Abstract. Variance component estimates were obtained in a North Carolina Design I experiment for several traits in pickling cucumber (Cucumis sativus L.) for a simulated once-over mechanical harvest. The reference population was random-mating and derived from 18 inbred lines obtained from several U.S. breeding programs. Environments sampled were the spring and fall of a single year. Data indicated most of the genetic variance was additive for all traits except fruit color. Evidence for relatively large genotype by environment interaction variances were found for number of fruit, length to diameter (L/D) ratio, and fruit firmness. Heritabilities, based on full-sib families grown in 2 replications in each of 2 seasons, for dollar value and number of fruit, were .19 and .17 respectively. Genotypic and phenotypic correlations for number of fruit and dollar value were high indicating selection for increased number of fruit would be effective in increasing crop value.

Materials and Methods

The research was conducted at the Horticultural Crops Research Station in Clinton, N.C. Environments sampled were the spring and fall of a single year, and hence referred to as seasons. The reference population used in this study was random-mating and constructed from 18 monocious lines obtained from breeding programs throughout the U.S. These inbred lines were used to make F l's and double crosses. The double crosses were random-mated in the greenhouse for one generation so that the reference population would be in Hardy-Weinberg equilibrium. No monocious lines were included in the population. Gynoe- cious plants would set fruit earlier than monocious plants and since plots were harvested when the first size #4 fruit appeared segregation for the gynoeccious character could disrupt the har­ vest scheme. If yield is controlled by many genes, a single gene should not greatly influence the variance component estimates. The mating design used to estimate the variance components in this reference population was a N.C. Design I. Construction and analysis of this design was given by Comstock and Robinson (3). In this study 56 plants, chosen at random, were designated as “males” and each was mated to 4 plants, also chosen at random, designated as “females.” The families were divided into 14 sets, with 4 half-sib families grown in 2 replications per set, in a randomized complete block design. In the spring, sets 1–7 were planted 10 days before sets 8–14, and in the fall, 7 days before sets 8–14. This was done to lengthen the harvest period and facilitate a once-over harvest. The planting dates were May 14 and 24, 1976, for the spring crop and July 29 and August 5 for the fall crop. Plots were single 2.4 m (8 ft) rows spaced 1.5 m (5 ft) apart. Previous work (13) had indicated this to be an efficient plot size for estimating the mean difference of the traits of interest. Excess seed was planted and stands were thinned to 25 plants per plot. All plots were hand harvested when the first fruit reached size #4 (> 5.1 cm in diam), which previously was suggested as the optimum time for a once-over harvest (9). Since the time of appearance of the first size #4 fruit was not uniform, all plots for a given set were not harvested on the same day. Fruit counts and weights were determined for 4 size grades so that dollar values could be computed.

The fruit quality traits examined were exterior fruit color, L/D ratio, fruit firmness, flesh firmness, and carpel wall thickness. Fruit color was determined by subjectively rating the fruit on a scale of 1 (uniformly dark green) to 5 (very light green). A sample of 5, size #3 fruit, when available, was used for all other quality determinations. Firmness readings were made with a USDA Fruit Pressure Tester (Mangen) equipped with a 0.95 cm tip (1). Fruit firmness readings were taken on the darkest shoulder of the upper third of size #3 fruit. Flesh firm­ ness readings were determined from the bottom third of the same fruit after rotating the fruit approximately 120° and after removing the skin. Fruit were cut transversely and the carpel wall thickness was determined as the shortest distance between the skin and the placental tissue. Days to harvest was computed as the number of days from seeding to harvest.
Genetic expectations of the design components were derived using the following assumptions: 1) regular diploid behavior, 2) no maternal effects, 3) either no linkage or linkage equilibrium, 4) no selection of individuals from which the estimates were obtained, and 5) no epistasis. Heritabilities among full-sib families grown in 2 replications in each of 2 environments were computed as follows:

$$h_i^2 = \frac{1}{2} \frac{a_i^2}{s_i^2}$$

where $a_i^2$ was the estimate of additive genetic variance and $s_i^2$ the phenotypic variance for full-sib family means. For traits with evidence of dominance, $a_i^2$ was estimated by $4a_i^2$, where $a_i^2$ has been shown to estimate the covariance among half-sibs and under the assumptions given contains $\frac{1}{2} a_i^2$. For traits for which the dominance variance ($s^2_d$) was negative, or positive and less than its standard error, the sums of squares for males and females within males were pooled. $a_i^2$ was then estimated as $2a_i^2$, where $a_i^2$ is the variance among full-sib families and with the assumptions of no dominance or epistasis contains $\frac{1}{2} a_i^2$. With traits for which the dominance by environment interaction component ($s^2_{dm,E}$) was negative, or positive and less than its $se$, the additive by environment interaction variance component ($s^2_{am,E}$) was estimated by pooling the sums of squares for males by environments and females within males by environments, so that $a_i^2$ was estimated by $2a_i^2 + s^2_{am,E}$. $s^2_{am,E}$ is the full-sib family by environment interaction component and with the assumptions of no dominance or epistasis contains $\frac{1}{2} a_i^2$. $s^2_{am,E}$ was estimated as $a_i^2/4 + s^2_{am,E}^2/2 + s^2_E$, where $s^2_E$ is the pooled error variance, $s^2_{am,E}$ and $s^2_E$ are as defined above.

Cross products were computed for all pairs of characters. Mode and Robinson (10) have shown that the mean product $s_{ij}$ was the phenotypic variance for full-sib family means. Hence, $s^2_{ij}$ was the estimate of additive genetic variance and $s^2_{iJ}$ was estimated from the full-sib family means grown in 2 replications in each of 2 environments estimated as:

$$r_{Aij} = s_{Aij} / (s^2_{AI} \cdot s^2_{AJ})^{1/2}$$

where $s_{Aij}$ was the estimated additive covariance component, and $s^2_{AI}$ and $s^2_{AJ}$ are the estimated additive variance components for the characters i and j respectively. The phenotypic correlation ($r_{Pij}$) for unrelated full-sib family means grown in 2 replications in each of 2 environments was estimated as:

$$r_{Pij} = s_{Pij} / (s^2_{Pij} \cdot s^2_{Pij})^{1/2}$$

where $s_{Pij}$ is the phenotypic estimate of covariance and $s^2_{Pij}$ and $s^2_{Pij}$ were phenotypic estimates of components of variance for traits i and j respectively.

### Results

Analysis of value/plot and number of fruit/plot resulted in large male by environment interaction variances and negative male variance components. This appeared to be due to the plot to plot variation in number of plants bearing fruit at harvest. Commercially, some of that non-uniformity in the fruit setting pattern is overcome by use of gynoecious hybrids. Therefore, to remove some of this variation in fruit set a covariance analysis was conducted using number of plants with fruit as the covariate for the traits fruit number, value, and fruit wt. If number of plants with fruit was environmentally determined then the effect of the covariance analysis would be to remove random variation and increase the precision of the estimates. However, if number of plants with fruit were genetically determined, then the effect of the covariance analysis would be to decrease the genetic variance of the adjusted traits. Each set in each environment was analyzed individually and then the analyses were pooled over sets and environments. Design component estimates for the adjusted yield traits and the quality traits are presented in Table 1. $s^2_{fm}$ was smaller than $s^2_{m}$ for the traits value, fruit number, fruit weight, L/D ratio, and days to harvest. $s^2_{m}$ was negative or less than its $se$ for all traits except fruit color (Table 2). The lack of evidence for dominance may have been due to lack of dominance or to the large $se$ associated with this component. However, lack of observed inbreeding depression in pickling cucumbers is evidence for lack of dominance; therefore for traits in which there was no evidence of dominance, $a_i^2$ was estimated from the full-sib family component ($s^2_{AI}$). The dominance by interaction variance components were also negative or less than their $se$ for all traits except L/D. $s^2_{AI}$ was estimated using the full-sib family by interaction component ($s^2_{Am,E}$) for all traits since $s^2_{Am,E}$ was negative for the trait L/D ratio.

The additive variance component was larger than its $se$ for all traits except fruit wt (Table 2). Since fruit wt changed very rapidly the errors associated with that trait were expected to be large. There was no evidence of dominance variance except for fruit color. This trait appeared to have been controlled by a few genes with evidence of dominance for genes conditioning lack of uniformity (stripping) of color (12). Fruit color was rated on a visual scale and uniformity was included in that rating. Dominance for stripping may have been responsible for the dominance variance for the fruit color trait.

### Table 1. Design component estimates from the combined analysis of a North Carolina Design I experiment with a random-mating population of pickling cucumbers (Yield traits adjusted for number of plants with fruit).

<table>
<thead>
<tr>
<th>Component</th>
<th>Value</th>
<th>Fruit no.</th>
<th>Fruit wt</th>
<th>L/D ratio</th>
<th>Fruit color</th>
<th>Days to harvest</th>
<th>Fruit firmness</th>
<th>Flesh firmness</th>
<th>Carpal wall thickness</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s^2_{fs}$</td>
<td>0.571</td>
<td>1.42</td>
<td>0.031</td>
<td>0.0178</td>
<td>0.105</td>
<td>1.81</td>
<td>0.547</td>
<td>0.320</td>
<td>0.190</td>
</tr>
<tr>
<td>$s^2_{m}$</td>
<td>0.480</td>
<td>1.37</td>
<td>0.185</td>
<td>0.0091</td>
<td>0.023</td>
<td>1.20</td>
<td>0.239</td>
<td>0.164</td>
<td>0.094</td>
</tr>
<tr>
<td>$s^2_{m}$</td>
<td>0.283</td>
<td>0.98</td>
<td>0.111</td>
<td>0.0034</td>
<td>0.011</td>
<td>0.35</td>
<td>0.134</td>
<td>0.067</td>
<td>0.045</td>
</tr>
<tr>
<td>$s^2_{m}$</td>
<td>0.117</td>
<td>0.32</td>
<td>0.117</td>
<td>0.0007</td>
<td>0.087</td>
<td>0.91</td>
<td>0.369</td>
<td>0.197</td>
<td>0.120</td>
</tr>
<tr>
<td>$s^2_{m}$</td>
<td>0.387</td>
<td>1.00</td>
<td>0.192</td>
<td>0.0007</td>
<td>0.018</td>
<td>0.21</td>
<td>0.134</td>
<td>0.075</td>
<td>0.037</td>
</tr>
<tr>
<td>$s^2_{E}$</td>
<td>-0.237</td>
<td>3.22</td>
<td>0.047</td>
<td>0.0052</td>
<td>0.010</td>
<td>-0.29</td>
<td>0.249</td>
<td>0.034</td>
<td>0.039</td>
</tr>
<tr>
<td>$s^2_{m}$</td>
<td>0.264</td>
<td>1.55</td>
<td>0.296</td>
<td>0.0027</td>
<td>0.016</td>
<td>0.22</td>
<td>0.166</td>
<td>0.088</td>
<td>0.055</td>
</tr>
<tr>
<td>$s^2_{E}$</td>
<td>-0.045</td>
<td>1.45</td>
<td>-0.164</td>
<td>-0.0011</td>
<td>0.009</td>
<td>-0.04</td>
<td>0.137</td>
<td>-0.031</td>
<td>0.063</td>
</tr>
<tr>
<td>$s^2_{E}$</td>
<td>0.279</td>
<td>1.05</td>
<td>0.126</td>
<td>0.0014</td>
<td>0.009</td>
<td>0.10</td>
<td>0.107</td>
<td>0.0041</td>
<td>0.033</td>
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<tr>
<td>$s^2_{E}$</td>
<td>0.290</td>
<td>2.06</td>
<td>0.179</td>
<td>0.0056</td>
<td>0.003</td>
<td>-0.27</td>
<td>0.148</td>
<td>0.060</td>
<td>-0.010</td>
</tr>
<tr>
<td>$s^2_{E}$</td>
<td>0.682</td>
<td>1.57</td>
<td>0.331</td>
<td>0.0030</td>
<td>0.016</td>
<td>0.24</td>
<td>0.170</td>
<td>0.097</td>
<td>0.045</td>
</tr>
<tr>
<td>$s^2_{E}$</td>
<td>9.025</td>
<td>21.30</td>
<td>4.865</td>
<td>0.0386</td>
<td>0.249</td>
<td>4.05</td>
<td>2.419</td>
<td>1.425</td>
<td>0.707</td>
</tr>
</tbody>
</table>

Estimates of additive by environmental interaction variances were larger than their standard errors for fruit number, L/D ratio, and fruit firmness. The additive by environment interaction component was larger than the additive component estimate for fruit number. Estimates of heritability were higher for the traits associated with quality, except for fruit color, than those for yield-related traits. Heritability for fruit wt was very low, presumably due to non-uniform size distributions when measuring this trait. Heritability for fruit color was lower than the additive component estimate for fruit firmness. The high positive correlation between number of fruit and dollar value shows that selection for increased fruit number is desirable because a low score for fruit color corresponded to dark green fruit. The phenotypic correlations were based on full-sib families grown in 2 replications in each of 2 environments.

Estimates of the genetic and phenotypic correlations are listed in Table 3. The genetic correlations for each pair of traits reflect the expected correlated responses in the first cycle of a selection program. Those genetic correlations may be due to linkage, pleiotropy, or both (15). The correlations due primarily to linkage could be expected to approach zero upon random-mating as the population achieved linkage equilibrium. The high positive correlation between number of fruit and dollar value shows that selection for increased fruit number could be expected to be effective in increasing yields. That was an important relationship since the grading process need to determine dollar value was laborious and time-consuming. The remainder of the genetic correlations between the yield and quality traits were small except for those involving days to harvest and fruit color. Because many of the genetic correlations were close to zero, they indicated that selection for improvement in yield can be done without adversely affecting quality.

The negative correlation between fruit number and fruit color was desirable because a low score for fruit color corresponded to dark green fruit. The phenotypic correlations were based on full-sib families grown in 2 replications in each of 2 environments.

**Implication for breeding.** Since most of the genetic variance was additive, recurrent selection within this populations should effectively utilize the genetic variance available. The low heritabilities and the large genetic by environmental interaction variances for yield traits indicate that the breeder should consider some type of family selection in this population. The monoecious material used in this study had large plot to plot differences in the number of plants bearing fruit. Harvesting of the monoecious material required daily checking to determine when to harvest. The genoecious character is considered necessary to achieve uniform fruit set essential for once-over harvests. Therefore, in addition to leading directly to a hybrid, this method could lead to increases in accuracy and increased efficiency in the selection process. A half-sib progeny test would allow the evaluation of gynoecious hybrids. In this scheme...
males would be selfed and crossed to a series of gynoecious
lines. If all or most of the genetic variance is additive then the
expected gain for this scheme is:

\[ \text{Expected gain (} \Delta G \text{)} = \kappa (1/2) a^2_A / (a^2_B)^{1/2} \]

where \( \kappa \) is the selection differential, \( a^2_A \) is the estimate of addi-
tive genetic variance, and \( a^2_B \) is the estimate of phenotypic
variance. For the half-sib progeny test, assuming no dominance,
\( a^2_B \) is estimated by \( a^2 = rs + a^2_{K \times A} + a^2_{K \times B} \) where \( r \) equals the
number of replications per season and \( s \) is the number of seasons
(5, 14). The direct response to selection based on half-sib
progeny test using the variance components for value, selecting
the best 5 percent of the families grown in two 25 plant
replications in each of 2 environments, is $18.00 per hectare
per cycle. The direct response to half-sib selection using the
fruit number would be preferable as fruit number can be deter-
mined more easily. This could allow for increased selection in-
tensities at the same cost.

Index selection could also be used to increase efficiency in a
selection program (8). Two or more highly correlated traits
could be combined to construct a selection index. A selection
index that would be useful in this population could be con-
built by combining fruit number and days to harvest. The
selection index calculated using these traits with economic
weights of 1 and 0 respectively was \( I = 0.096 X_1 + 0.413 X_2 \),
where \( X_1 \) is the half-sib family mean for fruit number and \( X_2 \)
is the half-sib family mean for days to harvest. The expected
gain using this index is 4441 fruit per ha per cycle which is a
66% increase over using fruit number alone.

The half-sib progeny test requires 3 generations per cycle;
therefore, the gain per generation would be only 1/3 the gain
per cycle. It is possible with cucumbers to complete a cycle of
selection each year since yield estimates are made at an immu-
minute fruit stage. The selfed seed from the males being evaluated
could be planted approximately a month after the half-sib
progeny being evaluated. By the time the progeny had been
tested the males would be ready to flower, and males selected
on the basis of their progeny test could be intermated with
ample time to produce seed. Selection with \( S_1 \) progenies could
also be carried out for highly heritable characters such as disease
resistance. The winter season could be used to generate the
half-sib families for the next cycle. Therefore, the gains per year
could equal the gain per cycle.

Low expected gains for fruit number and other traits with
low heritabilities suggest that unless the genetic variance asso-
ciated with these traits can be increased, progress is expected to
be slow or expensive in terms of land and labor. However, it
was previously shown that selection for genotypes with high
fruit numbers would be expected to be effective in increasing
yields. Therefore, a study designed to find and incorporate
multiple fruit setting genotypes might be the first step in
increasing yields.

In assessing the importance of genotype by environment
interactions it is important to define the environments of inter-
est. A large genotype by environment interaction variance for
spring and fall seasons could lead to 1 of 2 alternate selection
strategies (2). Different cultivars adapted to either spring or fall
seasons could be developed. Using this procedure the additive
by environment interaction variance would be combined with
the additive variance and thus increase the heritability and the
response to selection. Conversely the objective might be
development of varieties adapted to both spring and fall seasons.
In this case material would need to be tested in both seasons
and the genotype by environment interaction variance would
increase the difficulty of selecting superior genotypes. Genotype
by location interactions, if substantial, could be treated in a
similar manner; however, it is necessary to have some idea of
the relative magnitude of these interactions before an efficient
selection program can be developed.

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