

*Institute of Horticulture, Bet-Dagan;
The Hebrew University of Jerusalem, Rehovot (Israel)*

Quantitative Genetic Analysis of Traits in Avocado Cultivars*

U. LAVI, E. LAHAV, A. GENIZI, C. DEGANI, S. GAZIT and J. HILLEL

With 7 tables

Received January 12, 1990 / Accepted March 25, 1990

Abstract

This research is aimed at quantitative genetic analysis of several avocado traits and cultivars. The experimental material consists of our avocado breeding project in which data were collected from several crosses as well as selfings of cultivars. Parenthood was determined by isozymes and the seedling progenies were assessed for eight traits. A biometrical genetic approach for analysis of this breeding project is presented. Genetic profiles of the traits and cultivars were detailed by several characteristics: level of heterozygosity and dominance deviation, dominance of alleles, dominance direction, general evaluation of additive and non-additive genetic variance, maternal inheritance, and allelic differences among the various cultivars in major genes controlling the same quantitative trait. Five avocado cultivars: 'Fuerte', 'Hass', 'Ettinger', 'Tova', and 'Rosh-Hanikra', were characterized separately for each trait. Practical conclusions for the breeder regarding economically important quantitative traits are discussed.

Key words: *Persea americana* — additive genetic variation — non additive genetic variation — dominance — heterozygosity — maternal inheritance.

Considerable difficulties have been experienced in studying the genetics of fruit trees in general and of avocado in particular. Relatively little is known about the components of the phenotypic variability of quantitative traits in fruit trees. In only a few cases, has the herita-

bility of such traits been assessed, but with avocado excluded (HANSCHKE et al. 1966, HANSCHKE et al. 1972 a, b). The level of heterozygosity and partitioning the genetic variance of quantitative traits into their additive and non-additive components have not yet been assessed in avocado. This kind of genetic information is important for any systematic breeding programme.

The main problems which limit a systematic genetic study of avocado traits stem from the long juvenile period and the big tree size, which make the breeding programme long in time, small in number of seedlings, and hence quite expensive. Moreover, the very low fruit set typical for avocado, makes hand pollination impractical. In spite of these difficulties a few formal genetic studies of avocado have been reported. Some Mendelian genes have been reported to code several isozymes (DEGANI et al. 1986, GOLDRING et al. 1985, GOLDRING et al. 1987, TORRES et al. 1978). Both the flowering group and fruit skin colour were found to be controlled by several genes, although the exact mode of inheritance has not been elucidated (BERGH 1969).

A few years ago, an avocado breeding programme aimed at the production of better cultivars was initiated at the Agricultural Research Organization (ARO) in Israel. Hybrids between cultivars were produced by caging the parent trees with a net and putting a beehive inside. The progeny were tested by isozymes to distinguish between selfs and hybrids (DEGANI and GAZIT 1984). Over the years many

* Contribution from the Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel. No. 2778E, 1989 series.

crosses have been performed in the hope of detecting better cultivars resulting from new combinations of genes and alleles.

This manuscript describes the genetic and biometrical analyses of some quantitative traits, evaluated from progenies of crosses between and within avocado cultivars.

Materials and Methods

The research was performed at the Akko Experiment Station, in Western Galilee, Israel. Seeds were collected from trees caged under a net, using bees as the pollen vector. Crosses were performed in the following manner:

1. Two trees (cultivars) under a single net cage. Seeds were collected from each tree separately (reciprocals).
2. Individually caged trees, where the pollinator cultivar was either a grafted branch on the mother tree or flowering potted trees.

For selfings, single trees were caged. The harvested seeds were sown in the nursery, and one year later the seedlings were planted in the breeding orchard. The progeny of each cage were planted in a block, selfing progeny and hybrids were completely randomized within the block. The juvenile period was shortened by the use of autumn girdling (LAHAV et al. 1986).

Performance of the seedlings was assessed either by measurements or by visual scoring, as shown in Table 1. The values of the traits are the means of evaluation during two to five years. Means are important mainly for traits which are affected by "on and off" years. Fruit weight is the mean of all fruits in cases of low yield, or randomly harvested 10 fruits in cases of high yield. Fruit density is fruit number divided by tree volume, this trait takes into consider-

ation both tree size and number of fruits. Harvest duration expresses tree storage. Softening time was determined on mature fruits. Of the many cultivars involved in these experiments, results from only six will be presented here: 'Fuerte' (ROUNDS 1946), 'Hass' (GRISWOLD 1945), 'Ettinger' (STOREY and BERGH 1963), 'Tova', 'Horshim'-in some crosses (SLOR and SPODHEIM 1971, 1972), and a Mexican race seedling named 'Rosh-Hanikra II'. The last cultivar is a branching tree with numerous brownish-red lenticels on the young flush and a strong anise scent. The fruit is oval-pear, 150 gr. The fruit stalk is relatively short, slightly off centre. The fruit skin is black, very thin with a smooth and glossy surface. The seed is rounded and constitutes 25—30 % of the fruit's weight. The yellow flesh has a few fibres and a mild taste. 'Rosh-Hanikra II', a non-commercial cultivar, was used in the breeding project as a representative of the Mexican race due to its high productivity and early ripening.

To distinguish between hybrids and self-pollinated seedlings, the progeny were characterized by isozyme analysis of leaf tissue for 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. 1985) phosphoglucose mutase (PGM; EC 2.7.5.1) (TORRES et al. 1978), and triosephosphate isomerase (TPI; EC 5.3.1.1) (GOLDRING et al. 1987).

Six crosses between five to six cultivars (depending on the trait), and five selfings were the source of information for this study and will be named "set of crosses". The number of observations in the various crosses is given in Tables 2, 3, 4, and 5. Different trees of a certain cultivar were used for the various crosses due to the need for geographical proximity. However, for each cultivar all mother trees were assessed and found to be similar in all traits.

Table 1. Grades of quantitative traits in avocado trees

Note that in some traits a low grade indicates good performance, and *vice versa*

Trait	Grades						
	1	2	3	4	5	6	7
Tree size	Very tall	Tall	Medium	Short	Dwarf		
Flowering intensity	Profuse	High	Medium	Light	Very light	None	
Fruit density	Dense	Medium	Light	Very light			
Fruit weight	Grams						
Inflorescence length (cm)	≤ 5	6—10	11—15	16—20	> 20		
Seed size (% of fruit weight)	≤ 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
Harvest duration	Months						

Since no single comprehensive analysis of the data obtained from the "set of crosses" is feasible (see Results), three separate analyses were carried out:

I. Analysis of selfing progeny (Tables 2, 3): Selfing progeny of each cultivar was analyzed as a fixed effect one-way analysis of variance according to the following linear model:

$Y_{ij} = X + S_i + T_{ij}$, where:

Y_{ij} is the quantitative trait value of seedling j in cultivar i .

X is the mean of all selfing progeny.

S_i is the fixed effect of selfing of cultivar i .

$i = 1$ to 5 or 6 depending on the trait (see Table 3).

T_{ij} is the random effect of seedling j in cross i , $j = 1$ to n_{ij} , depending on the cross and the trait.

II. Analysis of orders (Table 4): Crosses between the six cultivars produced six male and female orders. In each order one cultivar is a common parent while the other parents are either the cultivar itself (selfing) or each of the other five cultivars (hybrids). Therefore, two-way factorial analysis of variance for fixed effects and unequal number of observations per cell was used, including progeny of selfing crosses of the same tree.

The linear model of this analysis is as follows:

$Y_{ijk} = E + M_i + F_j + (MF)_{ij} + R_{ijk}$, where:

Y_{ijk} is the value of the quantitative trait, measured on tree k , the progeny between parents i and j .

E is the average of the entire "set of crosses".

M_i is the fixed effect of cultivar i as male parent, for $i = 1$ to 6.

F_j is the fixed effect of cultivar j as female parent, for $j = 1$ to 6.

$(MF)_{ij}$ is the fixed effect of the interaction between cultivars i and j .

R_{ijk} is the random effect of seedling k in the cross between cultivars i and j .

k varies depending on the trait and the cross.

III. Analysis of crosses and reciprocals (Table 5): In only four crosses were data available for analysis of reciprocals. These four crosses were analyzed as fixed effects. The two reciprocals in each cross were analyzed as random effects within crosses. Within each reciprocal cross, information from different number of seedlings was available. Accordingly, the following linear model was used:

$Y_{ijk} = D + C_i + R_j(C_i) + T_k(R_j)$ where:

Y_{ijk} is the value of a given quantitative trait measured on seedling k of reciprocal cross j of the cross i .

D is the mean of this data set.

C_i is the fixed effect of cross i , for $i = 1$ to 4.

$R_j(C_i)$ is the random effect of reciprocal cross j , within cross i , for $j = 1$ to 2.

$T_k(R_j)$ is the random effect of seedling k in reciprocal cross j of cross i , for $k = 1$ to n_{ij} .

Within each cross, significance of the differences between the two reciprocal crosses was tested.

Results

The well-developed diallel models, as well as models dealing with incomplete diallel tables (GARDNER and EBERHART 1966, GRIFFING 1956, HAYMANN 1960, JINKS 1954) were not applicable to the data of the present study because the "set of crosses" represents a very incomplete diallel table.

The inherent huge variability in fruit production typical for the avocado affected the availability of data. Of the fifteen possible crosses (including selfing) among the five cultivars, only eleven were available. Furthermore the number of seedlings in each cross varied substantially ranging from 3 ('Fuerte' × 'Ettinger') to 382 ('Ettinger' × 'Tova'). The above-mentioned severe combination of difficulties produce statistical limitations particularly in the analysis of the interaction between males and females. Our genetic analysis is therefore based mainly on first order genetic statistics.

The genetic characterization of traits and cultivars were derived from the results given in Table 2 and from the variance presented in Tables 3, 4 and 5. Three main sources of information were used for this purpose: the cultivar performance, selfing progeny mean and the order mean. The genetic information as well as the statistical significance of the comparisons between these statistics, are detailed for each of the five cultivars as to each of the eight quantitative traits.

The overall genetic variance is expressed by the high statistically significant differences among order means (Table 4). This abundant genetic variation is supported by the significant differences between all crosses including selfing, found in most traits (Table 5). Part of this genetic variance is reflection of the genetic diversity between cultivars and the remainder which result from interaction between alleles and loci is exposed upon various crosses.

The genetic information resolvable from the biometrical analyses presented in Tables 2—5 is summarized for the traits in Table 6 and for the cultivars in Table 7. These Tables are the detailed summary of our results and are meant to serve as an aid for the avocado breeder.

Table 2. Cultivar performance, means \pm standard errors (S.E.) of selfing and order progeny

Trait	Statistics & significance	Cultivars				
		'Fuerte'	'Hass'	'Ettinger'	'Tova'	'Rosh Hanikra'
Tree Size	Cv. performance	2	2	2	4	2
	Self progeny: No.	7	5	132	15	18
	Mean \pm S.E.	3.4 \pm .48	3.0 \pm .32	3.8 \pm .08	3.2 \pm .32	3.2 \pm .29
	Sig. (self-parent)	*	*	***	*	***
	Order progeny: No.	183		702	207	54
	Mean \pm S.E.	3.7 \pm .09		3.1 \pm .05	3.3 \pm .08	2.5 \pm .23
	Sig. (order-self)	***		***	*	**
Flower intensity	Cv. performance	1	2	3	3	4
	Self progeny: No.	7	5	129	13	18
	Mean \pm S.E.	4.4 \pm .65	3.8 \pm .37	4.9 \pm .09	4.7 \pm .09	3.9 \pm .20
	Sig. (self-parent)	**	**	***	***	n.s.
	Order progeny: No.	184		698	265	54
	Mean \pm S.E.	4.0 \pm 0.12		4.6 \pm .06	4.7 \pm .08	3.8 \pm .18
	Sig. (order-self)	***		***	n.s.	n.s.
Fruit density	Cv. performance	3	1	2	1	1
	Self progeny: No.	4	4	32	5	9
	Mean \pm S.E.	3.7 \pm .25	3.7 \pm .25	3.3 \pm .16	2.8 \pm .58	3.8 \pm .15
	Sig. (self-parent)	n.s.	**	***	*	***
	Order progeny: No.	128		339	65	40
	Mean \pm S.E.	3.0 \pm 0.10		3.4 \pm .06	3.6 \pm .12	3.4 \pm .15
	Sig. (order-self)	***		n.s.	***	*
Fruit weight	Cv. performance	280	200	310	250	150
	Self progeny: No.	4	4	31	5	9
	Mean \pm S.E.	202 \pm 29.5	165 \pm 37.7	205 \pm 10.9	226 \pm 30.9	181 \pm 22.9
	Sig. (self-parent)	n.s.	n.s.	***	n.s.	n.s.
	Order progeny: No.	128		334	64	40
	Mean \pm S.E.	213 \pm 0.68		207 \pm .53	207 \pm 1.6	205 \pm 1.75
	Sig. (order-self)	n.s.		n.s.	n.s.	n.s.
Inflorescence length	Cv. performance	3.25	3.25	2.09	2	1
	Self progeny: No.	4	4	30	5	9
	Mean \pm S.E.	1.7 \pm .25	1.3 \pm .25	1.3 \pm .09	1.4 \pm .24	1.3 \pm .23
	Sig. (self-parent)	**	**	***	*	n.s.
	Order progeny: No.	114		312	57	40
	Mean \pm S.E.	1.9 \pm 0.18		1.3 \pm .07	1.5 \pm .13	1.1 \pm .2
	Sig. (order-self)	n.s.		n.s.	n.s.	n.s.
Seed size	Cv. performance	4	4	4	4	6
	Self progeny: No.	4	4	31	5	9
	Mean \pm S.E.	3.7 \pm .25	3.5 \pm .5	3.9 \pm .16	4.8 \pm .37	4.7 \pm .44
	Sig. (self-parent)	n.s.	n.s.	n.s.	n.s.	*
	Order progeny: No.	128		326	62	40
	Mean \pm S.E.	4.2 \pm 0.10		4.3 \pm .09	4.2 \pm .20	4.7 \pm .29
	Sig. (order-self)	***		***	**	n.s.

Table 2. (continued)

Softening time	Cv. performance	3	3	2	3	2
	Self progeny: No.	4	4	29	5	9
	Mean \pm S.E.	4.0 \pm 1.0	4.5 \pm .5	3.5 \pm .19	3.4 \pm .24	2.7 \pm .33
	Sig. (self-parent)	n.s.	n.s.	***	n.s.	n.s.
	Order progeny: No.	128		324	61	40
	Mean \pm S.E.	3.7 \pm .13		3.2 \pm .09	3.3 \pm .13	2.5 \pm .23
	Sig. (order-self)	n.s.		***	n.s.	n.s.
Harvest duration	Cv. performance	5	6	2	2	1
	Self progeny: No.	4	4	51	5	9
	Mean \pm S.E.	3.5 \pm 1.85	4 \pm 1.68	5.5 \pm .63	2.8 \pm .58	4.3 \pm 1.18
	Sig. (self-parent)	n.s.	n.s.	***	n.s.	*
	Order progeny: No.	128		327	62	40
	Mean \pm S.E.	4.4 \pm .32		5.2 \pm .28	6.1 \pm .45	3.8 \pm 0.87
	Sig. (order-self)	**		n.s.	***	n.s.

Cv. performance = grade of cultivar performance in each trait.

Self progeny: No. = number of selfing progeny in each cross.

Mean \pm S.E. = mean performance of selfing progeny or order progeny respectively \pm their standard error.

Sig. (self-parent) = Statistical significance of the difference between the mean of selfing progeny and the parent's performance.

* = .01 < P < .05; ** = .001 < P < .01; *** = P < .001; n.s. = non significant.

Order progeny No. = Number of order progeny in each cross. Note that the cultivar Hass was not involved in order crosses.

Sig. (order-self) = Statistical significance of the difference between the order progeny mean and the selfing progeny mean.

Genetic profile of traits (Table 6)

Similarity among cultivars: Homogeneity and differences between cultivars regarding each of the eight quantitative traits were assessed from the data in Tables 2—5.

Direction consistency of dominance deviation: The direction of dominance was deter-

mined only when the deviation of the selfing progeny from their parents was significant in most selfings (Table 2). Consistency of these deviations was interpreted as unidirectional dominance. Possibly bidirectional dominance was interpreted when the deviations were not consistent. In most instances whenever this characteristic could be determined, dominance

Table 3. Analysis of variance of selfings

Trait	Between selfings				Within selfings		
	df	MS	F	P	df	MS	CV
Tree size	5	3.21	3.21	**	173	1.00	30
Flowering intensity	5	4.70	3.94	**	168	1.19	25
Fruit density	4	1.13	1.52	n.s.	49	0.74	23
Fruit weight	4	30.85	<1	n.s.	48	40.57	32.5
Inflorescence length	4	0.22	<1	n.s.	47	0.31	40
Seed size	4	2.11	2.34	n.s.	48	0.90	23
Softening time	4	2.84	2.36	n.s.	46	1.20	30
Harvest duration	4	0.43	<1	n.s.	48	0.45	17

df — Degrees of freedom

MS — Mean squares

P — Significance of the differences between crosses: ** .001 < P < .01; n.s., non-significant.

CV — Coefficient of variation.

Trait	Between crosses ^{b)}			Between orders ^{c)}			Males × females			Within crosses			
	df ^{a)}	MS	F	P	df	MS	F	P	MS	F	P	df ^{d)}	MS
Tree size	15	7.8	6.7	***	10	8.26	7.12	***	5	6.88	5.92	1057	1.16
Flowering intensity	15	24.6	18.6	***	10	33.15	25.1	***	5	9.02	6.83	1048	1.32
Fruit density	15	5.2	8.1	***	10	4.9	7.66	***	5	5.97	9.33	396	0.64
Fruit weight	15	93.8	1.9	*	10	120	2.39	**	5	39.8	<1	390	50.15
Inflorescence length	15	2.5	6.4	***	10	3.6	9.23	***	5	.39	1.0	345	0.39
Seed size	15	5.1	3.7	***	10	6.9	5.0	***	5	1.46	1.07	379	1.38
Softening time	15	3.9	4.2	***	10	4.99	5.37	***	5	1.96	2.11	376	0.93
Harvest duration	15	38.6	3.9	***	10	46.8	4.81	***	5	22.18	2.27	380	9.73

df — Degrees of freedom

MS — Mean squares

P — Significance of the differences: * .01 < P < .05; ** .001 < P ≤ .01; *** P ≤ .001; n.s. non-significant

a) Selfings included.

b) The SS of this source of variation is not always the precise summation of the SS of the other two items due to unbalanced structure of the "set of crosses" table.

c) The male and female orders were pooled.

d) The number of seedlings varied among the different crosses.

Table 5. Analysis of variance of crosses and reciprocals

Trait	df	Between crosses ^{a)}			Between reciprocals within crosses			Between trees within crosses				
		MS	F	P	MS	F	P	MS	F	P	df	MS
Tree size	3	1.44	<1	n.s.	5.31	4.33	**	1.22	766	1.22	37	
Flowering intensity	3	32.12	19.50	**	1.65	1.31	n.s.	1.26	762	1.26	25	
Fruit density	3	6.70	7.53	*	0.89	1.68	n.s.	0.53	265	0.53	21	
Fruit weight	3	19.93	<1	n.s.	66.78	1.25	n.s.	53.25	260	53.25	36	
Inflorescence length	3	1.30	36.10	**	.04	<1	n.s.	.34	226	.34	40	
Seed size	3	6.38	8.20	*	.78	<1	n.s.	1.49	249	1.49	27	
Softening time	3	4.12	9.15	*	.45	<1	n.s.	.84	248	.84	29	
Harvest duration	3	69.69	4.50	n.s.	15.47	1.54	n.s.	10.07	250	10.07	54	

df — Degrees of freedom

MS — Mean squares

P — Significance of the differences: * .01 < P < .05; ** .001 < P ≤ .01; n.s. non-significant

CV Coefficient of variation

was unidirectional. When dominance direction was inconsistent, we considered only statistically significant cases because others could originate from bidirectional dominance as well as from heterozygosity and dominance deviation.

Allele differences among the various cultivars: Difference between alleles controlling the same quantitative trait locus (QTL) was determined by comparison between order means and selfing progeny means (Table 2). The conclusions are based on the fact that one common parent participates in both statistics but the other parent of the selfing progeny is substituted by the remainder of the various cultivars. Difference between these means was attributed to differences between alleles in the various cultivars. In addition, significant variance between selfing progeny means may also indicate such differences. Tree size is the only

trait which seems to be controlled in the various cultivars by different alleles, whereas for fruit weight, seed size, softening time and harvest duration, allele differences were not apparent.

Genetic variance: The experimental design analyzed in this study does not allow the partitioning of genetic variance into its additive and non-additive components. However, evaluation of their relative magnitudes in general terms was possible. General assessment of additive genetic variance was concluded from statistically significant variance both between crosses (Table 4) and between selfings (Table 3). High additive genetic variance was deemed to exist only when the variance between crosses was statistically significant, medium level of additive genetic variance when only the variance between selfing crosses was statistical-

Table 6. Genetic profile of the traits (Summary)

Cultivars: E — 'Ettinger'; F — 'Fuerte'; H — 'Hass'; R — 'Rosh-Hanikra'; T — 'Tova'

Trait	Similarity among cultivars	Consistency of dominance deviation	Allele differences among cultivars	Additive genetic variance	Non-additive genetic variance
Tree size	Homogeneous except 'T', short	Unidirectional	Large	Medium	Large
Flowering intensity	Heterogeneous 'F'-profuse 'R'-light	Unidirectional	Medium	Very large	Large, except 'R'
Fruit density	Heterogeneous 'R'-dense 'F'-light	Unidirectional	Medium	Low	Large, except 'F'
Fruit weight	Heterogeneous 'E'-large 'R'-small	Possibly bidirectional	None	Low	None, except 'E'
Inflorescence length	Heterogeneous 'F'-long 'R'-short	Unidirectional	Medium	Medium	Large, except 'R'
Seed size	Homogeneous except 'R'-large	Non determinable	None	Medium	None except 'R'
Softening time	Homogeneous	Non determinable	Low	Large	None, except 'E'
Harvest duration	Heterogeneous 'F'-long 'R'-short	Possibly bidirectional	Almost none	Large	Small, except high in 'E'

Table 7. Genetic profile of the cultivars (Summary)
 Cultivars: E — 'Ettinger'; F — 'Fuerte'; H — 'Hass'; R — 'Rosh-Hanikra'; T — 'Tova'

Profile	Tree size	Flower intensity	Fruit density	Fruit weight	Inflorescence length	Seed size	Softening time	Harvest duration
Cv. 'Fuerte'								
1. Cultivar performance	Tall	Profuse	Light	280 gr	3.2 cm	10—20 %	11—15 days	5 months
2. Heterozygosity and dominance deviation	Low	Medium	None	None	Medium	None	None	None
3. Cross of special performance	Smallest by selfing	Highest with 'T'	Highest with 'T'	Best size with 'T'	Largest with 'T'	Smallest by selfing	Longest by selfing	Longest with 'H'
4. Alleles responsible for increase	Dominant	Dominant	Codominant	Codominant	Dominant	Codominant	Codominant	Codominant
5. Maternal inheritance	None	None	None	None	None	None	None	None
Cv. 'Hass'								
1. Cultivar performance	Tall	High	Dense	200 gr	3.2 cm	10—20 %	11—15 days	6 months
2. Heterozygosity and dominance deviation	Low	Medium	Medium	None	Medium	None	None	None
3. Cross of special performance	Smallest by selfing	No difference	Higher with 'E'	Best size with 'F'	Largest with 'F'	Smallest by selfing	Longest by selfing	Longest with 'F'
4. Alleles responsible for increase	Dominant	Dominant	Dominant	Codominant	Dominant	Codominant	Codominant	Codominant
5. Maternal inheritance	None	None	None	None	None	None	None	None
Cv. 'Ettinger'								
1. Cultivar performance	Tall	Medium	Medium	310 gr	2.1 cm	10—20 %	6—10 days	2 months
2. Heterozygosity and dominance deviation	High	High	High	High	High	None	High	High
3. Cross of special performance	Smallest by selfing	Highest with 'H'	Highest with 'H'	No difference	No difference	Smallest by selfing	Longest by selfing	Longest with 'T'
4. Alleles responsible for increase	Dominant	Dominant	Dominant	Dominant	Dominant	Codominant	Recessive	Recessive
5. Maternal inheritance	In 'R' × 'E'	None	None	in 'E' × 'R'	None	None	None	None

Cv. 'Tova'												
1. Cultivar performance	Short	Medium	Dense	250 gr	2.2 cm	16—20 %	11—15 days	2 months				
2. Heterozygosity and dominance deviation	Low	High	Low	None	Low	None	None	None				
3. Cross of special performance	No difference	Highest with 'F'	Highest with 'F'	Best size with 'F'	Largest with 'F'	No difference	No difference	Longest with 'E'				
4. Alleles responsible for increase	Recessive	Dominant	Dominant	Codominant	Dominant	Codominant	Codominant	Codominant				
5. Maternal inheritance	In 'T' × 'H'	None	None	None	None	None	None	None				
Cv. 'Rosh Hanikra'												
1. Cultivar performance	Short	Light	Dense	150 gr	1.2 cm	26—30 %	6—10 days	1 month				
2. Heterozygosity and dominance deviation	High	None	High	None	None	Low	None	Low				
3. Cross of special performance	No difference	No difference	High with 'E'	No difference	No difference	No difference	No difference	No difference				
4. Alleles responsible for increase	Dominant	Codominant	Dominant	Codominant	Codominant	Dominant	Codominant	Recessive				
5. Maternal inheritance	In 'R' × 'E'	None	None	In 'E' × 'R'	None	None	None	None				

ly significant. Additive genetic variance is low for fruit weight and fruit density, medium for tree size, inflorescence length and seed size, large for softening time and harvest duration and largest for flowering intensity.

Non-additive genetic variance was presumed to exist from the deviation between the mean of selfing progeny and their parents (Table 2) as well as from the variance of the interaction: males × females (FALCONER 1960, HILLEL et al. 1972, MATHER and JINKS 1971). High levels of C.V. of the variances within crosses and within selfings were used to support the presence of the variance although part of the C.V. could result from non-genetic factors. Tree size, flowering intensity, fruit density, and inflorescence length, have high levels of non-additive genetic variance. In all fruit traits, namely, fruit weight, seed size and softening time, non-additive genetic variance was absent or very low. In all traits, except probably seed size, 'Ettinger' has abundant non-additive genetic variance.

The environmental variance was probably high in fruit weight, inflorescence length, and softening time. This finding was deduced from the low coefficient of variation within selfings of this trait, together with the indication for low non-additive genetic variance mentioned above.

Genetic profile of cultivars (Table 7)

Heterozygosity and dominance deviation: Heterozygosity level and dominance deviation which are confounded in the present study were assessed from the statistically significant difference between each selfing progeny mean and its parents' performance (Table 2), and from the interaction between females and males (Table 4). Tree size, flowering intensity, fruit density, and inflorescence length were characterized by a high level of heterozygosity and/or a high level of dominance deviation. The fruit traits: fruit weight, seed size, and softening time are of low heterozygosity or codominance mode of inheritance in most cultivars. In no trait was there a strong indication for low level of heterozygosity.

Cross of special performance: All crosses (including selfings) were compared in each trait within each cultivar to identify the best combination producing the optimal horticultural performance.

Alleles responsible for increased performance: In cases where the deviation between the selfing progeny mean and cultivar performance (Table 2) was statistically significant, a decrease in performance of the selfing progeny was interpreted as dominance of the increasing alleles at most loci which control the trait and vice versa. In most cases the increasing alleles were found to be dominant. Only in the case of softening time and harvest duration in some cultivars ('Ettinger' and 'Rosh-Hanikra') were the increasing alleles recessive.

Maternal inheritance: Maternal inheritance was considered to be apparent in crosses where the interaction Reciprocals \times Crosses was statistically significant. We used this criterion since comparison between the upper and lower triangles of the "set of crosses" table could be not informative due to possible maternal effects of opposite direction. In four crosses reciprocal comparisons were available for all traits: 'Tova' \times 'Fuerte', 'Tova' \times 'Ettinger', 'Rosh-Hanikra' \times 'Ettinger', and 'Horshim' \times 'Tova'. In most traits, maternal inheritance was not observed except for tree size and possibly in fruit weight in the cross 'Ettinger' \times 'Rosh-Hanikra' (Table 4).

In tree size, maternal inheritance was apparent in two crosses: (i) 'Rosh-Hanikra' \times 'Ettinger' (51 seedlings), tree size was larger by .8 scale grade than the reciprocal cross (20 seedlings, $P = 0.007$); and (ii) in 'Horshim' \times 'Tova' (240 seedlings), tree size is smaller by .7 scale level than the reciprocal cross (31 seedlings, $P = 0.002$). In fruit weight, the mean of the cross 'Rosh-Hanikra' \times 'Ettinger' is 65 gr. smaller than the mean of the reciprocal cross ($P = 0.005$).

Discussion

The lack of a suitable model for analyzing the results of this avocado breeding project allows the genetic characterization to be expressed in qualitative rather than quantitative terms.

All traits analyzed, except fruit weight were evaluated as scale measurements. It is important to emphasize that five of them: fruit weight, inflorescence length, seed size, softening time, and harvest duration were rated objectively by weighing (gr) or measuring (cm and days). The other three: tree size, flowering intensity, and fruit density, were carefully

scored by an avocado expert who evaluated the seedlings over 2—5 years of yielding and used parent cultivars for reference.

In the present report, we have shown that genetic variance (additive and non-additive) is pronounced in the avocado cultivars analyzed regarding all the quantitative traits analyzed. 'Ettinger' which was represented with the largest progeny number is distinguished by large non-additive genetic variance and high heterozygosity level for all traits. However, in some of the other cultivars there are indications of low heterozygosity level in some traits and low non-additive genetic variance. This finding may be a reflection of population structure or the result of being based on relatively small progeny.

Choosing parents for crosses in a breeding project should be based on the level of additive and non-additive genetic variance in the relevant traits. In cases of high additive variance, parents should be chosen on the basis of their phenotypes while in cases of high non-additive genetic variance, parent should not be chosen entirely according to their phenotypes. Crosses in the latter case should be aimed towards increasing the genetic variance in the progeny, hoping to create optimal gene combinations.

Based on the results reported in the present study, we can draw some practical breeding conclusions regarding the following avocado traits:

Tree size: Non-additive genetic variance is apparent. Therefore, trees of small size can be recovered among progeny of both selfings and crosses between cultivars. The selfing progeny of the tall 'Ettinger' gives the smallest tree size. Note that 'Tova' progeny (selfings as well as hybrids), tend to have a larger tree size than the cultivar itself.

Flowering intensity: The genetic variance is relatively high and significant, including both additive and non-additive components. Although 'Fuerte' has the highest flowering intensity, the mean of 'Fuerte's' progeny is similar to the progeny mean of other cultivars. Note that in all crosses, flowering intensity in each parent cultivar is greater than its mean progeny performance. Only the progeny of 'Rosh-Hanikra' resembled the cultivar performance. Selection among progeny of crosses between cultivars might yield genotypes of high flowering intensity.

Fruit density: The mean progeny performance of all cultivar crosses is lower than the fruit density of the cultivar. Due to large non-additive genetic variance, genotypes of higher fruit density might be obtained by selection among progeny of crosses between cultivars.

Fruit weight: Genetic improvement for fruit weight based on the cultivars analyzed in this research seems to be quite difficult, due to low additive and non-additive genetic variance. Since increasing alleles are probably dominant, screening among selfing progeny is advised only when decrease of fruit weight is the breeding objective. The fruit traits — seed size, softening time, and harvest duration have low non-additive genetic variance and noticeable additive genetic variance. Therefore screening should be done among progeny of specific cultivars (Table 6).

Seed size: 'Rosh-Hanikra' and its progeny have the largest seed size. 'Hass' progeny have a somewhat smaller seed size than the other cultivars, although the difference was not significant. Since the genetic variance of this trait is limited, small seed size is a breeding objective which is quite difficult to achieve.

Softening time: 'Rosh-Hanikra' and its selfing progeny have the shortest softening time, while the selfing progeny of 'Fuerte' and 'Hass' have the longest. Given these differences are of genetic origin, it is advisable to use 'Hass' and 'Fuerte' as parents to achieve long softening time.

Harvest duration: Selfing progeny of 'Ettinger' have the longest harvest duration, although the harvest duration of 'Ettinger' is limited compared with that of 'Fuerte' and 'Hass'. The dominant alleles seem to extend the harvest duration. Among the various orders, the progeny of 'Tova' have the longest duration. The variance within selfings is low, indicating small environmental effects.

Genetic analysis of fruit trees and especially avocado is quite limited, due mainly to the long juvenile period and the tree size. The present work suggests a biometrical analysis from which some preliminary conclusions could be drawn. It is important to note that availability of molecular markers such as RFLPs (BECKMANN and SOLLER 1983) and DNA fingerprint (DALLAS 1988, and our unpublished results) will probably revolutionize fruit tree breeding. Saturation of the tree genome with

such polymorphic markers will facilitate the establishment of genetic linkage between these markers and major genes controlling agriculturally-important quantitative traits. The breeder will overcome the above-mentioned barriers by assessing the molecular markers at the plantlet stage, thus being able to predict the mature tree performance.

Zusammenfassung

Quantitativ-genetische Analyse von Eigenschaften bei Stämmen und Sorten von Avocado

Folgende 8 Merkmale von Avocadostämmen und -sorten wurden einer quantitativ-genetischen Analyse unterzogen: Baumgröße, Blütenzahl, Dichte des Fruchtbehangs, Fruchtgewicht, Länge des Blütenstandes, Samengewicht, Nachreifezeit und Dauer der Ernteperiode. Für die meisten Eigenschaften konnte ausgeprägte genetische Variation beobachtet werden. Für jedes einzelne Merkmal wurden mehrere Parameter geschätzt. Das Ausmaß der Heterozygotie und die Dominanzabweichung waren für die Baumgröße sehr hoch und nahmen über die anderen Merkmale bis zum Samen- und Fruchtgewicht ab, für die nur geringe Werte ermittelt wurden. In den meisten Fällen erwiesen sich die für eine erhöhte Leistung verantwortlichen Allele als dominant, wobei in der Regel die Dominanz in gleicher Richtung verlief. Die Sortenunterschiede der Eigenschaften, die von den gleichen Allelen gesteuert werden, variierten von sehr stark bei der Baumgröße bis zu fast nicht mehr bemerkbar bei dem Merkmal Dauer der Ernteperiode. Das Niveau der additiven genetischen Varianz war bei den meisten Merkmalen hoch bis mittelhoch. Beim Fruchtgewicht und bei der Fruchtbehangsdichte wurde jedoch eine niedrige additive Varianz festgestellt. Bei 4 Eigenschaften war die nicht-additive Varianz groß, während sie sich bei den anderen 4 Merkmalen als sehr gering erwies. Für das Merkmal Baumgröße wurden Anzeichen einer mütterlichen Vererbung gefunden. Bei den Sorten 'Fuerte', 'Hass', 'Ettinger', 'Tova' und 'Rosh-Hanikra' wurden die Merkmale jeweils gesondert analysiert, um sowohl die oben erwähnten Parameter zu schätzen als auch um Kombinationen mit besonderer Leistung bestimmen zu kön-

nen. Es werden praktische Schlußfolgerungen gezogen, die helfen sollen, eine für die Avocado-Züchtung wirksamere Auswahl der Kreuzungseltern zu ermöglichen.

We thank the staff of the Akko Horticultural Experiment Station, and especially D. N. ZAMET, for his highly competent assistance. The Israel Fruit Board provided financial support for this research. We highly appreciate the critical reading of Prof. B. BERGH, Dr. A. CAHANER, and Prof. A. ASHRI.

References

- BECKMANN, J. S., and M. SOLLER, 1983: Restriction fragment length polymorphism in genetic improvement: Methodologies, mapping and costs. *Theor. Appl. Genet.* **67**, 35—43.
- BERGH, B. O., 1969: Avocado. In: FERWERDA, F. P., and F. DE WIT, *Outlines of Perennial Crop Breeding in the Tropics*. Publishers Veenman, B. Zonen, N.V. Wageningen, The Netherlands, pp. 23—51.
- DALLAS, F. J., 1988: Detection of DNA fingerprints of cultivated rice by hybridization with a human minisatellite probe. *Proc. Nat. Acad. Sci.* **85**, 6831—6833.
- DEGANI, C., and S. GAZIT, 1984: Selfed and crossed proportions of avocado progenies produced by caged pairs of complementary cultivars. *HortScience* **19**, 258—260.
- —, A. GOLDRING, S. GAZIT, and U. LAVI, 1986: Genetic selection during the abscission of avocado fruitlets. *HortScience* **21**, 1187.
- FALCONER, D. S., 1960: *Introduction to Quantitative Genetics*. Oliver and Boyd Edinburgh.
- GARDNER, C. O., and S. A. EBERHART, 1966: Analysis and interpretation of the variety cross diallel and related populations. *Biometrics* **22**, 463—493.
- GOLDRING, A., D. ZAMIR, and C. DEGANI, 1985: Duplicated phosphoglucose isomerase genes in avocado. *Theor. Appl. Genet.* **71**, 491—494.
- —, S. GAZIT, and C. DEGANI, 1987: Isozyme analysis of mature avocado embryos to determine outcrossing rate in a 'Hass' plot. *J. Amer. Soc. Hort. Sci.* **112**, 389—392.
- GRIFFING, B., 1956: A generalized treatment of the use of diallel crosses in quantitative inheritance. *Heredity* **10**, 31—50.
- GRISWOLD, H. B., 1945: The 'Hass' avocado. *Yb. Calif. Avocado Soc.* pp. 27—31.
- HANSCH, P. E., V. BERES, and R. M. BROOKS, 1966: Heritability and genetic correlation in the sweet cherry. *Proc. Amer. Soc. Hort. Sci.* **88**, 173—183.
- —, — —, and H. I. FORDE, 1972a: Estimates of quantitative genetic properties of walnut and their implications for cultivar improvement. *J. Amer. Soc. Hort. Sci.* **97**, 279—285.
- —, C. O. HESSE, and V. BERES, 1972b: Estimates of genetic and environmental effects on several traits in peach. *J. Amer. Soc. Hort. Sci.* **97**, 76—79.
- HAYMAN, B. I., 1960: The theory and analysis of diallel crosses. *Genetics* **45**, 155—172.
- HILLEL, J., G. SIMCHEN, and J. L. JINKS, 1972: Generalized selfing series as an experimental design. *Theor. Pop. Biol.* **3**, 466—490.
- JINKS, J. L., 1954: The analysis of continuous variation in a diallel cross of *Nicotiana rustica* varieties. *Genetics* **36**, 767—788.
- LAHAV, E., D. ZAMET, S. GAZIT, and U. LAVI, 1986: Girdling as a means of shortening the juvenile period of avocado seedlings. *HortScience* **21**, 1038—1039.
- MATHER, K., and J. L. JINKS, 1971: *Biometrical Genetics*. Cornell University Press, Ithaca, N.Y. pp. 83—96.
- ROUNDS, M. B., 1946: The 'Fuerte' avocado. *Yb. Calif. Avocado Soc.* pp. 54—56.
- SLOR, E., and R. SPODHEIM, 1971, 1972: Selection of avocado varieties in Israel. *Yb. Calif. Avocado Soc.* **55**, 156—157.
- STOREY, W. B., and B. O. BERGH, 1963: Some interesting early maturity avocados. *Yb. Calif. Avocado Soc.* **47**, 87—101.
- TORRES, A. M., U. DIEDENHOFEN, B. O. BERGH, and R. KNIGHT, 1978: Enzyme polymorphisms as genetic markers in the avocado. *Am. J. Bot.* **65**, 134—139.

Authors' addresses: U. LAVI, E. LAHAV, A. GENIZI, C. DEGANI, Agricultural Research Organization P.O. Box 6, Bet-Dagan 50-250; S. GAZIT, J. HILLEL, The Hebrew University, Faculty of Agriculture, P.O. Box 12, Rehovot 76-100 (Israel).

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.