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THE ORIGIN, SPREAD, & IMPROVEMENT OF THE AVOCADO, SAPODILLA & PAPAYA

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Cultivated plant species of importance were originated from three general sources, according to DeCandolle (5) namely, the Valley of the Euphrates, from whence came the grape, olive, date, fig, and walnut; China, where at a later date citrus fruits were derived; and lastly, tropical America, where the guava, cherimoya, granadilla, feijoa, and avocado appeared on horticultural horizon. A more recent speculation on development of economic plants is the excellent work by Vavilov (17), who, through the benefit of more extensive literature and personal travel, has provided more conclusive evidence concerning the origin of many crop species. He concludes that our economic plants originated in one of eight great world centers, with the Chinese centre being the earliest, and of great importance, and secondarily the Indian center, which has provided,, among other species, many citrus forms and the mango. The avocado, a plant of rather recent discovery and development, is mentioned by Vavilov to have originated in the Central American center.

Speculation in botanical history based on distribution of the plant family and genera strongly suggests that the *Lauraceae* or laurel family, of which the avocado is a member, developed primarily in the New World. More specifically, the genus *Persea,* which includes the principal edible fruits of the family, evolved in Central America. A few members of the genera, however, are found in North and South America, some in southeastern Asia, and one species, botanically isolated, in the Canary Islands.

Judging from accounts of early Spanish explorers and conquerors, the avocado as we know it must have been widely distributed in pre-Columbian times, though restricted in general to Central America.

An account by Oviedo in his report to Charles V of Spain in 1S26 defines rather clearly the "pear" trees of the New World which "have the colour and shape of a true pear, but with a thicker skin and having in the middle a seed like a peeled chestnut." The buttery texture of the ripened fruit is described and its flavour is mentioned as good.

New World floras of early botanists assumed that the genus *Persea,* or at least the edible species, was rather widespread throughout the islands of the West Indies and the mainland of tropical America early in the 17th century. There is some reason to question this sweeping assumption.

G. N. Collins, a plant explorer from the United States, searched carefully through the accounts of the earlier chroniclers and was able to show conclusively that the tree was unknown in the West Indies until after the Spanish conquest, though it was widely noted on the mainland.

Popenoe (11) somewhat later relates the account of Garcilaso de la Vega, who wrote of its introduction into Peru about 1475. The assumption is made that it was not native farther south than Ecuador at that time. The evidence, again gathered by Popenoe, suggests that the tree was not known east of Venezuela in pre-Columbian times. There is reason to believe that avocados were grown from northern Mexico through Central America into north wertern South America to Peru at the time of the Spanish conquest. That the fruit was well known and probably widely utilized is borne out by accounts of Bernabé Cobo, who only a century and a half after the conquests of Mexico and Peru described quite accurately the three horticultural races which we presently recognize. Since Popenoe's extensive collection and exploration in Central and South America, from whence he introduced many varieties of avocado into California, little has been added to our basic information concerning the possible origin of the fruit. The three great horticultural races of avocado noted by Cobo were verified by Popenoe, who divides the known forms into the Guatemalan and West Indian races under the botanical name of *Persea Americana,* Mill. And the Mexican race, now recognized as *Persea Americana* var. drymifolia, Mez. The nomenclature used here is probably most widely accepted at present. The distinguishing characteristics generally employed to separate the three groups briefly are as follows: Varieties of the Guatemalan race have large fruit with thick pebbled rind, medium oil content and are without anise in the leaf. Those of the West Indian race have medium to large fruit with moderately thin, but tough, smooth skin, low oil content and are without anise in the leaf. Mexican race varieties have small fruit, thin skin, high oil content and strong anise in the leaf. Difference in season of maturity, frost hardiness, and other characteristics may be found.

These rather well defined horticultural categories have served their purpose but indeed cannot encompass many new forms which have appeared as the result of several recent horticultural explorations. These searches have attempted to locate and introduce new species and varieties, with special emphasis directed toward the solution of the avocado root-rot problem. New species have been sought which are highly resistant or immune to the soil-borne organism, *Phytophthora cinnamomi.*

Several explorations made during the past ten years by Popenoe, Zentmyer {19), Schroeder (14), and others have disclosed many new avocado forms and close botanical relatives, such as the genera *Ocoteo, Nectandra,* and several species of *Persea* known previously only in herbaria. Many of these now have been established in California. Other *Persea* forms of special interest exhibit botanical and horticultural characteristics common to two or more of the three horticultural races. We can now demonstrate virtually all degrees of relationship and intermediate combinations between any two or three of the races. Thick skinned fruits with anise odor in their leaves—small fruits with delicate, thin skin typical of the Mexican race yet with little or no trace of anise in their leaves—these and many other combinations indicate a cross-breeding which must have occurred in the natural populations. Attempts to classify and to indentify such intermediate forms with certainty have proved difficult if not impossible in many cases.

While botanists in the recent past have worked entirely from limited herbaria, the extensive observations of a still wider collection of materials in the field have caused still other botanists to seriously question the strict classification and subdivisions of the genus *Persea.* There is some evidence to suggest that possibly all of the forms which now comprise the edible avocado may represent only a single species.

Breeding work conducted during the past decade at the University of California has provided only speculation on botanical and horticultural relationships between the several classical avocado forms. Though many difficulties arise in avocado breeding, nevertheless some results have been forthcoming which encourage further basic and applied work in this field.

When the avocado developed as a commercial industry in California about 1915, it was realized that the best varieties available lacked many characteristics, which would limit its expansion on a sound basis. Outstanding among these deficiencies were fruits of medium to small size with good keeping quality and especially the commercial requirements of regular and good yields. While ideas concerning the fruit characters of the perfect avocado have changed, the need for regular dependable bearing always has been apparent, especially in the variety of greatest importance, the Fuerte. Improved bearing behavior, therefore, is an objective of major concern to the plant breeder.

About 1935 the statement of the breeding problem was clearly formulated and the basis developed for a well oriented breeding program by Professor R.W. Hodgson of the department of Sub-tropical Horticulture. The establishment of the department at the Los Angeles campus shortly before that time provided the ideal environment pursuing the breeding program. Professor Hodgson immediately began a systematic assemblage of all suitable breeding materials as a variety collection of orchard trees and as trees growing in large 50 gallon tubs. The latter could be moved easily in and out of glasshouses or screen cages and likewise could be transported close to permanent trees in the field for caged-tree experiments. It was soon learned that moisture control in the canned trees was difficult to maintain, hence considerable fruit and tree loss resulted from accidental desiccation or over-irrigation. Permanent orchard trees proved more suitable as female parents.

Another fact learned early was the suspected unsatisfactory behavior of the Fuerte as a female parent. Frequently this variety sets a low percentage of hand or bee-pollinated flowers and will mature only a small portion of those fruits set. The Fuerte is, however, entirely satisfactory as a pollen parent.

Two general approaches have been utilized to obtain progeny materials. The caged-tree technique involves a permanent tree "A", the female parent, crossed with a canned tree "B" selected as a pollen parent. The pollen tree is placed under or near the female parent and a screen cage erected to cover both. A colony of bees is introduced to provide pollination. Four possible types of fruit can result from such an arrangement: either variety A self-pollinated or the hybrid A times variety B both on tree A. On tree B, there is variety B self-pollinated or the hybrid B times A. In such cases the hybrids are selected by comparison with a progeny planting of other known self-pollinated A or B seedlings.

In other hybridization work carefully bagged and emasculated flowers are used for controlled pollinations, but at great expense of time and labour and with discouragingly little returns. Under normal conditions an estimated million flowers may be borne by a single avocado tree. The number of fruit set and carried to maturity may only be 300 or 400. Likewise under actual experimental conditions using Fuerte as a female parent, over 10,000 flowers were emasculated and carefully hand pollinated. Only 25 fruits were set and further only 4 of these survived to maturity. Attempts are being made, therefore, to learn more of the basic physiology and factors which are concerned with fruit set and development, so that proper conditions can be provided or induced to give higher returns in the breeding program.

The use of varieties other than Fuerte as female parent has given slightly better returns from emasculation and hand pollination trials, but again such hybrids are indeed very costly.

A third method (1) used to secure hybrids is based on the fact that the avocado flower exhibits a strong tendency toward dichogamy, hence functions either as a female or as a male flower, depending upon time of day. Hence hand pollination with selected pollen can be utilized without emasculation and without fear of self pollination within the given flower. This rather hazardous assumption has been invoked in some cases where large scale hybridization has been desperately sought.

Seed of self-pollinated progenies from caged trees or selected from large single clone plantings in the field have been obtained in moderate quantity, hence at least & partial idea has been ascertained concerning the heterogeneity or genetical characters which may exist in the "pure lines" of such varieties.

Preliminary studies indicate a strong similarity of fruit form among the progeny at self-pollinated clones. F_1 progeny of Topa Topa selfed, for example, resemble the parent in fruit characters which are smooth, thin skinned, generally black in" color, and long oval in form with an oblique, prominent apical point. A comparable situation is found in F_1 of self-pollinated Mexicola. Both of these varieties are typical Mexican race varieties. The F_1 progeny of Fuerte, however, is highly variable in fruit form and other characters, a fact which fortifies our suspicion that this clone is highly heterozygous for many characters and is indeed a probable natural hybrid between a Mexican and a Guatemalan form. The very thick skin of the Guatemalan varieties has not appeared in progeny of Fuerte, though most other characteristics are evident to some degree.

Some early analysis of skin colour suggested rather strongly that black is a dominant and green a simple recessive Mendelian character. Such evidence was noted from an I\ population of the black Mexicola self-pollinated where black and green fruits occurred in the ratio of 3 to 1. This would indicate that green colour is inherited as a recessive character and hence green fruits theoretically would be homozygous for this feature. Subsequent appearance of black fruits in self-pollinated progenies from green fruits cast some doubt on the validity of the assumption concerning colour inheritance. It is probable that our theoretical pure green varieties such as Fuerte are really highly heterozygous for several characters, including colour. We have at present no good data to provide conclusive evidence on this problem.

The apparent natural hybridization between the Mexican and Guatemalan races—the latter representing two botanical species or at least a species and a distinctive botanical variety—is well exemplified by the Fuerte, the most important commercial variety, which provides approximately 75 to 85 percent of the production in California today. The Fuerte is an apparent natural hybrid originating in a dooryard in Atlixco near Puebla, Mexico. It has many intermediate characteristics of the Guatemalan and Mexican races in respect to frost hardiness, season of maturity, skin character, and other aspects. Varieties such as Puebla, Bacon, Zutano, and several other open-pollinated seedlings also display intermediate characteristics and are apparent natural hybrids. Such natural hybridization, which must occur frequently, has encouraged the plant breeder to attempt to synthesize new varieties directly in the F_1 generation by the selection of appropriate parents. A surprising, number of quite favorable combinations thus have appeared in F_1 progenies from such crosses. One typical example is a cross of Mexicola female parent times Fuerte pollen parent. Several F_1 progeny were obtained, most of which tended to resemble the Mexicola parent in fruit form and colour. At least one F_1 clone was approximately intermediate between the two parents in both fruit form and size. This particular clone also is green in colour, a very desirable characteristic in the commercial avocado. Unfortunately defects such as a fragile skin and comparatively inferior taste quality have prevented this particular fruit from receiving further attention. It will be utilized, however, in backcrossing to the high quality Fuerte in an attempt to improve its commercial potentialities.

Several comparable combinations such as Anaheim and Mexicola, Anaheim and Fuerte, Lyon and Mexicola, and others have given rise to extremely interesting F_1 progenies, though again none have provided fruits of sufficient quality to be utilized directly as a commercial clone. The character of high production in such clones as Mexicola and Anaheim has appeared in a large proportion of their progeny. We may be able to determine the genetical aspects or possible inheritance of this particular yield characteristic in the future.

Interspecific hybridization appears to be a reasonable objective in avocado breeding, though only limited progress can be reported on this aspect of the investigations. The diploid number or chromosomes in the basic species, *Persea Americana,* was determined by Eiden (6) to be 24. Bringhurst (2) analyzed several species in the collections at Los Angeles to show the diploid chromosome number of *P. borbonia, P. floccosa, P. nubigena,* and *P. longipies* also to be 24.

Hand pollinated, controlled crosses between several species of *Persea,* however, suggest that possibly physiological or other unsuspected barriers exist between most species, for very few progeny have been obtained from several crosses which have been attempted. Only a few crosses of two *Persea* species have been demonstrated by the production of half a dozen progeny *of*F_1 generation which, without doubt, are intermediate between the two parents in respect to vegetative characters. This cross made by Bringhurst utilized as one parent *Persea floccosa,* a highly pubescent plant with narrow lanceolate leaves, high yield, and considerable frost resistance. Among the female parents were Hass, Dickinson, and Anaheim, all with glabrous stems and broadly lanceolate leaves, good yields and only moderate frost hardiness. Hybridity of the F_1 progeny soon became evident. The leaf forms are narrowly lanceolate and highly pubescent, which are characteristics of *P. floccosa.*

Interspecific hybrids of *Persea* will be of considerable importance if factors for disease resistance and grafting compatibility can be combined.

Propagational trials have been underway in California to establish the degree of grafting affinity between *Persea* species and close relatives and those varieties of avocado of commercial importance (7). Simultaneous investigations have been conducted by the plant pathologists to determine the degree of resistance or immunity of the several stock plants to *Phytophthora cinnamomi* (20). The general status of these investigations can briefly be summarized by the statement that all species or relatives investigated thus far which show high resistance or immunity to *Phytophthora* are incompatible with scions of the edible avocado, whereas nearly all susceptible forms can be grafted to avocado successfully. Moreover, all resistant forms are compatible among themselves but cannot be united with any other susceptible forms. Hence we are now seeking by discovery in the field, or by breeding, an avocado rootstock which has both resistances to *Phytophthora* arid graft compatibility with the commercial varieties. Another approach to this problem is the development or discovery of a form which may have graft compatibility with the presently known resistant stocks and with the edible avocado. In the latter instance the use of the compatible form as an intermediate stem piece or sandwich, though it might not exhibit immunity itself, would indeed provide a means whereby the immune stocks could be further tested for their commercial longevity and production potential in the field.

THE SAPOTA OR SAPODILLA

Indeed the sapota, *Achras sapota* L., is a gift from tropical Central America. It is indigenous to Mexico, south of the Isthmus of Tehuantepec extending into Guatemala, and possibly into parts of Salvador and northern Honduras. It is still found native in the lowlands of Tabasco, Chiapas, and the western part of Yucatan in Mexico, and extends into British Honduras. It was introduced into Ceylon about 1802 but did not succeed on any commercial scale. It has been grown with success though not exploited commercially in Hawaii and is found commonly throughout tropical America from Florida to southern Brazil. Though introduced into California several decades ago, it is found only in special collections.

The botanical relationships within the Sapodilla nispero complex have been .reviewed by Gilly (8). He suggests that the generic notation *Achras* should be deleted in favour of the term *Manilkara.* Although the details of his arguments are presented, it appears that this point of view is not entirely acceptable to all botanists. Because the literature has consistently utilized the name *Achras* and because of the uncertainty of the evidence for change of name, it appears desirable to retain the usage of *Achras* at least for the present discussion.

The nomenclature concerned with the term sapota provides considerable confusion in the literature. The term sapodilla probably is most commonly used for the vernacular name of *Achras sapota* L. A number of other fruits, however, are carelessly or inadvertently called sapotes though of entirely different families. Hence we have the white sapote, *Casimiroa edulis* (family Rutaceae), the black sapote, *Diospyros ebenaster* L family Ebenaceae), the green sapote, *Calocarpum viridii* (family Sapotaceae), the yellow sapote, *Lúcuma salicifolia* (family Sapotaceae), and the sapote, *Calocarpum m&mmosum* (family Sapotaceae). This usage developed by Popenoe appears to be a reasonable approach to a complex problem, wherein agreement is not easily attained among horticulturists and botanists concerning the common name of a diverse number of fruits. While the sapodilla *(Achras sapota)* and sapote *(Calocarpum mammosum,* are frequently confused in their nomenclature and usage in the literature, indeed the two species are markedly distinct in character of leaf and fruit such that brief descriptions of these plant parts immediately indicate the species concerned. *Achras sapote* has small glabrous leaves up to 5 inches in length, whereas the leaves of *Calocarpum mammosum* are large and pubescent, up to 15 inches long. Fruits of *Achras sapote* are generally spherical and small, up to 3 inches, with none to ten or twelve hard black seed. *Calocarpum* fruits, on the other hand, are generally elliptic or oval in form, 3 to 16 inches long with a single large elliptic seed.

It would appear that the usage of the terms *sapodilla* or chiko for the species *Achras sapote* would be more satisfactory than the general term sapote. The term *sapodilla* is derived from the Spanish *zapatilla,* which means small sapote. The Mexican name *chicozapote* has been shortened to *chico,* which implies small. The term *naseberry* frequently is used in the West Indies and parts of India. Chiku is also used in Marathi. The name ya, a Maya word, is still used to designate the fruit in Yucatan, Mexico.

While the sapodilia has been propagated primarily by seed, considerable success has been attained by shield budding in Florida and by grafting and layering or marcottage in

India. Seedling trees are variable in both fruit character, the age of bearing and season of maturity, hence successful exploitation of sapodilla fruits will be enhanced by the selection of superior clones or the development of better varieties by plant breeding techniques. Whereas during the past two decades some seedling selection has been undertaken, there has been little evidence of endeavors to improve the varieties by direct plant breeding. The cytogenetics of *Achras sapote* is unknown. Aside from a determination (5) of the basic chromosome complement of 2n=26, there appears little information on this plant.

Seedling selection, on the other hand, has been responsible for the introduction into the trade and literature of several named varieties, primarily in Florida and parts of India, where the sapodilla has received the most attention from a scientific, horticultural point of view. Though the fruit has been grown in Florida for many decades, only within the past two decades has any attempt been made to propagate and utilize the better clones. The variety Prolific, introduced in 1941, was an open-pollinated seedling with fruit of medium large size, good quality, and early bearing. A second selection, Russell, was a seedling with large fruit, good quality but much slower to bear and with lighter yields. Six other selections have been under observation and trial but not propagated extensively.

The cultivation of the chiku in the Bombay area and other parts of India has resulted in extensive study and selection of clonal materials. Twelve varieties have been described (3) of moderate to major importance in the commercial marketing of the sapodilla in Madras alone. Among these clones are mentioned Kittabarti, Bangalore, Dwarapudi, Cricket Ball, Jonnavalosa I, Jonnovalosa II, and others.

From Bombay at least 7 varieties of importance have been selected and described. They include such clones as Kali, Large Calcutta, Long, Bhuri, Jingar and Vanjet. Without doubt there are many other clones utilized for small or commercial plantings in the United Province area and in Ceylon which are not recorded. It would appear from a perusal of the literature that much remains to be accomplished in the systematic pomology and horticulture of the sapodilla, namely in the adequate description of the best known clones and outstanding seedlings, and in the critical testing and evaluation of the materials under several environmental conditions.

The successful development of sapodilla in the Philippines has been responsible for some varietal selection work there. The Ponderosa chico, a large fruited form, has been described (9). Studies on the blooming and fruiting habit indicate a possible dichogamy may be operative in restricting fruit set under their conditions, in which the flowers tend to mature their pistils considerably after full bloom.

The major objectives in clonal selection in the sapodilla appear to be large size fruit, good quality, and seedlessness. Fruit size, while variable from season and within a given tree, has been markedly improved by selection. Fruits regularly 3J to 4 inches in diameter are now available in some clones. The quality of the improved clonal selections is markedly superior to the ordinary seedling fruit in respect to flavour, storage-ability, and reduced number of seed. Several virtually seedless or actual seedless clones are known and have been grown on a semi-commercial basis. Some of these are said to be of outstanding quality. Apparently production of seedless fruits is not as dependable as those having a few or many seed. Fruit quality, however, is said to be excellent in some seedless forms, though seedlessness generally is achieved at the expense of fruit size. Large size seedless fruits have been reported, however.

The sapodilla, though it can be grown over a wide area and will tolerate a considerable range of climatic conditions, is restricted commercially in respect of good quality fruit to certain regions. The plant has been grown widely throughout the milder climates of India, especially in the areas of Bombay, Bengal, and Madras, where it reaches its best quality and production. Proximity to the coast appears to be beneficial.

Though size should not be a limiting factor in selection of sapote varieties, nevertheless small size is definitely an undesirable character. Large size fruits with adequate quality should prove most desirable. Form of fruit probably will be of minor concern, though if distinctive, it conceivably could identify the variety in the trade and prove a natural trademark. Other things being equal, a round fruit should provide better handling characteristics from the point of view of machine sorting and sizing, uniform packing or nesting. Pointed or irregularly shaped fruits always are sources of potential trouble because broken or injured points are sources of disease infections. The economic loss in handling fruits of irregular shape is high in many instances.

Seedlessness in most fruit varieties is a characteristic usually of distinct advantage, especially if the fruit is utilized as a dessert or salad. Utilization of fruits in products and by-products need have little concern for seeds in most cases, as these can be easily removed by proper screens or other mechanical means. Ideal sapodilla fruits, however, should be at least of low seed count or seedless, if this can be achieved with simultaneous good production and maintenance of acceptable and attractive flavour. Selection for flavour must be based on local tastes.

THE PAPAYA

The native home of the cultivated papaya, *Carica papaya,* most certainly is tropical America, but its precise locale is apparently lost in antiquity and may never be known. DeCandolle and others have suggested that it originated in southern Mexico, though our present forms may have been developed as a natural cross between other species native to this region. DeCandolle points out that the species has no Sanskrit name and that the modern Indian name is derived from the American word papaya, which is a corruption of the Carib term *ababai.* The use of the term papaw or pawpaw is unfortunate for this is also applied to the unrelated *Asimina triloba.* The papaya was early considered an exotic plant in the Malaya Archipelago, having been introduced by the Portuguese. It was not reported in the Pacific Islands at the time cf Cook's voyages, though it spread rapidly and widely shortly thereafter. Evidence leads to the belief that it was introduced on the coasts of Africa and Asia after the discovery of America. Seeds were taken from India to Naples, Italy, in 1626. It was widely distributed in the islands of the Pacific by 1800.

The family Caricaceae as a whole is practically restricted to continental America, though it was known in the West Indies, namely Jamaica, at least in 1756, Nearly all the species described are dioecious except *C. papaya,* which is highly variable in sex form, and the more recently known species, *C. monoica,.* which is entirely monoecious.

Because the seed have a moderate period of longevity, it is likely that the papaya spread rapidly throughout the tropics following the discovery and exploration of the New World. It has existed nearly everywhere in the tropics practically as long as man has recorded modern history.

The Dutch traveler Linschoten in 1598 describes the fruit brought from the Philippines to Malaya and hence to India. He called the fruit "Papaios" and mentions it "is very like a Mellon". Since that time numerous descriptions from various parts of the world indicate its rapid and wide distribution such that practically all tropical areas, and indeed most sub-tropical lands, have long considered the papaya as a common dooryard plant. Commercial production, has been attempted only in comparatively recent times, probably because the plant was so common and widespread as to preclude the need for large plantations. More recently the development of rapid transportation has justified the attempt to supply the great temperate zone markets with this exotic delicacy of the tropics.

Though normally dioecious in nature, the sex expression of the papaya has been one of the most perplexing and lacking in explanation. Only in recent years has there been an understanding of the basic facts concerned with flowering and fruit form production, as the result of extensive investigations into the genetics,, inheritance and environmental responses by several investigators throughout the world.

The earliest botanical accounts of papaya described the general vegetative • characteristic of the plant, but the accounts of the floral morphology vary considerably. The very extensive range of floral characters which have been catalogued and illustrated have indeed confounded the horticulturists and most botanists-, until of late, when some degree of order was established among a mass of apparently conflicting data.

While several review papers have appeared which help clarify the rather complex floral situation and account for the highly variable fruit forms, the studies by Storey (15) present a concise and illuminating summary of the general knowledge in this field. He describes the papaya tree as bearing staminate, hermaphrodite or pistillate flowers. This together with strong tendencies toward carpeloidy, staminoidy, and petaloidy have given rise to the description of at least fifteen sex forms in the literature. These may be reduced to three general types, however; namely, those with 1-long, pendulous, cymose inflorescences, which are male forms but which may produce bisexual flowers ; 2-short peduncles with no more than 15 flowers and the flowers bisexual in form but occasionally becoming female sterile; and 3-trees with short peduncles, fewer than five flowers per cluster, purely pistillate forms, very stable in nature and monotypic:

While extensive studies have been on the relationship between vegetative characters and sex, it appears that no correlation can be established with certainty sufficient to be of value. Sex can only be predicted from among progeny materials from controlled pollinations. It has been firmly established by Hofmyer (10) and confirmed by Storey and others that sex in papaya is controlled by a single gene with three aliéis in which

M_1 — staminate

M_2 — hermaphrodite

m — pistillate

Furthermore, M_1M_1, M_1M_2, M_2M_2 are lethal in zygote. Thus M_1 m is male, M_2 m is hermaphrodite, and mm a female. Further cytological and genetical investigations have demonstrated that two sets of factors may modify the sex expression of male and hermaphroditic plants, causing seasonal shifting from female fertility to sterility, and then shifting back again and causing stamens to become careploid or fused with the pistil. Apparently these factors depend upon several pairs of genes and upon certain physioiogical conditions which must be present for these gene pairs to function.

The significance of these modifying genes in respect to sexual expression is indeed of concern to the horticulturist and in a more practical way to the grower. Upon utilization of such knowledge it would appear that selection of suitable parent materials will be of permanent importance to maintain and improve fruit quality in respect to form and to increase yields of fruit throughout the season.

Cytological studies have shown that papaya has a pairs of chromosomes identical in morphology. The only detectable difference is a possible precocious separation of one pair in anaphase of meiosis in male and hermaphroditic plants.

Qualitative characters have appeared as mutant genes of several types, such as:

a — albino—recessive to normal green

d — draft—recessive to short

dp — diminutive plant (short, slender, small)

cp — crippled leaf—recessive to flat leaf

rg — rugose leaf—upward puckersng

w — wavy leaf

r — red flesh—recessive to yellow

Y — yellow flower—dominant to white

P — Purple stem end petiole—dominant to green

B — gray seed coat—dominant to black.

All these are autosomal except YPB and are not associated with the sex chromosomes.

Several quantitative characters have been well established, such as fruit shape, by the flower type in addition to basic varietal differences. Likewise fruit size and fruit weight have been demonstrated to represent a mean of the inbred parental lines. Dwarf plants, important from several practical considerations, are related to the internode lengths, for these produce a normal number of leaves and fruit of normal size. The diminutive plants, on the other hand, are small in all respects and genetically quite different from dwarfs.

Propagation of papaya by open pollinated seed is still the universal method of reproduction. A slight refinement of this empirical method is to plant at least three plants to a hill with the hope and on assumption that at least one will develop as a pistillate or hermaphrodite. If pure staminate pistillate forms were utilized as parents, at least 40% of such progeny plantings would be staminate, hence discarded in the final selection. Based on well founded and demonstrable genetical behavior, it is now possible to obtain seed from controlled pollination, by selfing and intercrossing of hermaphrodites, a uniform gynodioecious progeny from an original polygamous form. Such controlled pollinations are now utilised widely for commercial seed production in Hawaii. As the result of such applications, yields have increased as much as 114 percent overall since the breeding studies were initiated in 1936. While the primary factor in such phenomenal increase in yield has been primarily that of breeding and selection, certain improved culture techniques, as well as more effective insect and disease control, must be mentioned in this account.

It is now quite possible to select certain desirable varieties and to control pollination of hermaphroditic forms within these varieties to produce pure lines of the variety which give rise only to hermaphroditic or pistillate plants.

While the papaya of commerce, *Carica papaya,* has been most widely grown and utilized, there is some indication that other species of the genus *Carica* may become of potential value in horticulture throughout the world. The mountain papaya, *C. candamarcensis,* a species of considerable cold hardiness, is utilized directly as a fruit for cooking and canning in Chile and comprises the basis of a moderate industry there. This species is said to be native to the mountains of Colombia and Ecuador in South America. The facts concerning its actual distribution in the native state and its spread throughout the world are practically unknown. It is well established in Florida and California and is reported growing in most of the sub-tropical areas of the world. Likewise other species of *Carica,* now of minor importance, are mentioned frequently from nearly all tropical and sub-tropical research centres of the world, with very little information from which one can discern their actual date of introduction. One is led to conclude, however, that the several species are of considerable interest to researchers primarily because of their potential value in the plant breeding programs.

The brief account of crossing relationships in the genus *Carica* given hy Sawant (12. 13) summarizes nicely our information on this topic. The inherent resistance of *C. monoica* to virus diseases such as Bunchy Top has invoked an intensive search of some of the other 40 species to seek breeding stock which might carry immunity or high resistance, and to attempt the incorporation of such immunity into the ordinary papaya, which is highly susceptible. A wide range of interspecific and reciprocal combinations have been made by Sawant, Warmke, and others utilizing some of the lesser known species such as *C. goudotiana, C. monoica, C. candamarcensis, C. caulifora, C. gracilis,* and *C. erythrocarpa.* It appears possible to induce hybridization between many of the species but that well demonstrated barriers may exist in some cases. These natural barriers operate at different times in respect to fruit development, hence indicate, in part, the degree of compatibility between the species. For example, fruit of *C. goudotiana X C. papaya* will drop at 2-2| months with a 00% set at the beginning. The same species, *C. goudotiana* X *C. monoica* pollen holds its fruit 1-2| months with 15% set, and when crossed with *C. caulifora* holds the fruit 3-4 weeks with 5-6% set. Sawant gives other examples to indicate both close and distant relationships between species in respect to their fruit setting and retention when hybridized.

It appears likely that upon extended investigation and concerted efforts all species within this group will eventually be utilized widely in hybridization, possibly with each other or perhaps with *C. papaya* as one parent. The evidence concerning the stability of these interspecific hybrids is meager at present and experience with them does not warrant conclusive statements at this time. Several years ago Dr. R. B. Seaney, a plant breeder formerly with our department, was able to efíect a crossing of *Carica canda marcenáis* with *G. monoica* which has resulted in an F_x hybrid of considerable interest. The mountain papaya, *G. candamarcensis,* is a hardy species having a palmate, rather thick leaf with moderate pubescence. The species is entirely dioecious. The fruit is 3-4 inches long, pointed and distinctly pentangular in cross-section, yellow in color and highly aromatic when mature. It does not attain perfection for eating fresh under conditions at Los Angeles, but can be cooked. *C. monoica* has a small, three-lobed leaf, glabrous, thin and dark green. The species is monoecious. The fruit is oval in form, about two inches long, and round in cross-section. It can only be eaten when cooked, hence has been given the name Peruvian cooking papaya (16). Upon cooking the flavor is suggestive of a fine quality cooked apricot. The cooked leaves of this species also are utilized for food.

The hybrid *C. candamarcensis X C. monoica* is intermediate in most of the characteristics described for the two parent species. While the genetical analysis •of this cross and its breeding behavior and cytogenetics has not been ascertained as yet, the hybrid nevertheless is of sufficient interest to bring to the attention of horticulturists at this time.

The hybrid appears to develop in size more rapidly than either parent, hence to exhibit heterosis or hybrid vigor. It is in general distinctly more fruitful and bears its fruits tenaciously in dense clusters which envelop the stem along almost its entire length. The individual fruits are intermediate to large in size, generally oval in form, slightly pentangular to rounded in cross-section, and very seedy. The seed characters are intermediate between those of the parents.

This particular hybrid has attracted considerable attention, primarily because of its ornamental value. The attractive yellow-orange fruit together with the short petioled papaya-like leaf is being utilized locally by landscape architects to attain tropical effects in those areas where climatic conditions will not allow the growth of the regular papaya. The fruit of this particular cross is again not edible as a fresh fruit. The more basic analysis of this hybrid remains to be done, but the value of its gross vegetative and fruiting characteristics is being exploited at this time.

Other crosses between such forms as *C. papaya, C. quercifolia, C. pentandra* and *C. monoica* and *G. candamarcensis* have been attempted, but because of limited trials and completely negative results to date no conclusive statements can be drawn concerning their affinity.

While the papaya has been grown on a limited commercial scale in California, there is little likelihood that it will ever attain more than a curiosity in the collectors' garden because of its tenderness to frost. There is need for the development of new, exotic fruits, among these the papaya, which will tolerate the limiting environmental conditions primarily as ornamental plants, not necessarily for potential commercial fruit production. It must be remembered, however, that the canning papaya is unknown as such in California and other areas and could possibly attain commercial importance if properly exploited.

LITERATURE CITED

1. Bergh, B. O. (1957). Avocado breeding in California. *Proc. Florida State Hort. Soc.* 70: 284-290.
2. Bringhurst, R. S. (1954). Interspecific hybridization and chromosome numbers in *Persea. Proc. Amer. Soc. Hort. Sci.* 63: 239.
3. Chema, G. S., S. S. Bhat, and K. C. Naik, (1954.) Commercial fruits of India. Calcutta, p. 422.
4. Darlington, C. D., and A. P. Wylie. (1955). Chromosome Atlas of flowering plants, pp. 1-519. London.
5. DeCandolle, A. (1884). Origin of cultivated plants. *London* 486 p.
6. Elden, H. van. (1935). Genetic and breeding aspects of the papaya *(Carica papaya).* XI erne Cong. Internatl. d'Hort. [Borne] Compt. Rend. Sec. IV, Theme 7. 2 p.
7. Frolich, E. F., C. A. Schroeder, and G. A. Zentmyer. (1958). Graft compatibility in the genus *Persea. Calif. Avocado Soc. Yrbk.* 1957 ; 102-105.
8. Gilly, C. L. (1943). Sapodilla-nispero complex. *Trap. WoodsJ3 :* 1-22.
9. Gonzales, L. C., and P. A. Feliciano. (1953). The blooming and fruiting habit of the *Ponderosa chico. Philip. Agri.* 37 : 384.
10. Hofmyer, J. D. J. (1953). Sex reversal as a means of solving breeding problems of *Carica papaya. African Jour. Sei.* 19 : 228-232.
11. Popenoe, Wilson. (1936). Origin of the cultivated races of avocados. *Calif. Avocado Soc. Yrbk.* 1935 : 184-194.
12. Sawant, A. C. (1958). Crossing relationships in the genus *Carica. Evolution* 12 : 263-266.

13. Sawant, A. C. (1958). A study of the interspecific hybrid *Carica monoica x C couliflora. Proc. Amer. Soc. Hort. Sei.* 71 : 330-333.
14. Schroeder, C. A. (1954). New avocado research materials from Mexico. *Calif. Avocado Soc. Yrbk.* 1954 : 89-91.
15. Storey, W. B. (1953). Genetics of the papaya. *Jour. Hered.* 40 : 70-78.
16. Swingle, C. F. (1947). The Peruvian cooking papaya, *Carica monoica,* a promising new fruit and vegetable for the United States corn belt. *Proc. Amer. Soc. Hort. Sei.* 49: 137-138.
17. Vavilov, N. I. (1950). The origin variation, immunity and breeding of cultivated plants. *Chronica Botánica* 13 (1/6) : 1-366. Waltham, Mass.
18. Warmke. H. E., E. Cabanallas, and H. J. Cruzado. (1954). A new interspecific hybrid in the genus *Carica. Proc. Amer. Soc. Hort. Sci.* 64 : 284-288.
19. Zentmyer, G. A. (1957). The search for resistant rootstocks in Latin America. *Calif. Avocado Soc Yrbk.* 1956 : 101-106.
20. Zentmyer, G. A., and C. A. Schroeder. (1957). Resistance of species of *Persea* to avocado root aot. *Calif. Axocado. Soc. Yrbk.* 108-107.

DISCUSSION

T. Gopalan Nayar: The wild species of papaya exist in Nilgiris *(Carica candamarcensis)* and this may be taken in account in tracing the origin of this fruit?

C. A. Schroeder: The species *Carica candamarcensis* is generally considered to be endemic to the northern part of the South America because it has been introduced to many areas of the world and is a hardy species therefore its escape into the wild places, might be expected.

*A. V. Richards: T*he three fruits—avocado, sapodilla and papaya discussed by you in this paper are of economic importance in Ceylon. The avocado is fast becoming a popular fruit in the mid-country wet zone around Kand. The varieties which have done well are of the West Indian group, the most popular one being the Pollock which produces large attractive fruits. The Fuerte variety has proved unsatisfactory as the fruits do not ripen properly. In regard to sapodilla the problem is to find a quick growing stock on which it is compatible. The wild palu *Mimusops hexandra* is not quick growing to be used as rootstock. The plants take one to two years to be ready for bud grafting.

The papaya is grown in Ceylon more for the production of papain which was once a thriving industry, than for the yield of fruit for desert. The variety grown for the desert purpose is the Solo from Hawaii when has a distinctive flavour of its own.

C. A. Schroeder: Concerning the adaptability of avocado to Ceylon there is a rather large number of varieties in Florida from which seedlings could be raised and tested some of which presumably would be better adapted to the specific condition than are the standard varieties such as the Pollock and the hybrid Fuerte. It has always been my opinion that use of seedlings in an unknown area is the best test for adoption of a species. Use of clones provides very little range of variability and may prove quite unsatisfactory. This approach can also be applied to the testing of the adaptation of sapodilla to any given area.

With our modern knowledge of the basic genetics of papaya it is possible to develop local varieties selected for good flavour or size and to be incorporated into the seedling strain, fruiting characters or sex forms of commercial value.

R. S. Boy: Has any work been done on the breeding of disease resistant varieties of papaya especially against mosaic?

C.A. Schroeder: The mountain papaya has been found to be resistant to mosaic. Hybrids from mountain papaya and other commercial varieties have been found to be mosaic resistant.

S. Krishnamurthy: It is seen from the paper that in hybridisation work with avocado, the fruit set is very low, only 25 fruits having set from 10,000 flowers hand pollinated. Under the circumstances has the use of plant regulators (plant hormones) been attempted or considered for improving the fruit set?

C. A. Schroeder: The plant hormones were tried and they have helped only to some extent.