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Inheritance of parthenocarpy in summer squash (*Cucurbita pepo* L.)

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ABSTRACT. The inheritance of the tendency to set parthenocarpic fruit in the summer squash (*Cucurbita pepo* L.) line Whitaker was studied. Two parental lines, Whitaker (parthenocarpic) and Caserta (non-parthenocarpic), and the F_1 and F_2 generations and backcrosses to both parents were tested. The parthenocarpic tendency of individual plants was scored on a scale from 1 (non-parthenocarpic fruit) to 5 (parthenocarpic fruit). The Whitaker line produced parthenocarpic fruit and had a mean score of 4.2, whereas Caserta did not set parthenocarpic fruit and had a score of 1.55. The heritability estimates indicated that genetic gains from selection were feasible. The additive-dominant model showed a good fit, with epistasis being negligible or nonexistent. The hypothesis of monogenic inheritance with incomplete dominance was not rejected within the degree of dominance range from 0.2 to 0.5. These results indicate that parthenocarpy is controlled by a single locus, with incomplete dominance in the direction of parthenocarpic expression.

Key words: *Cucurbitaceae*, Genetic control, Heritability, Whitaker

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INTRODUCTION

Summer squash (*Cucurbita pepo* L.) is normally a monoecious crop. Male flowers occur at the end of slender stems and have three anthers, whereas female flowers occur at the end of short peduncles and have a thick style and a two-lobed stigma; a swollen ovary occurs at the base of the corolla and is divided into 3-5 sections. Female flowers produce more nectar and attract more bees than do male flowers. The pollen grains are large and well-suited for transportation by insects. The flowers open early in the morning and close around noon of the same day, never to reopen (Free, 1992; Nepi and Pacini, 1993).

Pollinating agents, usually bees, are necessary to transfer pollen from male to female flowers. Wind does not pollinate *Cucurbita* spp. Wolfenbarger (1965) reported that summer squash plants visited by pollinators outyielded plants grown in insect-proof greenhouses by 500%. Similarly, Skinner and Lovett (1992) showed that squash plants caged to exclude pollinators produced no fruit.

Pollen viability in a newly opened male flower is about 92% but drops to 75% by the time the flower closes that same morning, and is only 10% by the next day (Nepi and Pacini, 1993). Female flowers must therefore be pollinated as early as possible on the day the male flower opens, while the pollen is still viable.

Fruit development after pollination and fertilization is triggered by the coordinated action of growth hormones provided and/or regulated by the pollen grains, pollen tubes and developing seeds (Gillaspy et al., 1993). Parthenocarpy involves development of the ovary into a fruit without fertilization and seed formation, under the influence of exogenous hormones or endogenous genetic stimuli.

Most of the currently grown greenhouse cultivars of slicing cucumbers can set parthenocarpic fruit, and parthenocarpic pickling cultivars are of major importance. Parthenocarpy in summer squash has received less attention, but may enable squash to be grown in greenhouses and in the field out-of-season, when staminate flowers or pollinating insects may be absent. The sharp reduction in bee populations in many areas of the world has adversely affected crop pollination.

'Whitaker' is a recently released parthenocarpic summer squash line developed by researchers at Cornell University. This line is resistant to three viral diseases and sets parthenocarpic fruit (McCandless, 1998). The source of the ability to set parthenocarpic fruit is uncertain (Robinson and Reiners, 1999). The aim of the present study was to determine the mode of inheritance of parthenocarpic fruit in Whitaker squash.

MATERIAL AND METHODS

The experiments were done at the Vegetable Crops Experimental Station of the Federal University of Lavras, Lavras, MG, Brazil. The lines Whitaker and Caserta were used to obtain the F_1 generation (Whitaker x Caserta). Whitaker sets parthenocarpic fruit, whereas Caserta is a traditional *C. pepo* cultivar grown as summer squash in Brazil, but does not set parthenocarpic fruit.

The F_1 (Whitaker x Caserta) plants were either self-pollinated to produce the F_2 generation or crossed to both parents to produce the reciprocal backcross families BC_{11} (= Whitaker x F_1) and BC_{12} (= Caserta x F_1). Fifty-one Whitaker plants, 94 Caserta plants, 53 F_1 (Whitaker

x Caserta) plants, 204 F_2 plants, 75 BC_{11} plants, and 86 BC_{12} plants were evaluated.

Female flowers were protected with paper bags one day before anthesis to prevent visitation by insects. Three female flowers per plant were bagged and scored separately. Any open flowers were removed to prevent the setting of open-pollinated fruit. Fruit development was scored seven days after the flowers had been bagged. A scoring system of 1 to 5 was used, as follows: 1 = fruit length <9 cm, or fruit base weak and/or necrosed, 2 = fruit length 9-11 cm, 3 = fruit length 11-13 cm, 4 = fruit length 13-15 cm, and 5 = fruit length >15 cm. Individual plant scores were calculated as the mean of the values for the three flowers scored per plant.

Means and variances were calculated for each generation in order to determine the genetic parameters. The environmental variance ($\hat{\sigma}^2_E$) was estimated as the geometric mean of the variances of the P_1, P_2 and F_1 generations. Genetic variance ($\hat{\sigma}^2_G$), and its additive ($\hat{\sigma}^2_A$) and dominance ($\hat{\sigma}^2_D$) components, as well as broad (H^2) and narrow-sense (h^2) heritability, were estimated. Analysis of the generation mean was used to test the fitness of a simple additive-dominant model and to estimate the mean degree of dominance (MDD) (Mather and Jinks, 1977). The number of segregating genes was estimated according to Wright (1934).

Test for the hypothesis of monogenic inheritance

The data were used to test hypotheses of monogenic inheritance under different presumed degrees of dominance, as described by Gomes et al. (2000). The assumptions and procedures used in this test are summarized as follows:

a) The data from all generations (P_1, P_2, F_1, F_2, BC_{11}, and BC_{12}) were assumed to have a normal distribution.

b) A truncation point (TP) was established, below which were located most of the P_2 (Caserta) plants and above which were most of the P_1 (Whitaker) plants. The TP chosen was a score of 3.

c) The means and variances of P_1 and P_2 were assumed to be equal to the respective estimates obtained from the experimental data.

d) Based on a normal distribution, the frequencies of P_1 and P_2 plants equal to or greater than the TP were estimated.

e) The true mean of the F_1 generation was admitted to be:

$$\overline{F}_1 = \left(\overline{P}_1 + \overline{P}_2\right)/2 + MDD \cdot \left(\overline{P}_2 - \overline{P}_1\right)/2$$

where $\overline{P}_1$ and $\overline{P}_2$ are the respective parental means and MDD is the presumed degree of dominance under consideration. The true variance of the F_1 population was assumed to be equal to the respective variance obtained from the experimental data.

f) Under the hypothesis of monogenic inheritance, the expected plant frequencies for F_2, BC_{11} and BC_{12} ≥TP were calculated as the weighted average of the expected frequencies in P_1, F_1 and P_2. The weights for the P_1, F_1 and P_2 generations were 1:2:1 for the F_2 generation, 1:1:0 for BC_{11} and 0:1:1 for BC_{12}.

g) The frequencies of P_1, P_2, F_1, F_2, BC_{11}, and BC_{12} plants ≥TP were calculated by multiplying the expected frequencies by the total number of plants tested per generation.

h) The expected numbers of plants ≥TP were compared with their respective observed values in each generation. The significance of the deviations was estimated with a χ^2 test, with

four degrees of freedom. The frequency of expected plants in P_1 was added to that of P_2 in order to avoid expected frequencies equal to zero.

i) Significant χ^2 values would lead to rejection of the hypothesis of monogenic inheritance under the presumed degree of dominance. On the other hand, non-significant χ^2 values would lead to the acceptance of such a hypothesis. The values of χ^2 for each MDD assumed were plotted against their respective hypothetical MDDs. The range of MDD values for which χ^2 values fell below the critical $\alpha = 0.05$ value represented the MDD range for which the hypothesis of monogenicity could not be rejected.

Tests of genetic control using maximum likelihood estimators

An alternative method based on maximum likelihood estimators, proposed by Silva (2003), was used to test the hypotheses of monogenic inheritance and/or the presence of polygenic (or modifier) loci that could affect the trait. Based on the means and variances (Mather and Jinks, 1977), the data were assumed to have normal distributions, as follows:

$$P_1: N\left(\mu - [a] - A, \sigma^2\right)$$

$$P_2: N\left(\mu + [a] + A, \sigma^2\right)$$

$$F_1: N\left(\mu + [d] + D, \sigma^2\right)$$

$$F_2: \frac{1}{4}N\left(\mu + \frac{[d]}{2} - A, \sigma^2 + V_A + V_D\right) + \frac{1}{2}N\left(\mu + \frac{[d]}{2} + D, \sigma^2 + V_A + V_D\right) + \frac{1}{4}N\left(\mu + \frac{[d]}{2} + A, \sigma^2 + V_A + V_D\right)$$

$$BC_{11}: \frac{1}{2}N\left(\mu + \frac{[a]}{2} + \frac{[d]}{2} - A, \sigma^2 + \frac{V_A}{2} + V_D - S_{AD}\right) + \frac{1}{2}N\left(\mu - \frac{[a]}{2} + \frac{[d]}{2} + D, \sigma^2 + \frac{V_A}{2} + V_D - S_{AD}\right)$$

$$BC_{12}: \frac{1}{2}N\left(\mu + \frac{[a]}{2} + \frac{[d]}{2} + A, \sigma^2 + \frac{V_A}{2} + V_D + S_{AD}\right) + \frac{1}{2}N\left(\mu + \frac{[a]}{2} + \frac{[d]}{2} + D, \sigma^2 + \frac{V_A}{2} + V_D + S_{AD}\right)$$

where μ = constant reference value, A = additive effect of the major gene, D = dominance of the major gene, [a] = polygenic additive effects, [d] = polygenic dominant effects, V_A = additive variance associated with polygenic effects, V_D = dominance variance associated with polygenic effects, S_{AD} = additive x dominance deviation associated with polygenic effects, and σ^2 = environmental variance.

The frequencies of BC_{11} and BC_{12} consisted of two normal densities whereas F_2 had three normal densities. In this model, the mean and variance components associated with polygenic effects are unaltered, and only effects that are correlated with a major gene usually show any change. All of the parameters were estimated by using the maximum likelihood method and several genetic models were constructed (Table 1).

Table 1. Genetic models tested for the resistance to parthenocarpy in summer squash.

Models	Estimated parameters
1 = major gene with additive and dominance effects + polygenes with additive and dominance effects	μ, A, D, [a], [d], V_A, V_D, S_{AD}, σ^2
2 = major gene with additive and dominance effects + polygenes with additive effect only	μ, A, D, [a], V_A, σ^2
3 = major gene with additive effect only + polygenes with additive and dominance effects	μ, A, [a], [d], V_A, V_D, S_{AD}, σ^2
4 = major gene with additive effect only + polygenes with additive effect only	μ, A, [a], V_A, σ^2
5 = polygenes with additive and dominance effects	μ, [a], [d], V_A, V_D, S_{AD}, σ^2
6 = polygenes with additive effect only	μ, [a], V_A, σ^2
7 = major gene with additive and dominance effects	μ, A, D, σ^2
8 = major gene with additive effect only	μ, A, σ^2
9 = environmental effects only	μ, σ^2

Tests were done using the LR (Modd et al., 1974) and the maximum likelihood method:

$$LR = -2\ln\frac{L(M_i)}{L(M_j)}$$

where LR is the likelihood ratio, $L(M_i)$ and $L(M_j)$ are maximum likelihood functions of models i and j, and model i is hierarchical to model j. The tests were done using the statistical software package Monogen v. 0.1 developed by Silva (2003) and available from E. Bearzoti upon request.

RESULTS AND DISCUSSION

The appearance of fruit from non-pollinated parthenocarpic flowers was similar to that from pollinated flowers. The ovaries of some bagged flowers enlarged somewhat after anthesis but aborted before reaching marketable stage. Mature fruits produced from closed pistilate flowers were entirely seedless, thus confirming that they were parthenocarpic.

The Caserta and Whitaker lines had mean scores of 1.55 and 4.2, respectively (Table 2), thereby reforcing the clear distinction between these parental lines with regard to the occurrence of parthenocarpic fruit. The broad and narrow-sense heritability estimates were 0.52 and 0.35 for the Caserta and Whitaker lines, respectively. The number of genes (estimated according to Wright, 1934) controlling parthenocarpy in 'Whitaker' was ~1 (Table 3).

A simple, additive-dominant model explained the segregation data (Table 3). The lack of significant deviations from the proposed model (as shown by the χ^2 test) indicated that no epistatic gene action was involved in controlling parthenocarpy in the Whitaker line. The estimated mean degree of dominance was 0.30, indicating partially dominant gene effects in the direction of parthenocarpy (Table 3).

Estimates of χ^2 for the hypotheses of monogenic inheritance indicated that the hypotheses could not be rejected for mean degrees of dominance between +0.2 and +0.5 (Figure 1),

Table 2. Means and variances for parthenocarpy in summer squash (*Cucurbita pepo*).

Generations	Score	Variances
Whitaker (P_1)	4.16	0.7499
Caserta (P_2)	1.55	0.6150
F_1 (Whitaker x Caserta)	3.33	1.2393
F_2 (Whitaker x Caserta)	2.91	1.7150
BC_{11} (= Whitaker x F_1)	3.54	1.5542
BC_{12} (= Caserta x F_1)	2.47	1.2705

Table 3. Estimates of broad (H^2) and narrow-sense (h^2) heritability, mean components, number of genes (η), and mean degree of dominance (MDD) for parthenocarpy.

Parameters	Estimates
H^2	51.61
h^2	35.29
m	2.8197 ± 0.009
[a]	1.2738 ± 0.009
[d]	0.3775 ± 0.020
χ^2	0.0508^{ns}
MDD	0.30
η	0.97 (~1)

m: parental mean; [a]: additive mean effect; [d]: non-additive (dominance) mean effect; χ^2: chi-square test for fitness of the additive-dominant model; ns: not significant.

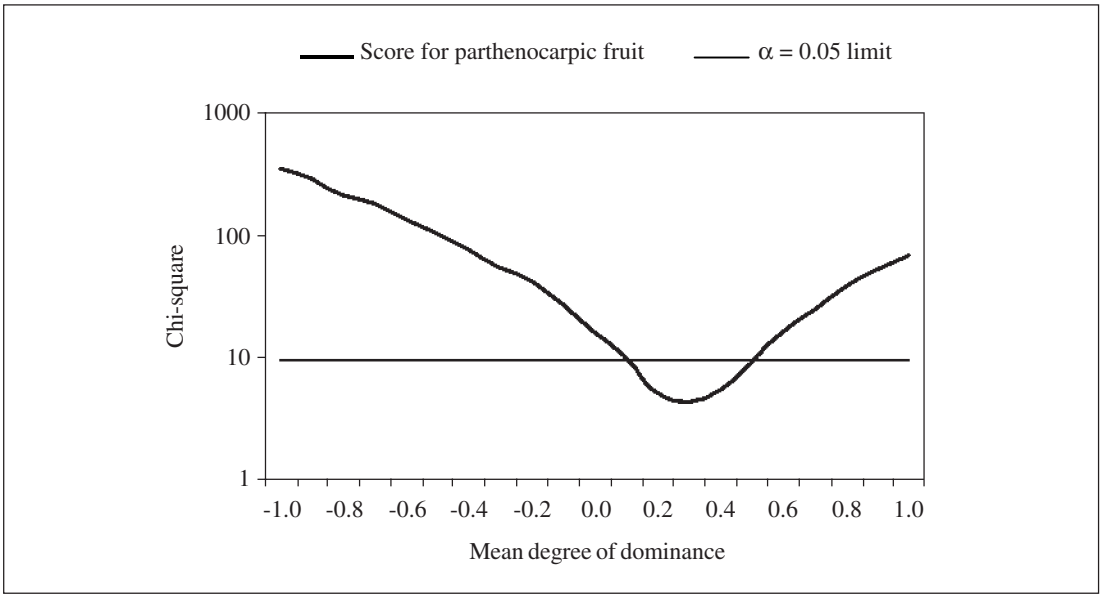

Figure 1. Monogenic hypothesis test under different presumed degrees of dominance for parthenocarpy in summer squash.

which suggested that parthenocarpy in the Whitaker line was controlled by one gene, with incomplete dominance in the direction of parthenocarpic fruit.

The inheritance tests done using the maximum likelihood approach are shown in Table 4. When model 1 was compared to model 5, the existence of a major gene plus polygenic effects was tested against the existence of polygenic effects alone. The test of this hypothesis was rejected, indicating that a major gene was involved in controlling this trait. When model 1 was compared to model 7, the existence of a major gene plus polygenic effects was tested against the hypothesis of a single major gene effect only. This hypothesis could not be rejected, indicating that there is no evidence of polygenic effects in the control of parthenocarpy (Table 4). When model 7 was compared to model 8, the existence of a major gene with additive and dominance effects was tested against the hypothesis of a major gene with an additive effect only. Since this hypothesis was rejected, we conclude that parthenocarpy in the Whitaker line is controlled by one gene with significant dominant effects.

Table 4. Hypotheses of inheritance for parthenocarpy tested using the maximum likelihood method.

Tests	χ^2_c	Degrees of freedom	Probability
1 *vs* 5	10.0247	5	0.0067
1 *vs* 7	1.3963	5	0.9247
5 *vs* 6	10.5170	3	0.0146
7 *vs* 8	10.6751	1	0.0011
7 *vs* 9	228.6306	2	0.0000

In this analysis, the methods of Gomes et al. (2000) and Silva (2003) yielded the same conclusion, namely, that parthenocarpy in *C. pepo* cv. Whitaker is controlled by a single gene locus, with partial dominance for the Whitaker allele that induces parthenocarpy.

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