit shapes of oblate, spherical, oval, and elongate in the literature (58). Baines and Kang (2) reported that in a cross of a cylindrical-fruited monoecious plant with a flat-fruited andromonoecious type, the F_1 was intermediate. They postulated a single gene without dominance as the governing factor. There are several alleles for fruit shape in muskmelons, and the dominant genes for round fruit from the two different sources in the present study might behave differently in crosses with other fruit shapes. These two sources of dominant round-fruited genes are of value, however, in transferring the round-fruited character to the unacceptable oblong monoecious and gynoecious types.

Figure 5. Fruit shape of Morden Monoecious, the gynoeceious line, the hybrid between the two lines, and typical fruit shape of hybrids between Gyn 1 and round-fruited andromonoeceious varieties.



Gyn X Morden Mon F,



*Morden
Monoecious*



*Typical
Gyn X Andromonoecious F,*



Gynoecious

Staminate Flower Induction Studies

Chemical Treatments

None of the chemicals used induced staminate flowers on Gyn 1. Various growth responses were induced by certain of the chemicals, but none altered the gynoeceous sex expression.

Environmental Treatments

Shock treatments of cold, heat and daylength were also ineffective in the induction of staminate flowers on Gyn 1. These results suggested the gynoeceous plants would remain gynoeceous if exposed to adverse conditions naturally. This stability is necessary for successful use in hybrid seed production.

Graft Studies

Effects of different cucurbit rootstocks.--The grafts of Gyn 1 scions onto different cucurbits substantiated differences between rootstocks for staminate flower induction. The induced pollen bearing flowers were not normal staminate flowers, but were mostly staminate flowers with rudimentary stigmas. These flowers are referred to as staminate flowers as they are bearers of viable pollen equivalent to normal staminate flowers.

Table 22 shows the response of Gyn 1 on the various rootstocks in the field. The pumpkin rootstock was significantly better than all the other rootstocks with the

Table 22. Comparative induction (to anthesis) of staminate flowers on Gyn 1 scions by different rootstocks in field.

Rootstock	Mean No. Staminate Flowers*
<u>Cucurbita pepo</u>	3.6 a
<u>Cucurbita moschata</u>	2.4 ab
<u>Cucumis sativus</u> (monoecious)	1.7 bc
<u>Cucumis sativus</u> (gynoecious)	1.6 bc
<u>Cucumis melo</u> (hermaphrodite)	1.6 bc
<u>Cucumis melo</u> (andromonoecious)	1.5 bc
<u>Cucurbita ficifolia</u>	1.3 bc
<u>Citrullus vulgaris</u>	0.3 c
Gyn 1 (inverted graft)	0 c
Gyn 1 (graft)	0 c
Gyn 1 (ungrafted)	0 c

* Means followed by different letters are significantly different at 5% level. Duncan's Multiple Range Test.

exception of squash. The absence of staminate flowers on the inverted graft of Gyn 1 demonstrated that the girdling effect alone did not affect staminate flower induction. The few staminate flowers (0.3-3.6) produced indicated that field-grown grafted plants would not produce enough pollen for increase of gynoeceious seed by bee pollinations. The lack of sufficient staminate flowers for adequate pollination in the field might be due to abortion of early flowers before anthesis. Abortion is accentuated by wind, less than optimum growing conditions and transplanting shock.

Zubov (64) reported various changes in muskmelon scions grafted onto pumpkin including increased cold and anthracnose resistance, doubled average length of vines and fruit weight, and taste variations depending upon the variety of pumpkin stock. In the present study, there were no visual changes in the gynoeceious scions on different rootstocks. Gynoeceious scions on different rootstocks resembled the Gyn 1/Gyn 1 and Gyn 1 control plants in all growth and fruit characteristics.

Field grown vs. greenhouse grown grafted plants.--

An alternative to growing the grafted plants in the field would be to grow them in the greenhouse and hand pollinate field plants with the greenhouse pollen. By using forceps and detaching each individual anther, approximately four pistillate flowers can be pollinated with one staminate flower. This method of increasing

gynoecious seed is not prohibitive compared to hand pollinations for hybrid seed production. For each successful pollination of the gynoecious plants with the greenhouse grown pollen, the return would vary from 200 to 500 seeds per fruit. The hybrid seed that could be produced with these gynoecious plants from one hand pollination would approach exponential proportions, assuming a realistic 1000 seeds per plant from bee cross-pollinations. It is estimated that one hand pollination to increase the gynoecious parent is equivalent to 5000 hand pollinations for hybrid seed production. The grafting procedure is not limiting, as the grafts are easily and quickly made, and a minimum of 90% scion survival is common.

Effects of stock size and scion age and size.--Since chemical treatments and field grafting did not produce sufficient staminate flowers, the most efficient stock size and scion age and size combinations for staminate flower induction in the greenhouse were determined.

Table 23 shows the number of staminate flowers induced to anthesis with the different graft combinations. Induction of staminate flowers was not increased by either larger stocks or by the scion size. Seedling scions (S) did not differ from scions taken from laterals (L) on older plants. The check plants, ungrafted Gyn 1 and Gyn 1/Gyn 1, were gynoecious with only two of the plants having one perfect flower each as the plants approached

Table 23. Effects of size of stock and size and age of scion on mean number of staminate flowers induced to anthesis in greenhouse.

Scion Size and Age*										
Stock Size	bud			1 leaf			2 leaves			F test
	$\bar{S}$	$\bar{L}$	$\bar{X}$	$\bar{S}$	$\bar{L}$	$\bar{X}$	$\bar{S}$	$\bar{L}$	$\bar{X}$	
2 leaf	22.7	23.0	22.9	29.7	20.3	25.0	24.5	19.0	21.8	23.2 N.S.
$\bar{X}$	S = 25.7 L = 20.8									
4 leaf	26.8	29.8	28.3	16.0	23.0	19.5	30.7	14.8	22.8	23.5 N.S.
$\bar{X}$	S = 24.5 L = 22.5									
6 leaf	26.0	11.8	18.9	33.0	31.0	32.0	22.7	20.5	21.6	24.2 N.S.
$\bar{X}$	S = 27.3 L = 21.1									
8 leaf	15.8	35.5	25.6	19.0	20.0	19.5	23.0	29.8	26.4	23.8 N.S.
$\bar{X}$	S = 19.3 L = 28.4									
$\bar{X}$	bud = 23.9 N.S.			1 leaf = 24.0 N.S.			2 leaves = 23.1 N.S.			
$\bar{X}$	S = 24.2 N.S.			L = 23.1 N.S.			No significant interactions			

* S = seedling, L = lateral from flowering plant...

senescence. The most suitable stock is one with two true leaves. It is more succulent for grafting and does not require support as do older stocks.

Origin and description of induction stimulus.--An experiment was conducted to learn if the stimulus for staminate flower induction originated from the root or the foliage of the pumpkin stock. Data were taken to determine the duration of induction.

Table 24 shows that the stimulus for staminate flower induction came from the foliage of the pumpkin rather than from the roots. The effect of pumpkin roots was easily circumvented by using pumpkin interstocks. There were no differences between mean number of staminate flowers induced, nodal extremities of induction, and mean node of induction between scions on the pumpkin rootstock and the pumpkin interstock.

Scheduling staminate flower induction.--In using greenhouse induced staminate flowers for field pollinations to increase gynoecious seed, scheduling the field plants is important. The field plants should be ready for pollination when the staminate flowers are at anthesis since the induction stimulus is temporary and is terminated after the twentieth node of the scion. This scheduling could be accomplished by planting the pumpkin rootstocks two to three weeks after the gynoecious plants are planted. Scions from the field plants could be used for grafting.

Table 24. Effect of pumpkin rootstock vs. pumpkin interstock on mean number of staminate flowers induced, nodal extremities of induction, and mean node of induction of staminate flowers on Gyn 1 scions in greenhouse.

	Gyn 1/Pumpkin	Gyn 1/Pumpkin/Gyn 1	F test
Mean number of staminate flowers induced	51.4	57.5	N.S.
Mean nodal extremities of induction	6-20	6-18	N.S.
Mean node of induction	10.0 $\pm$ 3.26	10.2 $\pm$ 2.95	N.S.

It is evident from the data that most induced staminate flowers are produced on laterals rather than the main runner. Therefore, laterals on the scion should be encouraged and not pruned as is practiced in growing muskmelons in the greenhouse for seed production.

Gynoecious cucumber response to pumpkin rootstock.--

Gynoecious cucumber scions did not respond to the pumpkin rootstock. Replicated trials using Gyn 1 scions and gynoecious cucumber scions on pumpkin stocks resulted in numerous staminate flowers on Gyn 1, but no staminate flowers on the gynoecious cucumbers. It is postulated that different stimuli are responsible for staminate flower induction in these two members of the same genus. This evidence supports the supposition that different stimuli are involved since gibberellin induces staminate flowers readily on gynoecious cucumbers, but has no induction effect on gynoecious muskmelons.

CONCLUSIONS

Genetics of Sex Expression

Gynoecious sex expression was controlled by multiple modifying genes in addition to the major genotype A-gg. Disruption of the combination of modifiers conditioning gynoecious sex expression by crossing with monoecious, andromonoecious, and hermaphroditic sex types resulted in mostly gynomonoecious plants for the A-gg genotype in the segregating F_2 , BCP_1 , and BCP_2 populations. The different major sex types had different complements of the modifying genes. The segregation behavior was similar whether the gynoecious type was the seed parent or the pollen parent, and illustrated lack of cytoplasmic differences for gynoecious sex expression. Gynomonoecious plants had $3/4$, $1/2$ and $1/4$ ovary perfect flowers and staminate with rudimentary stigmas in combinations or singly depending upon the modifier complement. Apparently, different modifiers were responsible for the different types of partial ovary perfect flowers. The highest percentage of gynoecious segregates was recovered from selfed gynomonoecious plants that had only $3/4$ ovary perfects.

Heterozygosity for the major genes A and G did not affect the expression of the modifiers. Monoecious and

andromonoecious plants infrequently exhibited the partial ovary perfect flowers in segregating populations, after crossing these two sex types with the gynoeceious type. The percentage of gynoeceious progeny in crosses of gynoeceious, AAgg, with the double recessive hermaphrodite, aagg, varied depending upon the complement of modifier genes of the hermaphrodite. A higher percentage of gynoeceious progeny was present in the F_1 if the hermaphroditic parent had only $3/4$ ovary perfects. Recovery of a homozygous gynoeceious type after the combination of modifiers has been changed by crossing to different sex types apparently requires several generations of selfing.

Inheritance of Fruit Shape

The oblong fruit shape of Gyn 1 was dominant to the fruit shape of several round-fruited andromonoecious varieties. A gene for round fruit dominant to the fruit shape of Gyn 1 was found in the andromonoecious Japanese hybrid, Sweetie. The round fruit shape of Morden Monoecious was also dominant to the fruit shape of Gyn 1. Genetic studies of these two factors for round fruit shape showed that they were single dominant genes.

Staminate Flower Induction

Chemical spray treatments with auxins, growth retardants, kinins, gibberellins, a morphactin, and an ethylene releasing growth regulator were ineffective in

inducing staminate flowers on Gyn 1. Environmental treatments of cold, heat and daylength were equally ineffective.

Grafting onto different cucurbit rootstocks demonstrated differential induction. Pumpkin rootstocks resulted in the highest number of staminate flowers on gynoecious scions. The induced flowers were not true staminate flowers, but were mostly staminate flowers with rudimentary stigmas. The amount of pollen on the graft-induced flowers was equivalent to normal staminate flowers. No effects other than induction of staminate flowers were observed as responses to the different rootstocks.

There were no differences in the numbers of staminate flowers induced due to different pumpkin stock sizes. Scion size did not affect induction, and scions from mature gynoecious plants did not differ from seedling scions. The girdling effect alone of grafting did not influence staminate flower induction.

Pumpkin stocks did not differ from pumpkin interstocks in either the number of staminate flowers induced, or the nodal extremities of induction, or the mean node of induction. The stimulus from the pumpkin stock is apparently endogenous to the foliage of the pumpkin.

Pumpkin stocks were not effective in inducing staminate flowers on gynoecious cucumbers. It is postulated that different stimuli are responsible for staminate flower induction in gynoecious muskmelons and cucumbers.

F₁ Hybrid Feasibility of Gynoecious
Muskmelon

Gynoecious sex expression in muskmelon deserves considerable attention for use in the production of hybrid seed. A gynoecious line was developed with the more desirable round fruit shape which is necessary for production of round-fruited hybrids. Two different methods of increasing seed of gynoecious lines may be used. Hand pollinations of gynoecious plants in the field, with pollen induced by grafting in the greenhouse, appears to be more satisfactory than sibbing with a hermaphroditic sister line. Hand pollinations with induced staminate flowers are facilitated by ease of making grafts and the high percentage of scion survival. It is estimated that one hand pollination to increase the gynoecious parent, with subsequent hybrid seed production by bee pollinations, would produce as much hybrid seed as 5,000 hand pollinations with the present method of making hybrids.

The difficulty in obtaining the homozygous gynoecious type is not prohibitive. Gynomonoecious segregates in the seed parent would contribute a minimum of pollen for contamination, as the perfect flowers usually occur after the plants are of sufficient size to have set fruit. The per cent inbreds in the hybrid seed from gynomonoecious pollen probably would not surpass the per cent inbreds observed in hand-pollinated commercial hybrids.

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