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Genetics of Skin Color, Flowering Group, and Anise Scent in Avocado

U. Lavi, E. Lahav, C. Degani, and S. Gazit

The genetic information available on subtropical fruit trees in general, and on avocado in particular, is quite limited. The genetics of skin color, flowering group, and anise scent in avocado (*Persea americana* Mill) have been studied. Progeny distribution of seedlings originating from crosses between all possible phenotypes in the above-mentioned three traits have been presented. The results rule out a model of one or two loci for any of these traits. It is quite probable that these traits are coded by several loci having several alleles in each locus. The various phenotypes probably result from various heterozygous combinations in several loci. This knowledge is relevant for both the genetics and breeding of avocado.

Avocado (*Persea americana* Mill) is a diploid having $2n = 24$ chromosomes. Fruit skin color in most commercial cultivars is green or purple including light and dark hues of both colors. Flower groups are classified according to Stout (1923) into A and B. Group A cultivars exhibit the first

Table 1. Progeny distribution in the fruit skin color trait

Parent phenotype	Progeny phenotype			
	Green	Purple	No. of families	Green/purple
Green × green (selfings)	121	14	9	8.6
Green × green (crosses between cultivars)	273	20	19	13.6
Green × green (total)	394	34	28	11.6
Green × purple	10	4	1	2.5
Purple × green	71	48	3	1.5
Purple × purple (selfings)	5	4	1	1.2
Total	480	90	33	5.3
Reciprocal crosses				
Green × green (Ettinger × Tova)	37	1	1	37.0
Green × green (Tova × Ettinger)	102	3	1	34.0
Green × purple (Ettinger × Rosh-Hanikra II)	10	4	1	2.5
Purple × green (Rosh-Hanikra II × Ettinger)	13	12	1	1.1

opening of functional female flowers during the morning hours. These flowers close near midday and reopen in the functional male stage the following afternoon. In B cultivars, the female opening occurs in the afternoon, and the male (second) opening occurs the following morning. Anise scent in the leaf is present in the Mexican race and absent from Guatemalan and West Indian races.

Bergh (1975) reported several studies aimed at understanding the genetics of several traits. Skin color was concluded to be inherited as a typical polygenic character, and flowering group was affected by segregation at a number of loci. Data concerning the genetics of leaf anise scent, skin color, or flowering group traits were not reported. This article reports the genetics of these traits.

Materials and Methods

The parent and progeny plots were located at the Akko Experiment Station in Israel. We collected seed from crosses and selfings by caging trees under a net, using bees as the pollen vector (Lavi et al. 1991). The harvested seed was sown in a nursery, and one year later we transplanted the seedlings into breeding plots. The progeny of each cage were planted randomly in one block. Progenies of different cages were randomized in the orchard. The juvenile period was shortened by the use of autumn girdling (Lahav et al. 1986).

We recorded fruit skin color, flowering group, and leaf anise scent traits over a 2-year period. Skin color was classified as green or purple, flowering group as A or B, and leaf anise scent as present or absent.

The cultivars used were Anaheim, Fuerte, Irving, Nabal, Regina, Rincon, Wurtz

(Rounds 1950), Ettinger (Storey and Bergh 1963), Hass (Griswold 1945), Pinkerton, Reed (Platt 1976), Rosh-Hanikra II (Lavi et al. 1991), Horshim, and Tova (Slor and Spodheim 1971–1972).

To distinguish between hybrids and self-pollinated seedlings, we characterized the progeny by isozyme analyses of leaf tissue (Degani and Gazit 1984). However we cannot rule out the possibility that a few individuals were wrongly classified.

The number of observations in the various crosses varied from four to 387, for a total of 1,688 seedlings.

Significance was determined by the chi-square tests.

Results

Fruit Skin Color

There were nine selfing crosses of the green × green type. The ratio of green/purple among the progeny varied from 3–20 to one, (3–20:1) and on the average was 8.6. There were also 19 crosses between various cultivars with green skin color. The ratio of green/purple among these progeny varied from 2–37 to one (2–37:1) and on the average was 13.6. No significant differences were found between the two ratios (8.6 and 13.6) (Table 1).

There was only one cross of green × purple, resulting in 10 green and four purple progeny. There were three crosses of the purple × green type, resulting in a progeny distribution ranging from 1.1:1 to 2.2:1 green to purple with an average of 1.5:1. One selfing represented the purple × purple cross, resulting in a progeny distribution of 1.2:1. The ratio of green/purple in selfings green × green (8.6) was significantly different ($P = .013$) from the same ratio for purple × purple selfings (1.2).

Table 2. Progeny distribution in the flowering group trait

Parent phenotype	Progeny phenotype				N.S.
	B	A	No. of families	B/A	
A × A (selfings)	11	9	4	1.2	
A × B	148	111	7	1.3	
B × A	32	17	6	1.9	
B × B (selfings)	35	13	2	2.7	
Total	226	150	19	1.5	N.S.
Reciprocal crosses					
A × B (Tova × Ettinger)	54	38	1	1.4	} N.S.
B × A (Ettinger × Tova)	8	8	1	1.0	
A × B (Rosh Hanikra II × Ettinger)	15	1	1	15.0	} N.S.
B × A (Ettinger × Rosh-Hanikra II)	9	3	1	3.0	

Table 3. Progeny distribution in the leaf anise scent trait

Parent phenotype	Progeny phenotype		No. of families	No anise/anise	
	Anise	No anise			
Anise × anise (selfings)	29	225	3	7.8	} P = .001
Anise × anise (crosses between cultivars)	24	57	3	2.4	
Anise × anise (total)	53	282	6	5.3	
Anise × no anise	11	59	4	5.4	} P = .001
No anise × anise	119	555	7	4.7	
No anise × no anise (selfings)	17	257	4	15.1	
No anise × no anise (crosses between cultivars)	65	270	9	4.2	
No anise × no anise (total)	82	527	13	6.3	
Total	265	1,423	30	5.4	
Reciprocal crosses					
Anise × anise (Ettinger × Rosh-Hanikra II)	11	9	1	0.8	} P = .02
Anise × anise (Rosh-Hanikra II × Ettinger)	13	35	1	2.7	
Anise × no anise (Ettinger × Tova)	7	55	1	7.9	} P = .0045
No anise × anise (Tova × Ettinger)	102	285	1	2.8	
No anise × no anise (Horshim × Tova)	49	191	1	3.9	} N.S.
No anise × no anise (Tova × Horshim)	6	25	1	4.2	

Flowering Group

There were four crosses of the A × A type, all of them selfings (Table 2). The ratio of B/A among the progeny varied from 4:1 to 1:3, the average being 1.2:1. There were seven crosses of the A × B type, and the ratio of B/A among the progeny varied from 1:1 to 15:1, the average being 1.3:1. There were six crosses of the B × A type, and the ratio of B/A among the progeny varied from 1:1 to 3.5:1, the average being 1.9:1.

There were two crosses of the B × B type, and the ratio B/A among the progeny varied from 2.1:1 to 4:1, the average being 2.7. No significant differences were detected between the crosses.

Leaf Anise Scent

There were six crosses in which cultivars having anise scent (+) were crossed with phenotypically similar cultivars (Table 3). Three of these were selfs in which the ratio of progeny with no anise scent to those with anise scent (-/+) varied from 1:1 to

11:1, the average being 7.8. In crosses between cultivars, the ratio ranged from 13:1 to 1:1, the average being 2.4. There was a significant statistical difference between selfing and nonselving crosses (P = .001).

Four crosses between cultivars with anise scent (+) and cultivars without (-) expressed ratios of -/+ among progeny from 3:1 to 8:1, the average being 5.4:1. Seven crosses of the -/+ type had ratios of -/+ among progeny that varied from 4:1 to 48:1, the average being 4.7:1. No significant differences were detected between the above mentioned crosses.

There were 13 crosses in which cultivars having no anise scent (-) were crossed with phenotypically similar cultivars. Among these, four were selfings having a -/+ ratio varying from 1:1 to 85:1, the average being 15.1:1. The ratio of -/+ among progeny originating from the nine crosses between various cultivars having the (-) phenotype varied from 3.9:1 to 10:1, the average being 4.2:1. A significant

statistical difference was detected between selfing and nonselving crosses (P = .001), as well as between anise × anise (selfings) and no anise × no anise (selfings) (P = .003).

Discussion

The genetic knowledge presented here is applicable to breeding programs in which these traits are either the breeding target or markers.

We analyzed the progeny of four classes of crosses for each trait—namely, X × X; Y × Y; Y × X; and X × Y (where X and Y represented the alternative phenotypes of each trait). In all three traits, in all four types of crosses, the average X/Y ratio among progeny was one, or much higher than one, with wide variation in the ratio between the different crosses. It is interesting, however, that selfings of either phenotype—that is, skin color green × green or purple × purple; flowering group B × B or A × A; and no anise × no anise, as well as anise × anise scent—resulted in more progeny of the first phenotype (green, flowering group B, and no anise, respectively). These results (Tables 1–3) rule out the possibility of a single gene coding for these traits.

As for a more specific genetic explanation, we based our suggestion on prior knowledge (Lavi et al. 1991) that described high levels of heterozygosity as well as a pronounced nonadditive variance component in several multigenic avocado traits. We have no evidence of the differential penetrance of different genes and alleles, nor do we have evidence of lethal effects. Therefore, we would like to suggest that our results can be explained by the assumption that the traits are coded by several loci with several alleles in each locus, while the various phenotypes result from various heterozygote combinations. Because of insufficient data, we do not intend to suggest a detailed model for each trait. However, in general, the genetic explanation for the inheritance of these traits could be based on a threshold value beyond which the phenotype shifts from one phase to the other, as has been suggested for cleft lip and other traits (Carter 1969).

From the Department of Fruit Tree Breeding and Genetics (Lavi) and the Department of Fruit Trees (Lahav and Degani), Agricultural Research Organization, P.O.B. 6, Bet Dagan 50250, Israel, and the Department of Pomology, The Hebrew University, Faculty of Agriculture, Rehovot, Israel (Gazit). This is a contribution from the Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel. No. 3222-E, 1991 series. We would like to express our gratitude to the Akko and Bet Dagan Horticultural Experiment Stations and, in particular, to

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