

Genetic Variance Components and Heritabilities of Several Avocado Traits

Uri Lavi, Emanuel Lahav¹, and Chemda Degani¹

Department of Fruit Tree Breeding and Genetics, Agricultural Research Organization, The Volcani Center, P.O. Box 6, Bet Dagan 50250, Israel

Shmuel Gazit and Jossi Hillel²

Department of Horticulture, The Hebrew University of Jerusalem, Faculty of Agriculture, P.O. Box 12, Rehovot 76100, Israel

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ABSTRACT. Genetic variance components for avocado (*Persea americana* Mill.) traits were estimated to improve avocado breeding efficiency. The additive and nonadditive genetic variance components were calculated from the variances between and within crosses. In all nine traits examined, i. e. anise scent, fruit density, flowering intensity, fruit weight, harvest duration, inflorescence length, seed size, softening time, and tree size, a significant nonadditive genetic variance was detected. Additive genetic variance in all traits was lower and nonsignificant. The existence of major nonadditive variance was indicated also by narrow-sense and broad-sense heritability values estimated for each trait. Therefore, parental selection should not be based solely on cultivar performance. Crosses between parents of medium and perhaps even low performance should also be included in the breeding program.

Breeding subtropical fruit trees, particularly avocado, is relatively inefficient because the genetic information available is quite limited (Bergh, 1975). Hence, the production of new cultivars is expensive and time consuming. At present, crosses are made without accurate prediction of progeny performance. Moreover, the choice of parents is based solely on their phenotypic performance. The genetic variance generally is assumed to be additive; therefore, combining alleles from the two parents will result in offspring having the desired performance (Hansche, 1983). A recent report on estimates of several genetic traits in avocado was based on genetic considerations rather than on quantitative genetic analysis (Lavi et al., 1991). It was shown that genetic variance (both additive and nonadditive) is large for most avocado traits. In four of the eight traits

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¹Dept. of Fruit Trees.

²Dept. of Genetics.

analyzed (tree size, flowering intensity, fruit density, and inflorescence length), relatively large nonadditive genetic variances were reported.

Our objectives were to conduct a quantitative analysis of several quantitative traits in avocado to estimate the variance components and narrow and broad-sense heritabilities to facilitate distinguishing between the additive and nonadditive components of the genetic variances.

Materials and Methods

FIELD SITE AND PROCEDURE. Parent and progeny avocado plots were located at the Akko Experiment Station in Western Galilee, Israel, lat. 32°55'N. 35°05'E, where rainfall occurs between November and February and averages ≈580 mm annually. Average minimum is ≈13 °C and the average maximum 25 °C. The soil is low-lime grumusol with 60% clay to a depth of 150 cm. All cultural practices were similar to those in commercial plantations. Microsprinkler irrigation was applied weekly during the dry season. Planting density was 1250 trees/ha.

PLANT MATERIAL AND PROCEDURES. Fourteen cultivars were used for crossing and selfing (Lavi et al., 1991). Twelve selfings and 12 crosses among these 14 cultivars produced between two and 431 progeny for each self- or cross- pollination and a total of 1638 seedlings (Table 1). The parent clones were sufficiently different in many traits to represent much of the variation that exists within avocado; these populations are also highly heterozygous. Thus, the production of well segregating populations does not depend on making many crosses.

Table 1. Parent avocado cultivars used for selfing and crossing.

| Parent cultivar | No. of progeny from selfings | Crosses | |
|-----------------|------------------------------|-----------------|----------------|
| | | Pollen parent | No. of progeny |
| Anaheim | 61 | z | --- |
| Ettinger | 235 | Fuerte | 9 |
| | | Pinkerton | 17 |
| | | Rosh Hanikra II | 71 |
| | | Tova | 431 |
| | | Tova | 50 |
| Fuerte | 7 | Fuerte | 123 |
| Hass | 5 | Ettinger | 40 |
| | | z | --- |
| Horshim | 2 | z | --- |
| Irving | 3 | Ettinger | 40 |
| Nabal | 85 | Reed | 11 |
| Reed | 23 | z | --- |
| Regina | 48 | z | --- |
| Rincon | 23 | z | --- |
| Rosh Hanikra II | 18 | z | --- |
| Tova | 22 | Horshim | 271 |
| | | Regina | 54 |
| Wurtz | z | Ettinger | 16 |
| Total | 532 | | 1106 |

^zNo seedlings available.

Individual trees or pairs of trees were caged for pollinations in the presence of a beehive. Several trees of a given cultivar were used as parents to perform all the pollinations described. As only seedlings of known parentage were of interest in this study, parental genotypes were verified by isozyme analysis. Seeds were extracted from mature fruit and sown in a container. Seedlings were raised for 1 year in a nursery then transplanted to the field. The progeny that originated from each caged tree were randomly grouped by rows. Trees were autumn girdled to shorten the juvenile period (Lahav et al., 1986).

Hybrid and self-pollinated progeny were distinguished by leaf tissue isozyme analysis with the following enzyme systems: leucine aminopeptidase (LAP; EC 3.4.11.1) (Degani et al., 1986), malate dehydrogenase (MDH; EC 1.1.1.37) (Degani and Gazit, 1984), phosphoglucose isomerase (PGI; EC 5.3.1.9) (Goldring et al., 1987) phosphoglucomutase (PGM; EC 2.7.5.1) (Torres et al., 1978), and triosephosphate isomerase (TPI; EC 5.3.1.1) (Goldring et al., 1987). Seedlings with alleles contrary to the assumed parentage were excluded even though individuals having the expected isozyme patterns possibly are not the progeny of the assumed pollen parents.

The characteristics of individual seedlings were assessed either by measurement or by visual scoring (Table 2), and data were averaged over 2 to 5 years. Combining data over several years was necessary because traits related to fruiting are affected by the alternate bearing habit of avocado. The parents' traits are regarded as parameters rather than statistics because they are reproducibly collected over the years. Fruit weight is the mean of all fruits per seedling in cases of low yield, or of ten randomly harvested fruits in cases of high yield. Fruiting density is based on tree size and number of fruits. Harvest duration is the ability to store fruit on the tree. Softening time was determined for mature fruits.

Table 2. Rating scale for quantitative traits in avocado fruit and trees.

| Trait | Rating | | | | | | |
|---|------------|--------|--------|------------|------------|-------|-----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Anise scent | Strong | Medium | Light | None | | | |
| Fruiting density | Dense | Medium | Light | Very light | | | |
| Flowering intensity ² | Profuse | High | Medium | Light | Very light | None | |
| Fruit wt (measured in grams) | | | | | | | |
| Harvest duration (recorded in months) | | | | | | | |
| Inflorescence length (cm) | <5 | 6–10 | 11–15 | 16–20 | >20 | | |
| Seed size (percentage of fruit wt) | <5 | 6–10 | 11–15 | 16–20 | 21–25 | 26–30 | >30 |
| Softening time (days from harvest to softening) | <5 | 6–10 | 11–15 | 16–20 | 21–25 | 26–30 | >30 |
| Tree size | Very large | Large | Medium | Short | Dwarf | | |

²Flowering intensity might partly reflect juvenility.

STATISTICAL MODEL. Multiple regression and covariance analyses were conducted with the Variance Components (VARCOMP) Type I SS and General Linear Model (GLM) procedures of SAS software (SAS Inst., Cary, N.C.). Each of the nine quantitative traits in both self pollinations and crosses between cultivars (Table 1) was analyzed in a one-way random effect model, taking into consideration the unequal number of progeny available for the analysis. The sources of variation were variation between parental means and variation between and within families.

Because our data represent an extremely incomplete diallel with unbalanced cell sizes, the well-developed diallel models were not applicable for this analysis. Instead, we used

the variance between and within crosses, covariances between progeny and parents, and the regression between them to estimate the genetic and environmental components of the phenotypic variances.

DEFINITIONS. VARIANCE COMPONENTS. Phenotypic variance [V(P)] is composed of genetic variance [V(G)] and environmental [V(E)] variance. Genetic variance is divided into additive variance [V(A)] and nonadditive variance [V(NA)]. The additive variance [V(A)] is the variance of breeding values (the value of an individual judged by the mean value of its progeny) and the chief cause for the resemblance between relatives and for the response of the population to selection. The nonadditive variance [V(NA)] is the genetic variance resulting from interaction of alleles (dominance) and/or interaction of loci (epistasis). The design of this study does not allow partitioning between these two nonadditive components (Falconer, 1989).

HERITABILITIES. Broad-sense heritability (h^2b) is the ratio of VG:VP. Partitioning of the genetic variance yields the ratio of VA:VP which is the narrow sense heritability (h^2n) of the character.

RATIONALE. ESTIMATES OF PHENOTYPIC VARIANCE COMPONENTS. Since the data from the hybrids and selfs were analyzed by simple one-way analysis of variance, the variance components between and within progeny populations (for both hybrids and selfs) were estimated from the relevant mean squares. These four variance components (σ^2 symbol in the first column of Table 3), jointly with the covariance between parents and progeny means [COV(op)] and the statistic named V(DE), are listed in Table 3, and their expected values in terms of genetic and environmental variance components are indicated. These six statistics were used to estimate the genetic and environmental variances (Table 4) including their standard errors as follows:

Table 3. Genetic and environmental variance components and the coefficients of their contribution to six statistics.

| Statistic ² | Genetic | | Environmental | |
|------------------------|------------------|----------------------|----------------|-----------------|
| | Additive V(A) | Nonadditive V(NA) | Random V(E) | Common V(EC) |
| σ^2BS | 1 | 0.25 | 0 | 1 |
| σ^2WS | 0.5 | 0.5 | 1 | 0 |
| σ^2BC | 0.5 | 0.25 | 0 | 1 |
| σ^2WC | 0.5 | 0.75 | 1 | 0 |
| COV(op) | 0.5 | 0 | 0 | 0 |
| V(DE) | 0 | 1 | 1 | 0 |

² σ^2BS = variance between selfs; WS = within selfs; BC = between crosses; WC = within crosses; COV(op) = covariance offspring-parents; V(DE) = a calculated statistic with the expected value of V(NA) + V(E).

Each has its own expected value [(Table 3) Falconer, 1989; Mather and Jinks 1971] in terms of additive [V(A)] and nonadditive [V(NA)] genetic variances and random [V(E)] and common [V(EC)] environmental variances, the latter environmental variance being the result of nongenetic factors common to all progeny of the same cultivar. (Note that, in this study, progeny of different cultivars were allocated randomly, but progeny of the same cultivar were grouped together in the same rows). Since simultaneous least

square estimates of the four variances (described above) from the six statistics (first column of Table 3) would leave only one degree of freedom for error, linear regression analyses were performed. In these analyses, each of the four variance components was estimated by using the six statistics as dependent variables and their expected values (for a given component, Table 3) as independent variables. The significance of the difference of each component from zero was determined as the significance of the regression coefficient (Mather and Jinks, 1971). To allow comparisons between traits, the least square estimates of the four components are expressed as percentages of the total.

ESTIMATES FOR HERITABILITIES. Estimates for the narrow-sense heritability (h^2n) were obtained from the regression coefficient of progeny means on the average of both parents. The parameters (with no error variance) describing the parents' traits are the independent variables in the fixed model of regression analysis. The broad-sense heritability (h^2b) was estimated as the ratio between the total genetic variance $[V(G)]$ and the phenotypic variance $[V(P)]$. These two variances were estimated as follows: $V(G) = V(A) + V(NA) = 2(\sigma^2BC + \sigma^2WC - \sigma^2WS)$ based on the expected values given in Table 3. The phenotypic variance, $V(P) = \sigma^2BC + \sigma^2WC$, was estimated as the sum of the variance components between and within all cultivar progeny groups. $SE(h^2b)$ was derived by using a standard formula for the variance of linear combinations of variances assuming normal distribution.

Results

VARIANCE COMPONENTS. The value of the nonadditive genetic variance is significantly higher than zero for all traits (Table 4). These values range between 36.3% in softening time and 49.3% in harvest duration. In contrast, the additive genetic variance varies from 25% to 66% of the nonadditive variance and is nonsignificant in all traits; however, significant environmental variance $[V(E)]$ was present and, except for one trait (flowering intensity), the estimate accounts for 33% to 35% of total phenotypic variance. The common environmental variance, $[V(EC)]$, was estimated by the combined least square estimates from variances between families (selfings and crosses). This variance was small and nonsignificant in all traits.

HERITABILITIES. The values of h^2n ranged from zero in fruit density and flowering intensity to quite high values in seed size (0.50) and softening time (0.48). In two traits, fruit weight and softening time, we could not estimate h^2b because $V(A) + V(NA)$ did not differ from zero; its other values ranged from 0.46 to 1. The ratio of $V(NA)/V(A)$, calculated as $[(h^2b/h^2n)-1]$, was not estimatable for four traits, but ranged from 1.6 to 7.3 in four of the remaining five traits. These results suggest the existence of pronounced nonadditive genetic variance.

Discussion

The choice of parents for hybridizing or selfing is probably the most important decision for a perennial fruit tree breeder. The usual goal is to combine complementary parental phenotypic virtues. Examples of such desired combinations in avocado are the crossing of 'Hass' with a parent having larger fruit size, or 'Fuerte', with a better yielding cultivar. The assumption for this approach is that much of the genetic variance is additive, so that there is a good chance to obtain offspring in which desirable traits from both

parents have been combined. In practice, however, progeny performance of most crosses is quite unpredictable.

Table 4. Least square estimates of the avocado variance components as percentages of the total variances.

| Trait | Genetic | | Environmental | |
|----------------------|------------------|----------------------|---------------------|-----------------|
| | Additive V(A) | Nonadditive V(NA) | Random V(E) | Common V(EC) |
| Anise scent | 20.0 | 42.6 ^{****} | 33.3 ^{***} | 4.1 |
| Fruit density | 21.6 | 39.8 ^{**} | 33.9 ^{***} | 4.7 |
| Flowering intensity | 26.9 | 46.9 ^{**} | 19.0 ^{***} | 7.2 |
| Fruit wt | 23.9 | 38.6 [*] | 34.7 ^{***} | 2.7 |
| Harvest duration | 12.0 | 49.3 ^{**} | 34.9 [*] | 3.8 |
| Inflorescence length | 16.9 | 45.4 ^{***} | 34.6 ^{**} | 3.1 |
| Seed size | 25.9 | 37.4 [*] | 33.7 ^{**} | 3.1 |
| Softening time | 26.0 | 36.3 [*] | 34.4 ^{**} | 3.1 |
| Tree size | 26.0 | 40.2 [*] | 33.4 [*] | 3.0 |

^z*,^{***},^{****}Significance of the difference of the original least square estimates from zero at $P < 0.05$, 0.01, or 0.001, respectively; absence of an asterisk indicates nonsignificance.

Table 5. Phenotypic variance V(P) and broad- (h^2b) and narrow-sense (h^2n) heritability values.

| Trait | V(P) ^z | h^2b ^y | SE | h^2n ^x | SE |
|----------------------|-------------------|---------------------|------|---------------------|------|
| Anise scent | 0.76 | 0.83 | 0.05 | 0.32 | 0.06 |
| Fruit density | 0.80 | 0.49 | 0.11 | -0.09 | 0.10 |
| Flowering intensity | 1.67 | 0.49 | 0.14 | -0.15 | 0.12 |
| Fruit wt | 50.19 | 0 | 0 | 0.35 | 0.07 |
| Harvest duration | 1.43 | 0.66 | 0.12 | 0.16 | 0.05 |
| Inflorescence length | 0.54 | 1.0 | 0.10 | 0.12 | 0.06 |
| Seed size | 1.47 | 0.77 | 0.08 | 0.50 | 0.10 |
| Softening time | 0.95 | 0 | 0 | 0.48 | 0.13 |
| Tree size | 1.22 | 0.46 | 0.12 | 0.18 | 0.07 |

^zFrom parent offspring regression.

^yFrom the ratio between the total genetic variance V(G) and the phenotypic variance V(P).

^xFrom the regression coefficients of progeny means on the average of both parents.

The estimates of nonadditive genetic variance given in this study and previously (Lavi et al., 1991) indicate that this variance is a major component of the total genetic variance and is significantly greater than zero in all traits. Estimates in this study were obtained for both the phenotypic variance components and for heritabilities. The relative value of V(A) presented in Table 4 actually reflects the narrow-sense heritability (h^2n) (Table 5). Although the estimates obtained by the two methods are not identical, they both suggest that, in most traits, the additive genetic component V(A) is not the major portion of the total variance. The high level of heterozygosity known to exist in several fruit trees, avocado included (Lavi et al., 1991 a), could explain the prevalence of a large nonadditive (dominant) genetic variance (Fisher, 1930). We emphasized, though, that our conclusions must be limited to the set of clones used in this study.

All traits analyzed in this study, except fruit weight, were linearly scored on a scale to allow quantitative statistical analysis. Harvest duration, inflorescence length, seed size, and softening time were actually measured. Anise scent, tree size, flowering intensity, and fruit density were carefully scored by an avocado expert who evaluated the seedlings during 2 to 5 years of yielding and with the parent cultivar for reference. For this reason, we do not think that the nonadditive components of the genetic variance have resulted from any subjectivity or nonlinearity introduced into the scoring of these traits by the experimenter (Mansche, 1983).

The choice of parents for crosses in a breeding project should be influenced by the relative magnitude of the additive and nonadditive genetic variance in the relevant trait. Where there is high additive genetic variance and high heritability values, parents should be chosen on the basis of their phenotypes. However, where high nonadditive genetic variance exists, parents should not be chosen entirely according to their phenotypes because offspring performance is less predictable. Crosses in the latter case should be aimed toward increasing the genetic variance in the progeny. We suggest that, in such cases, 10% to 30% of the crosses should include parents of inferior performance as well.

The broad-sense heritability of the various traits varied widely. Estimates possibly could be biased upwards because $V(EC)$ was included. However, since $V(EC)$ was found to be low and nonsignificant, we believe that the bias is negligible. The values of h^2_b for fruit weight and softening time are probably very small and could not be calculated. Tree size, fruit density, and flowering intensity had h^2_b values ranging from 0.46 to 0.49. Harvest duration, seed size, anise scent, and inflorescence length had high h^2_b values ranging from 0.66 to 1.0.

The importance of h^2_b originates from the fact that in the selection plots, best performing seedlings could result from either environmental or genetic factors. The higher the value of h^2_b , the higher the confidence that genetic factors are responsible for the seedling performance and, therefore, the smaller the number of grafted trees that must be made from the selected seedlings for the next phase of the evaluation.

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