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Variance component analysis of parthenocarpy in elite U.S. processing type cucumber (*Cucumis sativus* L.) lines

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Summary

Parthenocarpic (seedless) U.S. processing type cucumber (*Cucumis sativus* L.) germplasm can bear more high quality fruit when compared to their seeded counterparts. Knowledge of genetic components of variation for parthenocarpy would assist cucumber breeders to incorporate this economically important trait into commercial varieties. The inheritance of parthenocarpy in elite U.S. processing type cucumber was, therefore, investigated by examining the single-harvest yield of F_3 progeny derived from a mating between line 2A (P_1, parthenocarpic) and line Gy8 (P_2, non-parthenocarpic) grown in two fields (E-block and G-block at Hancock, Wisc.) in the summer of 2000. Environmental variance accounted for about 90% of total phenotypic variance in both locations. The degree of dominance genetic variance was 0.3 and 2.2 at G-block and E-block, respectively, and the minimum number of effective factors controlling parthenocarpy was estimated as 5 (G-block) to 13 (E-block). Estimates of heritability were significantly lower when based on individual plants within an F_3 family than on F_3 family mean performances. While narrow-sense and broad-sense heritability of individual plants within F_3 family was always $<$ 0.1, narrow-sense heritability for F_3 family mean performance ranged between 0.33 (E-block) and 0.62 (G-block), and broad-sense heritability ranged between 0.53 (E-block) and 0.67 (G-block). Thus, in this population, advanced generation selection for parthenocarpy based on F_3 family mean performance will be more effective than selection of individual plants within F_3 family.

Introduction

Cucumber (*Cucumis sativus var. sativus* L.; $2n = 2x = 14$) is one of the most economically valuable vegetable species of the Cucurbitaceae (Lower & Edwards, 1986). The average yield of processing cucumber in the U.S. increased from 4.1 metric tons per hectare in 1920 to 14.8 metic tons per hectare in 1984 [U.S. Department of Agriculture (USDA) 1940, 1984]. These yield increases were attained through the release of gynoecious and monoecious hybrids (Wehner, 1989), and are largely attributed to the incorporation of disease resistance genes, improved cultural practices and sex expression stability, and modified plant stature and fruiting habit (Peterson, 1978; Wehner, 1989; Wehner & Cramer, 1996).

Average yields in U.S. processing type cucumber production have plateaued at an average of 12.6 $\pm$ 0.2 metric tons per hectare in the last 19 years (Agricultural Statistics 1984 to 2002; http://www.nass.usda.gov:81/ipedb/). A phenomenon known as crown-fruit dominance or first-fruit inhibition (Tiedjens, 1928; McCollum, 1934) is thought to be the source of this yield limitation. In commercial cucumber, fruit with developing seeds from the first pollinated flower inhibits the development of subsequent fruits (Uzcategui & Baker, 1979). This yield inhibition phenomenon is particularly important in once-over mechanical harvest operations where yield maximization is dependent on the number of marketable fruits at a single harvest date.

Fruit set inhibition is less in seedless than seeded cucumber (Denna, 1973). Moreover, yield of

gynoecious parthenocarpic varieties is often higher than conventional commercial seeded varieties under optimum growing conditions (Denna, 1973; de Ponti, 1976; Sun, 2004). The higher yield potential of parthenocarpic cucumber is due to the fact that pollination is not a prerequisite for fruit set as it is in seeded cucumber. Thus, while poor pollination conditions often limits fruit set in seeded cucumber, parthenocarpic germplasm is less affected by such stresses (i.e., abiotic and biotic). Furthermore, parthenocarpic germplasm can develop fruits sequentially with little or no first-fruit inhibition. Under some growing conditions (e.g., glasshouse; no pollinators) non-parthenocarpic lines can, on occasion, develop parthenocarpic fruit. This phenomenon, called "spurious parthenocarpy", is inconsistent in its appearance, and is likely due to interplay between environment and a plant's physiology at anthesis or during fruit development.

Knowledge of the genetic characteristics of parthenocarpy would be useful in designing breeding strategies for improving yield in processing cucumber. The inheritance of parthenocarpy in U.S. processing type cucumber has been investigated using generation means analysis (Sun, 2004). The narrow-sense heritability estimates based on first-harvest yield data from two elite lines cross (2A × Gy8 2000) grown in a pollen-free, open-field environment was low (0.24). Thus, individual plant selection for this character in a parthenocarpic F_2 population would likely be relatively ineffective. Selection in an F_2-derived population obtained by self-pollination of F_2 individuals (e.g., F_3, F_4) would be, theoretically, more effective than on F_2 individuals because selection is based on family mean performance and variation among F_3 families increases due to selfing. Therefore, a study was designed to evaluate variance components, broad- and narrow-sense heritabilities, and the minimum number of genetic factors, in F_3 families derived from a line 2A (parthenocarpic) and Gy8 (non-parthenocarpic) mating. Such information is critical for continued improvement of this potentially important parthenocarpic processing cucumber population.

Materials and methods

Plant material

Two U.S. processing type cucumber inbred lines originating from the UW-Madison Cucumber Breeding Program (UW-CBP) were chosen for experimentation (Sun, 2004). The parthenocarpic line 2A is gynoecious (*gy*), normal leaf (*L*), and indeterminate (*De*), and has the ability to set multiple fruits without pollination under growing conditions typically found in North American climates. Likewise, the non-parthenocarpic U.S. processing type inbred line Gy8 is stable gynoecious, normal leaf, and indeterminate plant habit, but does not produce or bears only few fruits without pollination (Sun, 2004). These lines are morphologically similar, except for their parthenocarpic character.

Hybrid F_1 seed from a line 2A (P_1) × line Gy8 (P_2) mating was produced in a greenhouse at Cartago, Costa Rica in the spring of 1998. This F_1 was used to produce F_2 seeds in a greenhouse at Madison, Wisc. during the fall of 1998. Meristem cuttings of F_2 individuals were taken from plants grown in a greenhouse at Arlington, Wisc. in the spring of 1999, and self-pollination of these F_2 clones in a Madison greenhouse during the fall of 1999 resulted in 126 F_3 families.

Experimental design

Two parental lines, F_1, and F_3 families were planted at two open-field locations approximately 2 km apart at University of Wisconsin Research Station, Hancock, Wisc. in the summer of 2000. This growing region is where the majority of processing cucumbers are cultivated in Wisc. (rank fifth in U.S. production). The first planting occurred on June 20th (designed G-block), and the second planting was made on June 30th (designed E-block) in Planefield loamy sand (Typic Udipsamment; sandy, mixed mesic). The experimental fields were at least 2.5 km from other cucumber fields to ensure a pollen-free environment during fruit set. Each experiment was arranged in a randomized complete block (RCB) design with replicates, where there were three blocks in each location (G-block and E-block). In each block, the experimental units were three plots of each parental line and their F_1 hybrid progeny, and 126 F_3 family plots to total 135 plots per block (P_1: P_2: F_1: F_3 = 3:3:3:126). Plots consisted of eight plants spaced 15 cm apart in rows, where rows were on 1.5 m centers. This plant density (~38,000 plants per hectare) is typical of U.S. commercial open-field parthenocarpic cucumber production for multiple hand-harvest operations. Standard cultural practices for Wisconsin growing conditions were followed for the control of diseases and weeds. Nitrogen was applied through over-head irrigation system as needed at the rate of 32 kg per hectare once a week during vining and fruit development period. Plants were harvested once (47 and 45 days after

planting in E- and G-block, respectively) and measurements were taken on a single plant basis as the number of parthenocarpic fruits per plant. All fruits larger than 2.8 cm in diameter [U.S. Department of Agriculture (USDA) grade size number 2] were harvested when about 15% of the fruits reached 5.0 cm in diameter (USDA grade size number 4).

Data analysis

The parthenocarpic yield data from 126 F_3 families evaluated at two locations were analyzed both jointly and independently using the '*proc mixed*' procedure of SAS (SAS, 1999), where all effects were treated as random. Restricted maximum likelihood (REML) was used for estimating variance components. A best linear model was first performed using combined yield data from E- and G-block employing the model: $Y = \mu+L+B(L)+F+L\times F+B(L)\times F+e$; where Y is the yield as number of parthenocarpic fruits per plant, μ is the common effect, L is the location effect, $B(L)$ is the block effect, F is the F_3 family effect, $L \times$ F is the location $\times F_3$ family interaction, $B(L) \times F$ is the block $\times F_3$ family interaction, and e is the plant-to-plant variation within F_3 families. When the interaction between location and F_3 families was significant, Spearman (rank) correlation coefficients (Lehmann & D'Abrera, 1975) of predicted values of F_3 families in different locations were used to determine whether interactions were due to variation in the magnitude or the direction of the response from F_3 families. The parthenocarpic yield data from each location were then analyzed independently using the linear model: $Y = \mu + B + F + B \times F + p$ (Table 1). The variation within F_3 families was further partitioned into that due to heterogeneous effects within each F_3 family and environmental effects.

Table 1. Sources of variation for the analysis of variance of once-over harvest cucumber yield (parthenocarpic fruits/plant) in F_3 cucumber families evaluated at Hancock, Wisc. in 2000.

	Statistical parameter[a]		
Source	df	MS	EMS
Block (B)	$b-1$	M_{14}	$\sigma_p^2 + p\sigma_{B\times F}^2 + pf\sigma_B^2$
Family (F)	$f-1$	M_{13}	$\sigma_p^2 + p\sigma_{B\times F}^2 + bp\sigma_F^2$
Block × Family ($B \times F$)	$(b-1)(f-1)$	M_{12}	$\sigma_p^2 + p\sigma_{B\times F}^2$
Plants within family (p)	$bf(p-1)$	M_{11}	σ_p^2
Total	$bfp-1$		

[a]df = degrees of freedom, MS = mean squares, and EMS = expected mean squares.

The parthenocarpic yield data from two parental lines and their F_1 hybrid were also analyzed jointly and separately using the '*proc mixed*' procedure of SAS, where generation was treated as a fixed effect and the remaining effects were treated as random. The analysis of combined parthenocarpic yield data from two locations were performed using the linear model: $Y = \mu+L+B(L)+E(G)+G+L\times G+L\times E(G)+B(L)\times G+B(L)\times E(G)+e'$; where Y is the yield as number of parthenocarpic fruit per plant, μ is common effect, L is the location effect, $B(L)$ is the block effect, $E(G)$ is the entry effect within each generation, G is the generation effect (i. e., P_1, P_2, and F_1), $L\times G$ is the location × generation interaction, $L \times E(G)$ is the location × entry interactions, $B(L) \times G$ is the block × generation interaction, $B(L) \times E(G)$ is the block × entry interaction, and e' is the plant to plant variation within homogeneous entries. The parthenocarpic yield from each location was then analyzed separately using the linear model: $Y = \mu+B+E(G)+G+B\times G+B\times E(G)+p'$ (Table 2).

Due to the heterogeneous nature of the F_3 families and the different number of entries for each generation, least square means (lsmeans) comparisons among generations (i.e., P_1, P_2, F_1, and F_3) were performed using the *proc mixed covtest* procedure of SAS, where generation was treated as a fixed effect, and the block and block × generation interactions were treated as random effects (SAS, 1999).

Estimates of genetic variance

The expected genetic components of variances for F_3 were estimated using the formulae of Mather (1949), Mather and Jinks (1971), and Hallauer and Miranda (1988). Data from F_3 families allowed for the estimation of two sources of genetic variation: (1) variation among F_3 family means ($\sigma^2_{\bar{F}3}$), and; (2) mean variation of F_3 families ($\bar{\sigma}^2_{F3}$). Variance among F_3 family means had the expectation of $\sigma^2_{\bar{F}3} = \sigma^2_A + 1/4\,\sigma^2_D$, where σ^2_A and σ^2_D are additive genetic variance and dominance genetic variance, respectively. Mean variance of F_3 families was calculated as the average variation among plants within each F_3 family having an expectation of $\bar{\sigma}^2_{F3} = 1/2\,\sigma^2_A + \frac{1}{2}\,\sigma^2_D$.

At each location, $\sigma^2_{\bar{F}3}$ (i.e., $\sigma^2_A + \frac{1}{4}\,\sigma^2_D$) were obtained directly from the '*proc mixed covtest*' procedure in SAS for the estimates of variance components of F_3 families. The estimates of $\bar{\sigma}^2_{F3}$ (i.e., $\frac{1}{2}\,\sigma^2_A + \frac{1}{2}$

Table 2. Sources of variation for the analysis of variance of once-over harvest cucumber yield (parthenocarpic fruits/plant) of two cucumber parental lines and their F_1 progeny evaluated at Hancock, Wisc. in 2000

	Statistical parameter[a]		
Source	df	MS	EMS
Block (B)	$b-1$	M_{26}	$\sigma^2_{p'} + p\sigma^2_{B\times E(G)} + gpe\sigma^2_B$
Generation (G)	$g-1$	M_{25}	$\sigma^2_{p'} + p\sigma^2_{B\times E(G)} + pb\sigma^2_{E(G)} + pe\sigma^2_{B\times G} + bpeg\Sigma(G)^2/(g-1)$
Block × Generation ($B \times G$)	$(b-1)(g-1)$	M_{24}	$\sigma^2_{p'} + p\sigma^2_{B\times E(G)} + pe\sigma^2_{B\times G}$
Entry (Generation) (E)	$(e-1)g$	M_{23}	$\sigma^2_{p'} + p\sigma^2_{B\times E(G)} + pb\sigma^2_{E(G)}$
Block × Entry (Generation) (B × E(G))	$(e-1)(b-1)g$	M_{22}	$\sigma^2_{p'} + p\sigma^2_{B\times E(G)}$
Plants within entries (p')	$(p-1)bge$	M_{21}	$\sigma^2_{p'}$
Total	$bgep-1$		

[a]df = degree of freedom, MS = mean squares, and EMS = expected mean squares.

σ^2_D) were equal to the variance among plants within F_3 families (σ^2_p) minus the variance among plants within homogeneous entries ($\sigma^2_{p'}$; P_1, P_2, and F_1) (Tables 1 and 2). These two equations permitted the estimation of additive (σ^2_A) and dominance (σ^2_D) genetic variances. After solving these two equations, estimates of σ^2_A and σ^2_D were obtained as $\sigma^2_A = [4 \times \sigma^2_{\bar{F}3} - 2 \times (\sigma^2_p - \sigma^2_{p'})]/3$ and $\sigma^2_D = [8 \times (\sigma^2_p - \sigma^2_{p'}) - 4 \times \sigma^2_{\bar{F}3}]/3$; where $\sigma^2_{\bar{F}3}$, σ^2_p, and $\sigma^2_{p'}$ are estimates of variance components of F_3 families, plant to plant variation within F_3 families, and plant to plant variation within homogeneous entries, respectively. The variances (Var) of these genetic parameters (σ^2_A and σ^2_D) at each location were estimated using the following formulae:

$$\begin{aligned}\mathrm{Var}(\sigma^2_A) &= \mathrm{Var}\{[4 \times \sigma^2_{\bar{F}3} - 2 \times (\sigma^2_p - \sigma^2_{p'})]/3\} \\ &= [16 \times \mathrm{Var}(\sigma^2_{\bar{F}3}) + 4 \\ &\quad \times \mathrm{Var}(\sigma^2_p) + 4 \times (\sigma^2_p)]/9,\end{aligned}$$

and

$$\begin{aligned}\mathrm{Var}(\sigma^2_D) &= \mathrm{Var}\{[8 \times (\sigma^2_p - \sigma^2_{p'}) - 4 \times \sigma^2_{\bar{F}3}]/3\} \\ &= [64 \times \mathrm{Var}(\sigma^2_p) + 64 \times \mathrm{Var}(\sigma^2_{p'}) \\ &\quad + 16 \times \mathrm{Var}(\sigma^2_{\bar{F}3})]/9.\end{aligned}$$

Estimate broad- and narrow-sense heritability

Both narrow- and broad-sense heritabilities were estimated based on individual plants within F_3 families and F_3 family mean performances. While σ^2_A and σ^2_D for h^2_N among families were estimated using the formulae above (Mather and Jink, 1971), within F_3 family variances for $h^2_{N'}$ based on individual plant data were adjusted according to Hallauer and Mairanda (1988) employing a coefficient (1/2) to account for the degree of inbreeding.

The narrow-sense heritabilities of individual plants within F_3 families (h^2_{NP}) were estimated in two ways. Firstly, h^2_{NP} was estimated as $1/2\sigma^2_A/\sigma^2_{PP}$, where σ^2_A and σ^2_{PP} are the additive genetic variance and the phenotypic variance of individual plants within F_3 families, respectively. The phenotypic variance at each location was estimated as $\sigma^2_{PP} = \sigma^2_p = 1/2\sigma^2_A + 1/2\sigma^2_D + \sigma^2_{p'}$ (Table 1); where σ^2_p, σ^2_A, σ^2_D, and $\sigma^2_{p'}$ refer to variation among F_3 plants within F_3 families, additive genetic variance, dominance genetic variance, and variance within plots having homogeneous entries, respectively. The standard error (S.E.) of the narrow-sense heritabilities of individual plants within F_3 families were calculated as $\mathrm{S.E.}(h^2_{NP}) = [\mathrm{Var}(\sigma^2_A)]^{1/2}/(2 \times \sigma^2_{PP})$ (Hallauer and Miranda, 1988). Secondly, h^2_{NP} was estimated based on F_3 family means (h^2_{NF}) as $h^2_{NF} = 1.0208\sigma^2_A/\sigma^2_{PF}$; where σ^2_A and σ^2_{PF} are the additive genetic variance and the phenotypic variance based on F_3 family means, respectively. The coefficient 1.0208 was used to adjust for family size ($n = 24$; Keasey and Pooni, 1996). The phenotypic variance at each location was estimated as $\sigma^2_{PF} = (\sigma^2_p + p\sigma^2_{B\times F} + bp\sigma^2_{\bar{F}3})/bp$; where b, p, σ^2_p, $\sigma^2_{B\times F}$, $\sigma^2_{\bar{F}3}$ refer to the number of block, number of plants per plot, variation among F_3 plants within families, variation due to block × F_3 family interaction, and variation among F_3 family means, respectively. The multiplier associated with σ^2_A was obtained from summation of the additive genetic variance estimated among F_3 family means and among F_3 individuals (i.e., $1+ 1/bp$). The standard error (S.E.) of the narrow-sense heritabilities based on F_3 family means was calculated as $\mathrm{S.E.}(h^2_{NF}) = 1.0208 \times [\mathrm{Var}(\sigma^2_A)]^{1/2}/\sigma^2_{PF}$.

Broad-sense heritabilities of individual plants within F_3 family (h^2_{BP}) were calculated as $h^2_{BP} = (1/2\sigma^2_A + 1/2\sigma^2_D)/\sigma^2_{PP}$; where σ^2_A, σ^2_D, and σ^2_{PP} are the additive genetic variance, dominance genetic variance, and phenotypic variance of individual plants within F_3 families, respectively. The standard error of broad-sense heritabilities of individual plants within F_3 families were calculated as S.E. $(h^2_{BP}) = [\mathrm{Var}(\sigma^2_A) + \mathrm{Var}(\sigma^2_D)]^{1/2}/(2 \times \sigma^2_{PP})$ (Hallauer & Miranda, 1988). The broad-sense heritabilities based on F_3 family means (h^2_{BF}) were calculated as $h^2_{BF} = (1.0208\sigma^2_A + 0.2708\sigma^2_D)/\sigma^2_{PF}$, where σ^2_A, σ^2_D, and σ^2_{PF} are the additive genetic variance, dominance genetic variance, and phenotypic variance based on F_3 family means, respectively. The standard errors of broad-sense heritabilities based on F_3 family means were calculated as S.E.$(h^2_{BF}) = [1.0208^2 \times \mathrm{Var}(\sigma^2_A) + 0.2708^2 \times \mathrm{Var}(\sigma^2_D)]^{1/2}/\sigma^2_{PF}$.

Estimate of minimum number of genetic factors

The minimum number of effective factors (n) influencing parthenocarpy were estimated according to Castle (1921) and Wright (1968) using the correction factor suggested by Cockerham (1986) as $n = [(\bar{P}_1 - \bar{P}_2)^2 - (\sigma^2_{\bar{P}1} + \sigma^2_{\bar{P}2})]/(8 \times \sigma^2_A)$; where $\bar{P}_1$ and $\bar{P}_2$ are the estimates of the mean yield of parents P_1 and P_2, $\sigma^2_{\bar{P}1}$ and $\sigma^2_{\bar{P}2}$, are the estimates of variance of two parental lines means, and σ^2_A is the additive genetic variance.

Results and discussion

Generation means

The parental lines were consistently different for parthenocarpic fruit yield regardless of growing locations ($p \leq 0.01$) (Table 3). Mean fruit yields tended to be higher in E-block than in G-block, except for P_1 (2A; parthenocarpic) in which yields were higher in G-block. Significant differences in mean yield were not detected between the F_1 and F_3 generation in either locations ($p \leq 0.05$). However, both F_1 and F_3 progeny means were significantly different from the two parental lines at both locations ($p \leq 0.01$). The F_1 generation mean in E-block was higher than the mid-parent value, indicating a positive contribution of dominance effects for parthenocarpy. However, the F_1 progeny mean in G-block was lower than the mid-parent value (Table 3). Although open-field experiments were conducted for only one year, results confirmed an earlier finding from a generation means analysis of cross progeny derived from P_1 and P_2 (Sun et al. 2006a) that demonstrated that genotype performances vary across growing environments. Under dissimilar experimental conditions differences in magnitude (not in rank) between treatments would be expected given the environmental influence on parthenocarpic fruit development.

Analysis of variance components

When parthenocarpic yield data from two locations were combined, the estimate of variance components for the location effect was not significantly different from zero ($\propto = 0.05$; Table 4). However, the F_3 families reacted differently across locations as the estimate of location $\times$ F_3 family interaction was significantly different from zero ($\propto = 0.05$). The Spearman (rank) correlation coefficient value (r_s) of 0.24 for F_3 families between two locations was significant ($\propto = 0.01$), suggesting that the interactions detected between F_3 family and location were most likely due to changes in magnitude in these locations. However, the covariances between rankings of F_3 families in these two locations were weak ($r^2_s = 0.06$) which indicated that

Table 3. Least square means (lsmeans), variance (Var), and their standard errors (S.E.) for once-over harvest cucumber yield (parthenocarpic fruits/plant) of parental lines (2A and Gy8) and their F_1 and F_3 progeny grown in E-block and G-block at Hancock, Wisc. in 2000

	E-block		G-block	
Generation	Lsmeans ± S.E.	Var ± S.E.	Lsmeans ± S.E.	Var ± S.E.
P_1	3.11 ± 0.19^{a1}	1.65 ± 0.35	3.76 ± 0.29^{a}	3.82 ± 0.81
P_2	0.91 ± 0.10^{c}	0.51 ± 0.11	0.54 ± 0.13^{c}	0.59 ± 0.13
F_1	2.17 ± 0.16^{b}	1.25 ± 0.26	1.50 ± 0.16^{b}	1.07 ± 0.22
F_3	1.99 ± 0.02^{b}	1.14 ± 0.03	1.90 ± 0.06^{b}	2.27 ± 0.06

[1]Letters indicate lsmeans differences within columns at $\propto = 0.01$ level.

Table 4. Estimates of variance components and their standard errors based on once-over harvest cucumber yield (parthenocarpic fruits/plant) in 2A × Gy8-derived F_3 families grown in E-block and G-block at Hancock, Wisc. in 2000

Source	E-block	G-block	E- and G-block
Location (σ^2_L)	Na[a]	Na	0.00 ± 0.01
Block (location) ($\sigma^2_{B(L)}$)	0	0.01 ± 0.01	0.00 ± 0.00
Family (σ^2_F)	$0.07 \pm 0.02^{**,b}$	$0.27 \pm 0.05^{**}$	$0.06 \pm 0.03^{**}$
Location × Family ($\sigma^2_{L\times F}$)	Na	Na	$0.11 \pm 0.03^{**}$
Family × Block (location) ($\sigma^2_{F\times B\ (L)}$)	$0.07 \pm 0.02^{**}$	$0.21 \pm 0.04^{**}$	$0.14 \pm 0.02^{**}$
Plants within family (σ^2_p)	$1.00 \pm 0.03^{**}$	$1.80 \pm 0.05^{**}$	$1.40 \pm 0.03^{**}$

[a]Na = Calculations are not possible due to model partitioning.
[b]**Indicates that the value is significant at $\propto = 0.01$ level.

Table 5. Estimates of variance components and their standard errors based on once-over harvest cucumber yield (parthenocarpic fruits/plant) of two cucumber parental lines (2A and Gy8) and their F_1 progeny grown in E-block and G-block at Hancock, Wisc. in 2000

Source	E-block	G-block	E- and G-block
Location (σ^2_L)	Na[a]	Na	0
Block (Location) ($\sigma^2_{B(L)}$)	0.09 ± 0.14	0.01 ± 0.10	0.04 ± 0.07
Generation [$\Sigma(G)^2$]	Na	Na	Na
Entry (Generation) ($\sigma^2_{E(G)}$)	0	0	0
Location × Generation ($\sigma^2_{L\times G}$)	Na	Na	0.11 ± 0.15
Location × Entry (Generation) ($\sigma^2_{L\times E(G)}$)	Na	Na	0
Block (Location) × Generation ($\sigma^2_{G\times B(L)}$)	0	0	0
Block (Location) × Entry (Generation) ($\sigma^2_{B(L)\times E(G)}$)	0.17 ± 0.11	0.25 ± 0.18	$0.21 \pm 0.11^{*}$
Plant within entry ($\sigma^2_{p'}$)	$0.93 \pm 0.12^{**}$	$1.64 \pm 0.21^{**}$	$1.28 \pm 0.12^{**}$

[a]Na = Calculations are not possible due to the model partitioning.
[b]*,**Indicates that the value is significant at $\propto = 0.05$ and 0.01 level, respectively.

the direction of response of F_3 families was different across locations. Therefore, parthenocarpic yield data were subsequently analyzed separately by location. In either location, the estimates of variance component for block effects were not significantly different from zero ($\propto = 0.05$). However, the estimates of variance components for F_3 families were, as expected, significantly different from zero ($\propto = 0.01$; Table 4).

The application of the best linear model to parental line and F_1 progeny performance did not result in the detection of significant block, block × generation, entry within generation, and block × entry within generation interaction effects in both locations (Table 5). Significant generation (P_1, P_2, and F_1) effects ($p = 0.01$ in E-block; $p = 0.01$ in G-block) were, however, detected across locations. The detection of generation differences in this population support results of least square mean estimation reported herein (Table 3).

Estimates of variance components and heritability

The genetic variances for dominance detected by variance component analyses were relatively low in both locations (Table 6). These relatively low dominance variance estimates may be due to the diminishing importance of dominance variance usually obtained after selfing, or to the lack in efficiency of the experimental design used for detecting dominance variance (Kearsey & Pooni, 1996). In order to estimate the additive genetic variance and dominance genetic variance with equal precision, a North Carolina Design III (NCIII) (Comstock & Robinson, 1952) or Triple Test Cross (TTC) design (Kearsey & Jinks, 1968) could be employed in future evaluations of parthenocarpy in this population.

The relative values of additive and dominance effects are important for identifying inbred lines or F_1 hybrids having potential as commercial varieties (Kearsey

Table 6. Estimates of variance components, narrow- and broad-sense heritabilities, and the minimum number of effective factors (n) for once-over harvest cucumber yield (parthenocarpic fruits/plant) of progeny derived from a 2A × Gy8 mating grown in two locations (E-block and G-block) at Hancock, Wisc. in 2000

Parameter[a]	E-block	G-block
$\sigma^2_{\bar{F}3}$	0.07 ± 0.02	0.27 ± 0.05
σ^2_{F3}	0.07 ± 0.12	0.16 ± 0.22
σ^2_A	0.04 ± 0.09	0.25 ± 0.16
σ^2_D	0.10 ± 0.33	0.08 ± 0.59
n	13.2	5.0
Heritability based on individual plants within F_3 family		
σ^2_{PP}	1.00 ± 0.03	1.80 ± 0.05
h^2_{NP}	0.02 ± 0.04	0.07 ± 0.05
h^2_{BP}	0.07 ± 0.21	0.09 ± 0.21
Heritability based on F_3 family means		
σ^2_{PF}	0.13 ± 0.02	0.41 ± 0.06
h^2_{NF}	0.33 ± 0.66	0.62 ± 0.40
h^2_{BF}	0.53 ± 0.94	0.67 ± 0.56

[a] $\sigma^2_{\bar{F}3}, \sigma^2_{F3}, \bar{\sigma}^2_A, \sigma^2_D, \sigma^2_{PP}, h^2_{NP}, h^2_{BP}, \sigma^2_{PF}, h^2_{NF}$, and h^2_{BF} are variation among F_3 family means, mean variation of F_3 families, additive genetic variance, dominance genetic variance, phenotypic variance of individual plants within F_3 family, narrow-sense heritability based on individual plants within F_3 family, broad-sense heritability based on individual plants within F_3 family, phenotypic variance of F_3 family means, narrow-sense heritability based on F_3 family means, and broad-sense heritability based on F_3 family means, respectively.

& Pooni, 1996). Dominance variance was the main component of the total genetic variance in E-block (Table 6), where the dominance to additive genetic variance ratio was 2.2. These results indicate that dominance was important for parthenocarpic fruit development in this environment. In contrast, the contribution of the additive genetic variance to the total genetic variance in G-block was relatively large (Table 6). The average dominance to additive genetic variance ratio detected was 0.3, indicating additive gene effects for parthenocarpic fruit development were important in this growing environment. A possible explanation for this growing location difference is the instability of the parthenocarpy itself. Soil type differences (i.e., homogeneity) were neglible, but average temperatures were higher (∼3 °C) in G-than in E-block during fruit development. A testable hypothesis is that genes controlling parthenocarpic fruit development are affected differentially by growing environment. This might be examined by evaluating pure parthenocarpic lines across a wide range of growing environments.

The environmental variance among individual plants within the F_3 families examined was considerably larger than either the additive or dominance variance in both locations (Tables 4 and 6). This is due to the fact that variances within homogenous entries were relatively high in both locations [0.93 (E-block) and 1.64 (G-block)] (Table 5). These variances accounted for 93% (E-block) and 91% (G-block) of the total phenotypic variance of individual plants within the F_3 families examined. Heritability estimates (narrow- and broad-sense) based on individual plants within F_3 families would be predictably low because of the large environmental effect. Heritability estimates based on F_3 families mean performance would be greater than that of F_3 individuals since the heterogeneity within these F_3 families would predictably decrease after selfing. Thus, heritability comparisons in this population were made based on both individual plants within F_3 families and F_3 family mean performances.

Given the variance components detected (Table 4), estimates of broad-sense heritability (h^2_{BP}) based on individual plants within F_3 families were predictably low [0.07 (E-block) and 0.09 (G-block); Table 6]. These values were lower than heritability estimates (0.12) obtained through a generation means analysis of six basic generations (P_1, P_2, F_1, BC_1P_1, BC_1P_2, and F2) derived from a 2A × Gy8 mating at first-harvest evaluated in the summer of 2000 at Hancock, Wisc. (Sun, 2004). Narrow-sense heritabilities (h^2_{NP}) of individual plants within F_3 families ranged from 0.02 to 0.07 in E-block and G-block, respectively (Table 6). These h^2_{NP} values are lower than narrow-sense heritability estimates based on a first-harvest generation mean analysis (0.24) of cross progeny derived from 2A and Gy8 evaluated in 2000 (Sun, 2004). Such low heritabilities (h^2_{NP} and h^2_{BP}) were likely due to the combination of large variances among plants within homogenous entries and the selfing procedure used, which, taken collectively, decreased the genetic variation within F_3 families and increased the genetic variation among F_3 families. Such low broad- and narrow-sense heritability estimates based on individual plants within F_3 family indicates that a response to direct selection for parthenocarpic yield based on individual plants within F_3 families will likely not be effective in this population.

Broad-sense heritabilities (h^2_{BF}) based on F_3 family mean performances ranged from 0.53 to 0.67 in E-block and G-block, respectively (Table 6). Likewise, narrow-sense heritability (h^2_{NF}) based on F_3 family means ranged from 0.33 to 0.62 in E-block

and G-block, respectively (Table 6). Estimates of both broad- and narrow-sense heritabilities based on F_3 family means were significantly larger than those estimated from individual plants within F_3 families where experimental variances were the largest portions of the total phenotypic variance. In addition, the additive genetic component of variances estimated based on F_3 family means increased significantly compared to those estimated from individual plants within F_3 families (i.e., $1.0208\sigma_A^2$ vs. $0.5\sigma_A^2$). Thus, selection based on F_3 family means clearly would be more effective than that based on individual plants within F_3 families since experimental variances associated with F_3 family means were dramatically lower than that of individual F_3 plants.

Estimate of minimum number of effective factors

The estimated minimum number of factors controlling parthenocarpy ranged between 5 (G-block) and 13 (E-block) (Table 6), and reflects the quantitative nature of parthenocarpy in cucumber as reported in previous studies (de Ponti & Garretsen, 1976; El-Shawaf & Baker, 1981a,b; Sun, 2004). These estimates are considerably higher than estimates based on generation means analysis for parthenocarpy in cross progeny derived from a 2A × Gy8 mating at first-harvest at Hancock, Wisc. in 2000 (approximately two genes; Sun, 2004). Estimates of minimum number of effective factors derived from the simple model used for calculation herein are confounded by known epistatic interactions (Sun, 2004). Estimates of the minimum number of effective factors using Castle (1921) and Wright (1968) equations with the correction factor suggested by Cockerham (1986) are also heavily dependent on the mean difference between two parental lines. Thus, environmental factors (e.g., abiotic and biotic stresses) that affect mean differences between parental lines will alter estimates of the minimum number of effective factors. Our empirical data is supported by genetic mapping experiments that identified four genes for parthenocarpy in the 2A × Gy8 population that mapped to the same genomic regions (Sun, 2004; Sun et al., 2005b) as QTLs detected for seeded fruit yield at first-harvest (Fazio et al., 2003; G421 × H-19).

The analyses provided herein indicate that selection based on F_3 family means is preferable to selection based on individual plants within F_3 families. Even though parthenocarpic fruit development is highly affected by environments, the development of gynoecious U.S. processing type parthenocarpic cucumber for once-over mechanical operations using the population examined is possible. This could be accomplished through continued selfing combined with family or pedigree selection. In either case, use of extensive replication with large number of plants for each plot (perhaps 30–40) would assist in identifying unique genotypes by minimizing the large environmental effects associated with the expression of this trait.

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