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CHARACTER SEGREGATIONS IN AVOCADO RACIAL-HYBRID PROGENIES

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ABSTRACT

Two unusual characteristics of the West Indian race are desirable in California avocados: early fall maturity and tolerance of soil salinity. Since that race is too tropical in adaptation for satisfactory performance in California, its hybridization with local varieties of the hardy Mexican race was initiated by grafting scions of Arturo, Clifton, and Jalna into a tree of the West Indian race in the Hawaiian Islands. Of 45 resulting progenies planted at Riverside, 28 have fruited. A detailed analysis under 4 foliar and fruit characters is presented. The presence of West Indian characteristics, particularly type of pedicel and of skin, indicated that at least some of the progenies were derived from West Indian pollen; hence the hybridizíng procedure was successful. The presence of Guatemalan race characteristics indicated that these three so-called Mexican race varieties are in fact of Mexican-Guatemalan hybrid origin. There was no indication of Ínter-racial sterility.

INTRODUCTION

Our present understanding of the botany of the avocado is that all types and varieties belong to a single species, **Persea americana** Miller. As they occur in nature, however, avocados fall into three fairly well-defined subspecific classes which are separable on the basis of a number of more or less distinctive morphological and physiological characteristics. These classes are now usually treated taxonomically as intraspecific horticultural races.

The putative horticultural races are generally identified with the geographical regions to which they were thought to have been indigenous at the time that they were discovered botanically. These regions are: the highlands of south central Mexico; the highlands of central Guatemala; and the islands of the West Indies. Consequently, the races have come to be known as: Mexican, Guatemalan, and West Indian. According to Popenoe (6), however, it is now quite clear that the West Indian race did not origínale in the West Indian islands. He states, following extensive plant explorations, that a lowland continental origin, possibly in Colombia, is likely.

Popenoe also found that primitive avocado trees of the Mexican race abounded on the lower slopes of the Orizaba volcano in southern Mexico. The center of distribution of the apparent wild prototypes of the Guatemalan race was among pines and other temperate zone trees at altitudes as great as 9,000 feet in the Chichoy mountains near Tecpan, Guatemala; later he observed similar types near Vera Cruz, Mexico, and in mountain-top cloud forests in the Honduras (8), He described a very primitive, indigenous avocado type from the lowlands of Honduras as well as from somewhat higher elevations near San Jose in Costa Rica, which had a strong anise scent plus larger fruits with a tough, granular shell; these composite characteristics, together with the geographical location, suggest to us the interesting possibility that this type is closely related to the progenitor of all three of the avocado horticultural races now under cultivation.

In the early years of avocado culture, the West Indian and Guatemalan races were classified together as **P. americana,** while the Mexican race was considered to be a separate species known as **P. drymifolia** Cham. and Schlect. (5). Later, Hodgson (4) proposed, "What now appears to be the most reasonable and useful classification is that in which **P. drymifolia** is considered to be a botanical variety of **P. americana** and therefore becomes **P. americana** var. **drymifolia."**

The recognition and classification of three distinct groups in the avocado goes back more than 300 years, according to Popenoe (7). It remained for Popenoe himself, and only in this century, to formulate a working key (5):

"1. Leaves anise-scented; skin of fruit thin (rarely more than 1/32 inch in thickness) **Persea drymifolia**. Mexican race of horticulture.

2. Leaves not anise-scented; skin of fruit thicker (from 1/32 to ¼ inch in thickness) **Persea americana.**

a) Fruit summer and fall ripening; skin usually not more than1/16 inch thick, leathery in texture. West Indian Race.

b) Fruit winter and spring ripening; skin 1/16 to ¼ inch thick, woody in texture. Guatemalan Race."

This classification continues to be widely used by avocado workers. As noted by Ruehle (9), however, "This scheme of differentiation is becoming constantly less useful, both because of the increasing number of hybrid varieties and because intermediate types between Guatemalan and Mexican groups have been found growing wild in Mexico." To add to Ruehle's observation, it should be noted that individuals of the three races interbreed freely by natural cross-pollination when brought together in a common location. The variety Fuerte, which originated in Mexico, is thought to be a Mexican-Guatemalan interracial hybrid. Many varieties of California origin are known to be hybrids of similar origin. In Florida and in Hawaii, many of the important commercial varieties are hybrids of known origin between varieties of the Guatemalan and West Indian races. An exploration committee of the California Avocado Society found both Guatemalan-Mexican hybrids and West Indian-Mexican hybrids in Mexico in 1953 (3). The Hawaiian variety Sexton presumably has all three races in its pedigree. It resulted from the cross of Fuerte (Guatemalan x Mexican) with the Hawaiian variety Seyde

(West Indian).

Varieties of the Mexican and Guatemalan races and of hybrids between them have become important in the California avocado industry. Mexican varieties account for the fall crop (September-November), as well as providing the principal source of seeds for use as rootstocks in nursery operations. Guatemalan varieties account for the spring and summer crops (April-September). Hybrids, principally the variety Fuerte, account for the winter crop (December-March).

The West Indian race is virtually unknown in California. There are several reports in the literature of varieties of this race having been introduced into California for trial, principally from Hawaii and Florida where varieties of the race are the principal source of summer fruit (May-September). The most extensive trial seems to have been by Joseph Sexton of Goleta, who grew 15 varieties from Hawaii, and obtained several hundred seeds which he distributed widely to southern California growers (10). Mr. Sexton's trial came to naught, apparently, first because West Indian varieties usually fail to fruit properly, or even to flower, under California conditions; second, because of failure of varieties of the race to withstand even relatively mild frosts.

In recent years, there has been renewed interest in the West Indian race for two reasons: 1) individuals of this race have been found to be more tolerant of saline conditions and less liable to chloride-induced leaf tipburn than those of the other two races (2); 2) the need in California for a high quality, early-maturing fall variety especially for regions where climatic conditions make it difficult to hold fruit of the late-maturing varieties like MacArthur and Hass on the trees into the fall months.

In view of the lack of cold hardiness and general non-adaptability of the pure West Indian type in California, it was decided to hybridize trees of that race with varieties of our hardiest and earliest-fruiting type, the Mexican. This paper reports some early data obtained from populations of such hybrids.

MATERIALS AND METHODS

Attempts were made in 1954 and 1955 to obtain hybrids by hand— pollinating varieties of the Mexican race with pollen of a number of West Indian varieties air-mailed from both Florida and Hawaii. Not a single fruit set from these attempts. Because of these failures, we enlisted the aid of the Hawaii Agricultural Experiment Station. This seemed a promising approach for two reasons. First, the West Indian type of avocado abounds in Hawaii, especially in the Kona district of the Island of Hawaii, where there are numerous trees well isolated from any tree of the Guatemalan type. Second, the climatic conditions would minimize the chances for self-pollination, since under the warm, equable climate of Hawaii, the dianthesis cycle (11) is much more precise than it is in the cooler, more variable climate of southern California. No overlapping of first and second opening has ever been observed in Hawaii, consequently trees of both A and B flowering types must always be grown together if one is to expect fruit set on either. This is contrary to experience in California, where a single tree can produce fruit by means of self-pollination if one of the openings is sufficiently delayed by cold, so that at least a few male-functioning and female-functioning flowers are in anthesis at the same

time. Thus, open pollination in Hawaii would probably be much more productive of hybrid seed than the arduous, expensive hand pollination method (1).

In 1955, P. A. Peterson, who was then in charge of the avocado breeding project, sent scionwood of three varieties that were classified as the Mexican type to Hawaii for grafting into a West Indian tree. The varieties were Arturo, Jalna, and Clifton. As will be noted later, there is now good reason to believe that these varieties are not pure Mexican in type but rather are Mexican-Guatemalan hybrids. The grafting was performed by Edward T. Fukunaga, Superintendent of the Kona Branch Station. In the fall of 1957, some fruit was produced by the grafts. About a half dozen fruits each were collected from Arturo and Clifton and about 40 fruits from Jalna by R. A. Hamilton, Horticulturist in the H.A.E.S., who extracted and mailed the seeds to the Citrus Research Center at Riverside. From these, three seedlings of Arturo, five of Clifton, and 37 of Jalna were grown successfully and transplanted into the variety test orchard.

No descriptions of the West Indian tree to which the above varieties were topworked are available except that the fruit was purple, about 12 ounces in weight, and had a medium-sized, tight-fitting seed. A more detailed description would be interesting, but not necessarily meaningful in view of the fact that all seeds were obtained by open pollination and there were other West Indian trees nearby. Also, self-pollination, although not likely to occur, cannot be entirely excluded as a possibility.

Three seedlings of Arturo were grown to adult size, but, so far, only one of these has fruited. This, with a typical Arturo fruit, is illustrated in Figure 1.

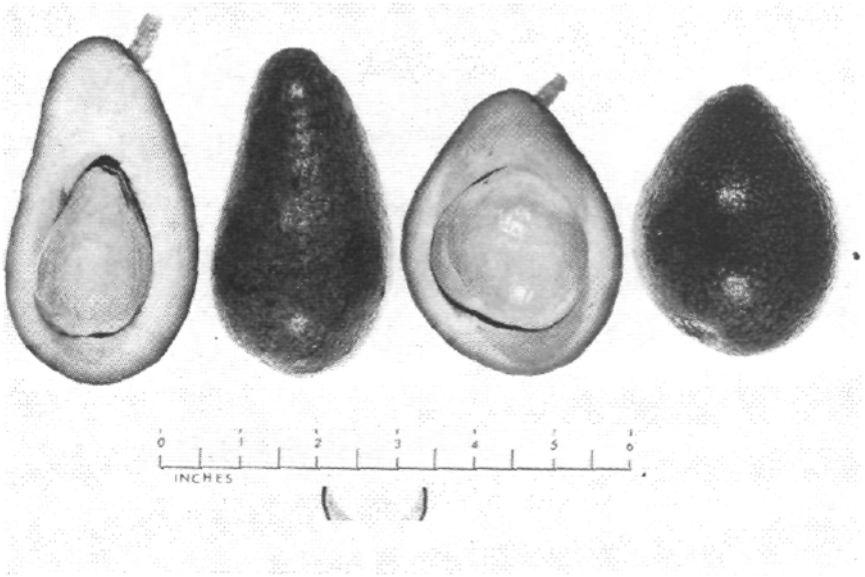

Figure 1. Fruit of Arturo (left), and seedling (right), which probably resulted from West Indian pollen.

Four out of five Clifton seedlings have now produced fruit. Three are shown with Clifton in Figure 2.

Twenty-three out of 37 Jalna seedlings have fruited. These exhibit a wide range of variation, from small and spherical to large and pyriform with long necks. Jalna is shown in Figure 3 with 12 of its seedlings, selected to show the extreme types and some of the intermediate types.

Figure 2. Fruit of Clifton (left), and three of its seedlings which probably resulted from West Indian pollen.

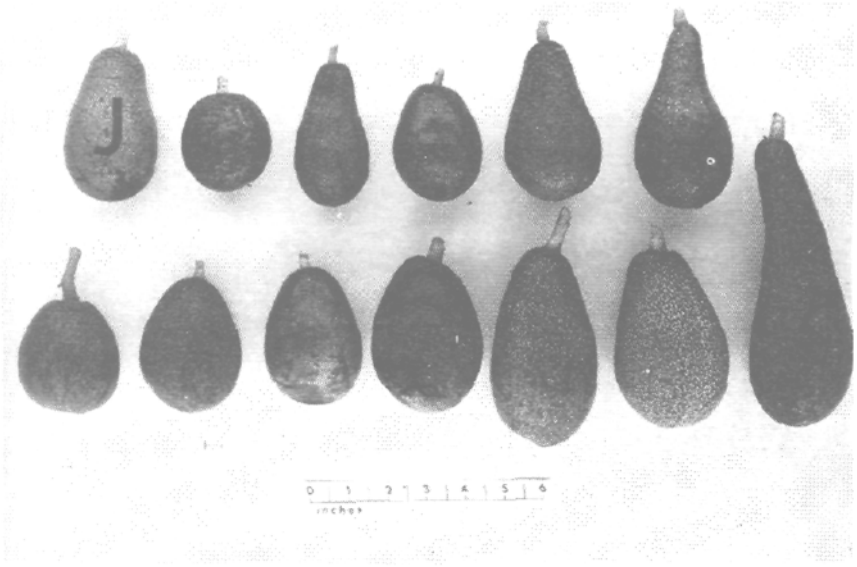

Figure 3. Avocado fruit variations among Jalna seedling trees from seeds produced in Hawaii. The fruit at the upper left, marked J, is Jalna itself.

Observations were made on the following vegetative characters: color and density of pubescence; odor of foliage; color of new growth flush; lenticel characters. Fruit characters observed were: type of pedicel; insertion of the pedicel on the fruit; orientation of pedicel attachment; fruit shape; fruit weight; type of skin; color of skin; presence or absence of end spot; presence or absence of corkiness; season of fruit maturity by months.

To determine possible commercial or breeding usefulness, other characters not reported on herein will be analyzed later: general vigor; productivity; tendency to alternate bearing; shelf life of fruit; seed loose or tight in ovarian cavity; adherence of seed coats to seed or to flesh; flesh flavor; and several others.

RESULTS AND DISCUSSION

Vegetative Characters

Pubescence.—Young vegetative growth varies among seedlings with regard to the color and density of epidermal hairs.

Odor of foliage.—Characteristically, the leaves of "true" representatives of the Mexican race have a strong, spicy odor, most often likened to that of anise. Representatives of the West Indian and Guatemalan races have not been reported to possess any distinctive odor. However, we detected a well-defined, different odor in the leaves of some of these seedlings; to some observers it resembled the odor of citronella, while to others it was suggestive of certain species of Eucalyptus, such as the lemon-scented gum.

Color of new growth flush.—Young leaves were in some cases green of variable shades, while in other cases they had anthocyanin coloration; because previous observations on avocados have shown that intensity of coloration may vary from locality to locality and year to year, no attempt is made to indicate degree in the table.

Lenticel characters.—These characters were rated on young growth, since on this type of growth the lenticels may be conspicuous and show some color, whereas on older wood they may become inconspicuous and have the color fade out.

Fruit Characters

Type of pedicel.—The late L. A. Walmsley noted from observations in Costa Rica (personal communication) that the pedicel offers useful diagnostic properties for differentiating the three avocado races. Pedicels which are more or less typical of each of the three races are illustrated in Figure 4.

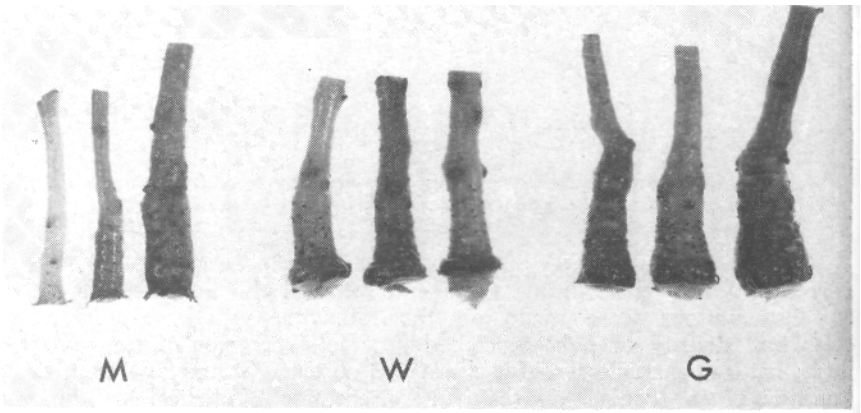

Figure 4. Pedicel types of horticultural races of avocado: M — Mexican; W — West Indian; G — Guatemalan. These examples were selected from trees that segregated out of a tri-racial hybrid.

The pedicel of the Mexican race (M) tends to be very nearly parallel-sided from its point of origin at the apex of the peduncle to its point of insertion into the fruit. In pure Mexican types, the pedicel margin is nearly continuous with that of the peduncle, and the point of insertion may be quite inconspicuous, as seen in the peduncle-pedicel at the left of the M group. In hybrid types, the pedicel may have a swollen appearance, so that its point of differentiation from the peduncle is quite distinct. Pedicels of the West Indian race are illustrated by the group of three marked W. There may or may not be slight tapering of the pedicel, so that it increases in diameter from the point of attachment on the peduncle to the point of attachment to the fruit. Its most distinctive feature, however, is a rather abrupt expansion into a conspicuous collar or round flange just at its point of insertion into the fruit. Walmsley (personal communication) has aptly likened this pedicel configuration to that of a nail head.

Pedicels of the Guatemalan type are illustrated by the group of three marked G. They tend to be heavier than the other two types, and to taper conspicuously from fruit to peduncle.

Insertion of pedicel on fruit.—There are three general categories of pedicel insertion on the fruit, in terms of the adjacent fruit level: sunken, flat, and elevated. Actually, individual pedicel insertions vary continuously among these three types, but for simplicity each seedling was classified as of the type that it resembled most.

Orientation of pedicel attachment.—The orientation of the attachment of the pedicel to the fruit varied from practically straight or transverse to quite oblique. Fruit shape.—This is classified as pyriform, oval, or spherical. For our files, a finer scale of classification is used, in view of the high degree of variation that is recognized within each of our three general categories. Some of the variation that occurred in a single seedling progeny set is shown in Figure 3.

Fruit weight.—An approximate measure of fruit size is provided by the weight in ounces. This is the measure commonly used in commercial packing houses. A mean weight was estimated; the range for any one seedling may include a maximum that is over twice the minimum fruit weight.

Type of skin.—The skins of Mexican race fruits typically are smooth and very thin. They are easily broken when the fruit is full ripe, simply by rubbing with the thumb. Characteristically, they are covered with a grayish bloom which makes them dull in appearance; they become glossy when wiped with a dry cloth, but do not acquire as high a sheen as do skins of the West Indian type. Smoothness is due to the fact that the lenitcels are not raised but are level with the surface. The lenticels, themselves, are very small, and tend to remain discrete, or to coalesce into groups of no more than two or three.

Skins of West Indian race avocados are smooth and shiny. They are somewhat thicker, and considerably tougher than those of the Mexican type. Much more pressure must be exerted to cause rupturing by rubbing with the thumb. There is a little bloom on the surface, but this is so sparse that it does not obscure the sheen. When polished with a dry cloth, the skin takes on a high luster. In the West Indian race, as in the Mexican race, the fruit lenticels are not raised but are level with the surface; this accounts for the smooth, almost slick, feel of the skin. Toward the basal end of the fruit, the lenticels tend to be discrete from one another or coalesced into groups of no more than two or three. Also, they are somewhat scattered. They become progressively more numerous, with greater coalescence, from the basal end to the apical end of the fruit.

Skins of avocados of the Guatemalan race tend to feel rough to the touch; they are tough leathery to woody in texture. They are not easily ruptured by rubbing with the thumb even under considerable pressure. Roughness is due to the lenticels, which are slightly raised. These are larger than those of the other two races, and often show a tendency to coalesce along longitudinal lines. The immature fruit may have some sheen, but this tends to be lost as maturity approaches. Bloom, if present, is very sparse, and seems to have no effect on sheen.

Skin color.—This is classified as green or purple. Again, large differences in color shade are present within these two groups. Virtually every description of the Clifton variety gives its skin color as green, but at least under Riverside conditions it is purple at full maturity.

End spot.—End spotting, i.e. the tendency for the epidermis to become corky or woody at the apex of the fruit in the region immediately surrounding the point of stylar attachment, is an inherited characteristic which varies in expression depending upon environment. Fruits were rated as affected markedly, slightly, or not at all.

Corkiness.—Corkiness is a condition similar to that of end spot. It may occur in various degrees anywhere on the fruit, but may or may not invade the stylar apical region. It originates in the lenticel, to which it may be confined, or by coalescence of lenticels it may invest virtually the entire fruit. Since corkiness is widely variable in expression under differing physiological conditions, it was recorded simply as present or absent.

Season of maturity.—This refers to the months during which fruit reaches maturity and continues to be palatable.

Arturo was rated as having light yellow, dense pubescence; faint anise odor; green color of new growth flush; and purplish red, conspicuous lenticels. Its fruit pedicels were intermediate between the Mexican and Guatemalan types (Fig. 4), with flat fruit

insertion, and oblique orientation; fruit shape, pyriform to oval; average fruit weight, 8 ounces; skin type, closer to Guatemalan than to Mexican; color, green; a little end spot was present; corkiness, present; season, September to December. The 3 presumed Arturo x West Indian progenies all had slight pubescence, light brown in one case and rated tawny in the other 2 seedlings; all 3 had faint anise odor and green growth flush like their maternal parent. The one seedling with fruits had a Mexican type pedicel, but with flat insertion and oblique orientation like Arturo; fruit shape, oval — much more squat than Arturo (Fig. 1); weight, 6 ounces; skin type, Guatemalan-like; green; considerable end spot; no corkiness; November-December maturity.

Clifton pubescence was rated light brown and sparse; anise odor, faint; new growth, with anthocyanin; lenticels, green and inconspicuous. Fruit pedicels, Mexican; pedicel insertion, flat; orientation, nearly straight; shape, oval; average weight, 10 ounces; skin type, Guatemalan; color, considerable purple when ripe; no end spot; corkiness, present; season, September to November, Its 5 progenies all had sparse pubescence, but the color was white in each case instead of light brown; 2 had faint anise odor, 2 had strong anise odor, and one had no noticeable leaf odor; 4 had anthocyanin coloration of new growth flushes like the maternal parent, whereas in the fifth it was absent; all 5 had conspicuous lenticels, which in 3 cases were green like Clifton, but in the other 2 seedlings were reddish brown. Four of the seedlings had set fruit: 1 had a Mexican-type pedicel like Clifton, whereas 2 had Guatemalan pedicels, and in the remaining seedling it was of West Indian type; 3 had flat pedicel insertions but the fourth had an elevated pedicel attachment; one had straight pedicel orientation, but 3 were oblique; 2 had fruits with an oval shape much like that of Clifton, while the other 2 were more pyriform; fruit weight varied from the Clifton average of 10 ounces down to about 7 ounces; skin type was Guatemalan in 2 cases, but the other 2 seedlings were of the West Indian type for this character; all 4 had green fruits at maturity; 2 had an end spot, unlike the female parent; 2 had no corkiness, unlike the female parent; all 4 had a shorter harvesting season, from October to November in the year observed. Jalna pubescence was rated light yellow, and dense; anise odor, strong; new growth, green; lenticels, green and inconspicuous. Jalna fruits had pedicels of the Guatemalan type; with sunken insertion; and straight orientation; shape, pyriform; average weight, 8 ounces; Guatemalan skin type; green at maturity; slight end spot; no corkiness, harvested September to November. Among the 37 Jalna seedlings from Hawaii were all degrees of pubescence density and all shades of pubescence color from white through light yellow and light brown to tawny; 13 had no particular leaf odor; in 6 the anise odor was faint, in 8 it was mild, and in only 5 it was rated "strong" like the Jalna parent; 5 had a citronella-like odor not hitherto reported; all but 2 seedlings had no appreciable anthocyanin in the new growth flushes; 10 had considerably more conspicuous lenticels than Jalna itself; in 4 cases the lenticels were brown instead of green. Of 23 seedlings with fruit, 11 were of Guatemalan pedicel-type, but 8 were rated as closest to the Mexican standard, and 4 were classified as West Indian; 4 had sunken pedicel insertion, 17 were flat, and 2 were elevated; only 5 had the straight orientations of Jalna; 13 were pyriform in shape, with 9 rated oval and one spherical (Fig. 3); average weight ranged from 5 to 10 ounces; 14 had the Guatemalan-type skin of Jalna, whereas Mexican and West Indian skin types numbered 2 and 7, respectively; all but 4 were green skinned; end spot varied from absent to pronounced; only 6 were free from

corkiness, although for 4 other seedlings this character was not recorded; maturity season was generally shorter than that of Jalna—some matured as early, while 10 were later and remained in good condition into December.

CONCLUSIONS

1) The appearance of "nailhead" pedicels (which are associated y with avocados of the West Indian race) and of West Indian type skins, indicate that hybridization was accomplished by open pollination. Success in this Initial experiment indicates that the method is a sound one for obtaining racial hybrids, and especially useful if one wishes to introduce germplasm of the West Indian race into breeding stocks for a climate like that of California. The open pollination method provides an inexpensive means of obtaining hybrid seeds in large numbers.

2) There are definite indications of characteristics associated with the Guatemalan race, particularly with regard to type of pedicel and type of skin. This strongly suggests what we have long suspected, namely that Arturo, Clifton, and Jalna, as well as many varieties that originated from open pollinated seeds of Mexican varieties and that are registered and described in check lists as Mexican, are actually Mexican-Guatemalan hybrids. The genetic behavior of these seedlings suggests also that the three taxons do belong to the same species, and that the Mexican race is no more distinct from the Guatemalan and West Indian races than they are from each other.

3) The wide range of character differences, which is illustrated only in part in Figure 3, emphasizes the great difficulty in attempting to determine parentage from seedling phenotype. A number of the fruit types in Figure 3 aro less like Jalna than they are like several other California avocado varieties.

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