Cytogenetical Studies in the Genus *Persea* (Lauraceae)

II. A Comparative Morphological Study on 61 Avocado Strains¹⁾

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In order to elucidate the variation in *Persea americana* complex (avocado) and to know the genetical relationships among strains and among races, morphological characters of 61 different avocado strains were analyzed statistically.

The analyses of variance on 30 morphological characters at four-months-old seedling stage so far recorded in these materials clearly demonstrated a great genetic diversity of the germ plasms. The great diversity agrees well with earlier studies. The analyses of variance also showed that 15 out of the 30 characters examined were useful in characterizing, at least, strains, and that 14 out of the 15 such characters were also useful to distinguish races of *P. americana*.

When six scattering diagrams were drawn based on six pairs of two characters which showed high F values among races and exhibited different extents of correlation to each other, it was found that Mexican-race strains tended to have smaller sizes than Guatemalan- or West Indian-race strains. Closer relationships were observed in the scattering diagrams between Guatemalan- and West Indian-race strains. Thus the genetic relatedness between Mexican and other races was concluded to be less closer, as compared with that between Guatemalan and West Indian races.

Introduction

The family Lauraceae distributes in the tropical to temperate regions in the world, and the four major genera of the family in the New World are *Ocotea*, *Nectandra*, *Phoebe* and *Persea* (ALLEN 1945). In the genus *Persea*, two species, *P. americana* Mill. and *P. schiedeana* Nees, are economically important because of their buttery fleshed fruits known commonly as avocado fruits, the former being more common (KOOP 1966) and the latter being rather local but known as "Chinini" (GARCÍA 1972). Some archeological evidences found in the Tehuacan Valley in Puebla, Mexico, suggested that avocado had already been cultivated on the nearby stream sides in 6500 B.C. (SMITH 1966).

In Mexico, *P. americana* distributes widely from the Pacific coast to the coast of the Gulf of Mexico and from southern to northeastern states. In Veracruz, this species grows together with *P. schiedeana* and some intermediate forms between them are observed. *Persea americana* grows together also with a few wild *Persea* species in some areas.

Persea americana has been taxonomically subjected to some discussion. This species, once classified into two different species (*P. americana* and *P. drymifolia*) or into three

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different species (above two and *P. nubigena*), is now treated as one species but with three different botanical varieties, *P. americana* var. *americana*, var. *drymifolia*, and var. *nubigena* (Koop 1966). From horticultural point of view, on the other hand, POPENOE (1920) identified three races in avocado's group, namely, Guatemalan, West Indian and Mexican races. HODGSON (1950) regarded the Guatemalan and West Indian races as *P. americana* and the Mexican race as *P. drymifolia*. According to the present taxonomical situation, the former two races are included in *P. americana* var. *americana* and the third race in *P. americana* var. *drymifolia*. However, because of the occurrence of natural hybridization, intermediate forms which can not be classified into any of the races with POPENOE's keys are observed. ANDERSON (1950) demonstrated a part of the variation of the *P. americana* complex, using a pictorialized scatter diagram of a few leaf characters. RHODES *et al.* (1971), employing a method of numerical taxonomy, also showed the phenotypic diversity of the complex, but they did not arrive to any clear conclusion.

The present study aims to elucidate the variation in the *P. americana* complex with statistical methods, and to obtain more information in order to clarify the relationships among the three races of the taxonomical complex.

Materials and Methods

The materials examined in the present study were 61 strains of *P. americana* as representatives of different geographical origins and of different races. Table 1 lists those avocado's strains examined.

Seeds were sown in wooden flats (63×38×15 cm) filled with sterilized soil, after remov-

Table 1. Strain numbers, cultivar names, origins, numbers of seedlings and races of *P. americana* materials used in the present study

Strain number ¹⁾	Cultivar	Origin ²⁾	Number of seedlings	Race ³⁾
1	unnamed	Uruapan, Mich.	9	Mex.
2	"	Xalapa, Ver.	4	"
3	"	Atlixco, Pue.	8	"
4	"	Zitácuaro, Mich.	4	"
5	Fuerte	Uruapan, Mich.	3	Guat. ⁴⁾
6	unnamed	Atlixco, Pue.	10	Mex.
7	"	Zitácuaro, Mich.	5	"
8	"	"	9	"
9	Fuerte	Uruapan, Mich.	8	Guat. ⁴⁾
10	unnamed	Atlixco, Pue.	4	Mex.
11	"	Texcoco, Méx.	4	"
12	"	Tehuacán, Pue.	3	"
13	"	Orizaba, Ver.	5	"
14	"	Tehuacán, Pue.	6	"
15	"	Jalatzingo, Pue.	4	"
16	Fuerte	Atlixco, Pue.	4	Guat. ⁴⁾
17	unnamed	Córdoba, Ver.	3	Mex.
18	"	Xico, Ver.	3	"
19	"	Zitácuaro, Mich.	6	"

Strain number ¹⁾	Cultivar	Origin ²⁾	Number of seedlings	Race ³⁾
20	unnamed	Atlixco, Pue.	4	Mex.
21	"	Pachuca, Hgo.	5	"
22	"	Córdoba, Ver.	5	"
23	"	Zitácuaro, Mich.	5	"
24	Selección	Zitacuaretiro, Mich.	8	"
25	"	"	12	"
26	unnamed	Tehuacán, Pue.	4	"
27	"	Uruapan, Mich.	10	"
28	"	Venados, Hgo.	6	"
29	"	Uruapan, Mich.	6	"
30	"	Atlixco, Pue.	4	"
31	"	San Juan Tezontla, Méx.	8	"
32	"	Córdoba, Ver.	4	"
33	"	Maltrata, Ver.	2	W.I.
34	"	San Juan Tezontla, Méx.	4	Mex.
35	"	Maltrata, Ver.	4	"
36	"	Xalapa, Ver.	7	"
37	López	Tacámbaro, Mich.	7	"
38	unnamed	Tecario, Mich.	7	"
39	Blanco	Tacámbaro, Mich.	7	"
40	unnamed	Las Marias, Mich.	9	"
41	"	San Rafael, Mich.	17	"
42	"	Tecario, Mich.	8	"
43	"	Cuautla, Mor.	4	"
44	"	Tacámbaro, Mich.	4	"
45	"	Caracuaro, Mich.	9	"
46	"	Cutzarandiro, Mich.	9	"
47	"	El Rincon, Mich.	12	"
48	"	Jometepepec, Mor.	5	"
49	"	San Miguel Taixpan, Méx.	4	"
50	"	San José Buenavista, Mich.	10	"
51	"	Pinos Altos, Mich.	8	"
52	"	Mérida, Yuc.	6	W.I.
53	"	Hawaii, USA	7	"
54	"	"	5	"
55	Beardsle	"	6	" ⁵⁾
56	Hashimoto	"	3	Guat.
57	Fuerte	"	7	" ⁴⁾
58	Grypina 12	"	5	" ⁵⁾
59	Hayes	"	6	"
60	Itzamna	"	4	"
61	Saint Claire	"	2	W.I.

1) Strains nos. 53 to 61 were kindly supplied by Prof. R. A. HAMILTON of University of Hawaii, Manoa, Hawaii, USA. Other strains from Mexico were collected by the authors.

2) Hgo.=Hidalgo, Méx.=México, Mich.=Michoacan, Mor.=Morelos, Pue.=Puebla, Ver.=Veracruz, and Yuc.=Yucatan.

3) Guat.=Guatemalan race, Mex.=Mexican race, and W.I.=West Indian race.

4) Said to be of a hybrid origin between Guatemalan and Mexican races.

5) Considered to be hybrids between Guatemalan and West Indian races.

Table 2. Characters examined in the present study

01	Average stem length between leaves (obtained by dividing seedling height by number of leaves).
02	Leaf color [(1) <i>light</i> , (2) <i>medium</i> , and (3) <i>dark green</i>].
03	Color of young leaf [(1) <i>green</i> , (2) <i>bronze</i> , and (3) <i>red</i>].
04	Aroma of crushed leaf [(1) <i>none</i> , (2) <i>weak</i> , and (3) <i>strong</i>].
05	Leaf shape [(1) <i>ovate</i> , (2) <i>elliptic</i> , and (3) <i>acute</i>].
06	Leaf apex [(1) <i>acuminate</i> , (2) <i>subacuminate</i> , and (3) <i>acute</i>].
07	Length of leaf blade.
08	Median width of leaf blade.
09	Petiole length.
10	Petiole sulcus [(1) <i>incomplete</i> , and (2) <i>complete</i>].
11	Color of midrib hairs [(1) <i>white</i> , and (2) <i>golden</i>].
12	Length of midrib hairs (100 hairs were measured in the central portion of the leaf).
13	Color of stem [(1) <i>green</i> , (2) <i>bronze</i> , and (3) <i>red</i>].
14	Median cotyledon width.
15	Median cotyledon length.
16	Stem diameter at bottom.
17	Leaf area.
18	Leaf blade with granular waxy secretion on under-surface [(1) <i>yes</i> , and (2) <i>no</i>].
19	Height of stem to the first leaf.
20	Height of stem to the second leaf.
21	Height of stem to the third leaf.
22	Height of stem to the fourth leaf.
23	Occurrence of twin seedlings (two or more seedlings from a seeds) [(1) <i>yes</i> , and (2) <i>no</i>].
24	Number of stomata per unit area (0.25 mm×0.17 mm) (about one square centimeter of leaf blade was obtained from the central region of leaf, and number of stomata was counted from the impression made by the SUMP method of the Suzuki's Universal Micro Printing, Tokyo).
25	Stomatal length (guard cells).
26	Stomatal width (guard cells).
27	Number of leaves.
28	Angle of divergence of the primary nerves of leaves.
29	Color of petiole [(1) <i>green</i> , (2) <i>bronze</i> , and (3) <i>red</i>].
30	Seedling height.

ing the seed coat and cutting about upper one third and lower 2 to 3mm of the cotyledons of the plumule. When seedlings grew 10 to 15cm in height, they were transplanted in the bench of the air-conditioned greenhouse, in which temperature was kept at $20\pm 2^{\circ}\text{C}$ and the light period was maintained to be about 16hr. They were planted randomly 10 cm apart from each other in a row, allowing 15cm distance between rows. The seedlings were fertilized twice a week with a nutritional solution ("Hyponex" of the Hydroponic Chemical Co. Inc., USA).

When the seedlings became four months old, 30 characters as listed in Table 2 were investigated. The leaf characters were determined on the fifth leaf from the base. The data of such morphological characters were analyzed employing the method of analysis of variance, in order to compare strains or races of *P. americana*. The correlations between characters were also studied, and the scattering diagrams of selected six pairs of characters were drawn to see if the materials examined could be separated into some groups.

Results

The morphological characters recorded varied greatly even within strains. The analysis

Table 3. Results of analyses of variance on 15 characters of 61 *P. americana* strains. Mean squares between strains and within strains (errors) are given

Character	Source of variation	
	Between strains d. f. = 60	Within strains (errors) d. f. = 300
01 Average stem length between leaves	0.9680**	0.2352
07 Length of leaf blade	33.6618**	6.1724
08 Median width of leaf blade	5.5000**	1.0071
09 Petiole length	60.8873**	16.5793
14 Median cotyledon width	550.0767**	9.5189
15 Median cotyledon length	790.0507**	11.2899
16 Stem diameter at bottom	7.3343**	2.5343
17 Leaf area	1460.7615**	264.6858
19 Height of stem to 1st leaf	93.1202**	14.3734
20 Height of stem to 2nd leaf	116.1285**	16.8253
21 Height of stem to 3rd leaf	106.4360**	22.1042
22 Height of stem to 4th leaf	160.7613**	38.5772
27 Number of leaves	97.9253**	31.0149
28 Angle of divergence	133.9650**	9.1061
30 Seedling height	3237.9508**	512.2849

** Significant at 1% level.

Table 4. Results of analyses of variance on 15 characters of 61 strains belonging to three races of avocado (*P. americana*). Mean squares attributable to races, strains and plants, and F values for races and strains are given

Character	Source of variation				
	Races d. f. = 2		Strains d. f. = 58		Plants d. f. = 300
	M. S.	F	M. S.	F	M. S.
Av. stem length btw. leaves	9.53	14.01**	0.68	2.83**	0.24
Length of leaf blade	328.10	14.80**	22.17	3.59**	6.17
Median width of leaf blade	48.53	13.99**	3.47	3.44**	1.01
Petiole length	615.80	12.80**	48.12	2.90**	16.58
Median cotyledon width	4207.34	10.30**	408.33	42.89**	9.52
Median cotyledon length	4030.46	5.72**	704.13	62.37**	11.29
Stem diameter at bottom	30.14	4.96*	6.08	2.40**	2.53
Leaf area	16205.02	35.36**	458.28	1.73**	264.69
Height of stem to 1st leaf	1764.16	48.44**	36.42	2.53**	14.37
Height of stem to 2nd leaf	2205.00	53.99**	40.84	2.43**	16.83
Height of stem to 3rd leaf	2160.54	63.58**	33.98	1.54**	22.10
Height of stem to 4th leaf	2547.01	44.81**	56.84	1.47*	38.58
Number of leaves	1064.84	15.39**	69.21	2.23**	31.01
Angle of divergence	861.06	7.58**	113.61	12.47**	9.11
Seedling height	379.49	0.11	3342.16	6.52**	512.28

* Significant at 5% level.

** Significant at 1% level.

of variance of each of the 30 characters recorded in this study indicated that the variations within strains were greater than the variations among strains for 15 characters. Thus such 15 characters were excluded from the following analyses which were to compare different strains or races.

The mean square values among strains (*i.e.*, variations attributable to strains) and within strains (errors) for 15 other characters which showed statistically significant differences among strains are presented in Table 3. The results of F-tests which are also indicated in the table prove statistically highly significant variations attributable to strains for all the 15 characters. Such differences among strains are significant at 1% level. These results clearly indicate that there must be genetic differences among the 61 *P. americana* strains examined.

Based on the indication of the genetic differences among strains for the 15 characters, analyses of variance were performed in order to detect differences among three races of avocado, Mexican, Guatemalan and West Indian races (47, 8 and 6 strains examined, respectively; but see footnotes of Table 1). The mean square values among races (*i.e.*, attributable to races) for the 15 characters are shown in Table 4, together with those among strains and plants (errors). The results of F-tests are also indicated in the table. Statistically highly significant differences among races are seen for almost all the characters, except for seedling height. It was also revealed again by F-test that the variations attributable to strains (classified into three races here) were statistically (mostly highly) significant for all the characters.

Correlation coefficients for all the possible 105 pairs of two characters from the 15 characters which exhibited statistically significant differences among strains were calculated and the resultant values are shown in Table 5. Significantly high correlation coefficients, positive and negative, were obtained in 79 out of the 105 combinations of characters.

Since the above analyses of variance showed significant differences among the three races, drawing scattering diagrams of some pairs of characters is desirable in order to obtain more detailed information. Selected for this purpose were six pairs of two characters which showed high F values for the variations attributable to races, and the six scattering diagrams drawn are shown in Fig. 1 (A to F). The characters included in the six pairs are average stem length between leaves, leaf area, heights of stem to the second, third, and fourth leaves, and length and median width of leaf blade. The F values for the variations attributable to races of these seven characters involved were 14.01, 35.36, 53.99, 63.58, 44.81, 14.80 and 13.99, respectively (see Table 4).

In the scattering diagram of the average stem length between leaves *vs.* the height of stem to the third leaf ($r=0.742$) drawn in Fig. 1A, the 61 strains examined would be separated into two groups. One group includes 46 out of 47 strains of Mexican race and two exceptional strains, one belonging to Guatemalan race (strain no. 5) and the other to West Indian race (no. 33). The other group includes most of Guatemalan- and West Indian-race strains, and one exceptional strain of Mexican race (no. 24). The scattering diagram of the leaf area *vs.* the height of stem to the second leaf ($r=0.593$) also seems to indicate the separation into two groups (Fig. 1B). Namely, one group seems to include all the 47 strains of Mexican race plus three exceptional strains (nos. 5 and 16 of Guate-

Table 5. Correlation coefficients between 15 characters of the seedlings of 61 *P. americana* strains

Character	07	08	09	14	15	16	17	19	20	21	22	27	28	30
01	.298*	.410**	.513**	.327**	.195	.582**	.458**	.711**	.722**	.742**	.782**	-.252*	-.141	.460**
07		.875**	.645**	.622**	.156	.479**	.937**	.507**	.514**	.525**	.516**	-.253*	-.297*	.174
08			.427**	.628**	-.364**	.430**	.976**	.530**	.526**	.519**	.507**	-.388**	-.298*	-.049
09				.650**	.053	.434**	.521**	.318*	.328*	.363**	.370**	-.112	-.088	-.544**
14					.058	.580**	.691**	.390**	.469**	.445**	.484**	-.162	-.242	.227
15						.111	-.040	.226	.061	.259*	.272*	-.638**	-.677**	-.346**
16							.482**	.455**	.507**	.538**	.564**	.218	-.114	.606**
17								.538**	.593**	.544**	.531**	-.327**	-.235	.027
19									.993**	.973**	.444**	-.245	-.327**	-.023
20										.990**	.980**	-.791**	-.312*	.005
21											.990**	-.521**	-.289*	.033
22												-.488**	-.275*	.086
27													.331**	.713**
28														.216

* Significant at 5 % level.

** Significant at 1 % level.

Fig. 1. Scattering diagrams of six selected pairs of two characters of 61 strains of *P. americana* (A to F). Symbols: $\cdot$ = Mexican race, $\circ$ = Guatemalan race, and $\triangle$ = West Indian race. The r values given are correlation coefficients between the two characters.

malan race and no. 33 of West Indian race), and the other consisted of other Guatemalan- and West Indian-race strains. Similar separation seems to be seen also in the scattering diagram of the leaf area *vs.* the height of stem to the third leaf ($r=0.544$, Fig. 1C). Almost all the Mexican-race strains (excepting one, see below) and one strain each of Guatemalan (no. 5) and West Indian (no. 33) races belong to one group, and most of Guatemalan and West Indian races and one exceptional Mexican-race strain (no. 24) constitute the other group.

Drawn in Fig. 1D is the scattering diagram of the height of stem to the second leaf *vs.* that to the third leaf ($r=0.990$). The 61 strains are separated into two groups also in this diagram. One of the groups includes 47 Mexican-, two Guatemalan- (nos. 5 and 16) and one West Indian-race (no. 33) strains, and the other does only strains of Guatemalan and West Indian races. Very similar scattering of 61 points into two groups is observed in Fig. 1E in which the height of stem to the second leaf and that to the fourth leaf are plotted ($r=0.980$). One strain of Mexican race (no. 24) is plotted at intermediate position between the two groups in this diagram.

On the other hand, no clear separation of groups is seen in Fig. 1F in which the correlation between the length and median width of leaf blade is shown ($r=0.875$). However, Mexican-race strains obviously tend to have smaller leaves in general than the strains of other races.

Discussion

The analyses of variance on 30 morphological characters at four-months-old seedling stage so far recorded for 61 *P. americana* strains clearly demonstrated a great genetic diversity of the germ plasms. This result agrees well with previous studies on the variability of *P. americana* complex carried out by POPENOE (1920), ANDERSON (1950) and RHODES *et al.* (1971). Such a great morphological diversity shows a clear contrast against the cytological uniformity, *i.e.*, the constant number of chromosomes ($2n=24$) and also that of satellite chromosomes (one pair) in different *Persea* species so far reported earlier, with a few exceptional chromosome numbers (tri- and tetraploids) found by one of the present authors (GARCÍA 1975). A great variation of peroxidase isozymes (GARCÍA and TSUNEWAKI 1977) and high enzyme polymorphisms (TORRES *et al.* 1978) have been also reported in the avocado.

The analyses of variance also showed that 15 characters as listed in Table 3 can be used to characterize, at least, strains, since the mean square values among strains (*i.e.*, variations attributable to strains) of the 15 characters were larger enough to prove statistically highly significant variations (Table 3). Almost all of those 15 characters, with only exception of seedling height, were proved to be also useful for characterizing different races of *P. americana* (Table 4).

Judging based on the correlation coefficients between every two characters of 105 combinations of the 15 characters (Table 5), average stem length between leaves is correlated with almost all other characters. The heights of stem to the first, second, third and fourth leaves are also highly correlated to each other as expected. High correlations of leaf area with the length and median width of leaf blade are also of course observed.

These characters mostly exhibited high F values among races (Table 4). Such high correlations between characters suggest that probably a few (or not many) specific genes are controlling such correlated characters.

More important for the purpose of the present study is to find any general tendency of those characters of avocado seedlings, which may distinguish different races. Out of the six diagrams in Fig. 1, which were drawn for the pairs of two characters having high F values among races and showing different extents of correlations to each other, five diagrams (Fig. 1A to E) exhibit a fairly clear separation of avocado strains into two groups. Namely, it is possible to see an obviously general tendency that Mexican-race strains tend to have smaller sizes than Guatemalan- or West Indian-race strains, in either of the characters plotted in those diagrams (similar but less clear tendency is also seen in Fig. 1F). Thus, the strains of Mexican race can be generally distinguished from the strains of Guatemalan and West Indian races, although there are a few strains of intermediate or exceptional forms. Some of the exceptional strains are considered to be those of hybrid origin between races. That is, the particular Guatemalan-race strains which are often located in the group of Mexican race in the scattering diagrams (Fig. 1A to E) are of the cultivar *Fuerte* collected in Michoacan and Puebla (strains 5 and 16, see footnotes of Table 1). *Fuerte* is considered to have been originated from natural hybrids between Mexican and Guatemalan races (POPENOE 1920). Other two strains of *Fuerte*, strains 9 and 57 (see Table 1), however, always fell in the Guatemalan-West Indian group in the diagrams. On the other hand, closer relationships are observed in the scattering diagrams between Guatemalan and West Indian races, although the former tends to have larger sizes in general (see Fig. 1).

Based on the results of the present morphological studies, it is possible to conclude that the genetic relatedness among the three races of *P. americana* can be demonstrated by comparing some morphological characters, and that the relatedness is less closer between Mexican and other races while that between Guatemalan and West Indian races is much closer. Indeed, no clear differences were found between the latter two races so far studied here.

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Persea 属における細胞遺伝学的研究

II. アボカド 61 系統の比較形態学的研究¹⁾

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アボカドは、メキシコをはじめ、北米南部から中南米にかけて広く栽培される重要な果樹であるが、その遺伝学的、系統分類学的研究は、あまり進んでいない。最も普遍的な栽培型のアボカドは、分類学上、かつて2種または3種に分けられていたが、現在では、1種 (*Persea americana*) として扱われ、3変種 (var. *americana*, var. *drymifolia*, var. *nubigena*) を含むものとされている。一方、園芸学上は、グアテマラ系、西インド諸島3系、メキシコ系の3系に分けられ、前2系は var. *americana*、メキシコ系は var. *drymifolia* に属するとされている。ただし、異系間の雑種形成が起こるため、3系への分類は必ずしも容易ではない。

この研究では、著者らがメキシコ各地から集めた52系統と、ハワイのハミルトン教授から提供を受けた9系統のアボカド (Table 1) について、発芽後4か月間空調温室で育てた芽生の30形質 (Table 2) を調査し、統計学的分析によって変異の程度とそれによる類縁度の解析を行なったものである。

分散分析の結果、調査した30形質中、15形質については系統間差異が有意であった (Table 3)。また、このうち14形質は、園芸学上の3系間でも有意差が見られた (Table 4)。これら形質間には、高い相関関係が見られる場合が多く (Table 5)、そのうち6組の2形質について相関図を画くと (Fig. 1)、一般にメキシコ系がグアテマラ系および西インド諸島系から区別でき、後2系間には明白な区分がつけられないことが判明した。それゆえ、グアテマラ系と西インド諸島系はより近い類縁関係にあり、メキシコ系はかなり離れていると考えられる。

異系間の雑種起原と考えられるもののうちには、形質相関図上でも中間型を示すものがいくつか見られた。