GENETIC VARIABILITY IN *CARICA PAPAYA*

AND RELATED SPECIES

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ABSTRACT

As part of an *ex situ* conservation of *Carica* germplasm in Hawaii, expeditions in 1992 and 1993 resulted in the collection and analysis of seeds of 131 accessions of *Carica papaya* from 9 countries in Central and South America (Mexico, Belize, Guatemala, Honduras, Costa Rica, Panama, Venezuela, Colombia, and Ecuador). Populations of wild small-fruited *C. papaya* (previously designated as *C. peltata*), and hybrids between the wild and domesticated were sampled from their native range on the Caribbean coast of Central America (Mexico, Belize, Guatemala, Honduras). Domesticated *C. papaya* specimens were also collected from Central and South America. The three types of *C. papaya* were examined for variability in nine enzyme systems (ACO, IDH, MDH, PGM, PGI, SKD, TPI, UGP, and 6-PGD) and 13 loci. Domesticated, hybrid, and wild *C. papaya* shared a Nei's genetic identity, *I*, of greater than 0.9, which is consistent with conspecific populations. The intrapopulational genetic variability results indicate that the greatest diversity exists in the Yucatan-San Ignacio-Peten-Rio Motagua area in Central America. In general, the wild *C. papaya* populations have greater isozyme variability than the domesticated populations. The hybrid populations have intermediate variability between the domesticated and the wild populations. The least diverse populations are found in South America where no wild populations are found.

Carica cauliflora, C. goudotiana, C. crassipetala, C. sphaerocarpa,
C. pubescens, C. microcarpa ssp. *baccata, C. microcarpa* ssp. *heterophylla,*

C. microcarpa ssp. microcarpa, *C. stipulata*, *C. pulchra*, and the natural hybrid

C. x *heilbornii* n.m. *pentagona* (babaco) were collected in Venezuela, Colombia, and

Ecuador. *Carica glandulosa*, *C. monoica*, *C. parviflora*, and *C. quercifolia* were

obtained from germplasm banks in Latin America or were already present in the USDA-

NCGR collection. Isozyme analysis indicated that *C. papaya* is distantly related to the

other *Carica* species included in this study and that none of the other *Carica* species could

have been a wild progenitor of *C. papaya* in the recent past. Recommendations on future

collecting expeditions and conservation of *Carica* genetic resources are suggested.

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CHAPTER 1

INTRODUCTION

A native plant of the American tropics, papaya (*Carica papaya* L.) is the best known and most important member of the family Caricaceae with regard to economic value. Consumed as breakfast fruits as well as drinks, the value of this delicious fruit is based on its high vitamin A and C content, easy digestibility, and desirable taste (Morton 1987; Smith et al. 1992). Global papaya production in 1993 was 5,663,000 tonnes, which represents a 47 percent increase since 1981 (Food and Agricultural Organization 1994). The world's leading papaya-producer nations in descending order are Brazil (1,750,000 tonnes), India (1,200,000 tonnes), Thailand (545,000 tonnes), Nigeria (500,000 tonnes) and Mexico (343,000 tonnes), with the United States much further down the list (29,000 tonnes) (Food and Agricultural Organization 1994). In addition to its value as an edible fruit, papaya latex harvested from unripe fruits or leaves contains papain, a proteolytic enzyme that is used as an active ingredient in meat tenderizer and is a significant export item for Tanzania, Uganda, Zaire, and Sri Lanka (Becker 1958).

In Hawaii, papaya ranks as the second most economically important diversified crop after macadamia nut with a value of production of almost $14 million in 1994 (Hawaii Agricultural Statistics Service 1995). Approximately 250 papaya farms in Hawaii, totaling some 1,000 hectares of harvested acreage, yield about 26,000 tonnes

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of fresh fruit and about 2,500 tonnes of processed fruit annually (Hawaii Agricultural Statistics Service 1995).

A threat that jeopardizes the papaya market (and other domesticated crops) is plant disease pressure. One of the most serious diseases to impact the papaya industry in Hawaii is the papaya ringspot virus (PRV) which first appeared in Hawaii in 1945 (Ferreira et al. 1992). Following the discovery of a new "mosaic" strain of the virus in 1959, papaya acreage on the island of Oahu decreased from a peak of 300 hectares in 1950 to a mere 16 hectares in 1991 (Ferreira et al. 1992). The decline in papaya production on Oahu was more than offset by increased papaya acreage on the island of Hawaii, where no PRV existed until recently. However, in May 1992, PRV disease arrived in the commercial production areas on the island of Hawaii, and it now threatens the long-term survival of the papaya industry in the state of Hawaii. Efforts are underway to develop PRV-tolerant or -resistant cultivars via cross protection and genetic engineering techniques (Ferreira et al. 1992; Fitch et al. 1992). Other diseases, such as root rot caused by the *Phytophthora* fungus, have also become serious problems in Hawaii (Chia et al. 1990).

Disease and pest problems in domesticated plants are often due to the fact that they possess only a subset of the genetic variability found in their wild progenitors (Allard 1988; Doebley 1989; Gepts et al. 1986; Ladizinsky 1985; Nevo et al. 1979). Future ability to counter pests and diseases successfully is further reduced by the loss of

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crop genetic resources through extinction of both wild and domesticated plant species. Wild plant species are driven to extinction through massive losses of habitat, and domesticated plant species have reduced genetic variability through the selection for high crop performance and uniformity (Fowler and Mooney 1990; Frankel 1974). The trend toward monoculture that relies on a few crop varieties has made agriculture more vulnerable to sudden changes in the environment and appearance of new diseases or pests.

This is depicted by the infamous southern corn leaf blight (caused by the fungus, *Helminthosporium maydis*), which resulted in a 50-percent loss in the corn crop in some southern states and a total loss of over 15 percent in the United States in 1970 (Simpson and Conner-Ogorzaly 1986). At that time, the U.S. corn industry relied almost exclusively on cultivars that were produced using male sterile double-cross hybrid plants derived from the same source of cytoplasm. The single gene that confers male sterility also makes plants highly susceptible to the southern corn leaf blight. Because some 80 percent of the U.S. corn crop that year was planted with hybrids having male sterile cytoplasm, the crop loss was high. This event signaled the need for the availability of an adequate store of disease-resistant germplasm to cope with the exigencies of nature.

In any plant breeding program, it is essential to maintain a germplasm collection or have access to new material in the gene pool from which potentially useful

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characters, such as disease resistance, may be incorporated into the crop (Simmonds 1979). The usefulness of the germplasm available depends in part on how thoroughly the materials have been characterized genetically and phenotypically (Bliss 1990). Evaluating the genetic variation in the germplasm is the first step towards understanding the scope and utility of material in the collection (Marshall 1990). By examining the genetic variability of the crop species throughout its home range, its center of diversity may be identified and its center of origin hypothesized (Doebley 1989; Gepts 1990; Vavilov 1939). This is important for collecting genetic resources to be used for crop improvement, and for planning ultimate conservation strategies (Frankel and Bennett 1970). Breeding programs benefit from the information obtained from analyses of genetic variability and molecular systematics of crop species. Such knowledge allows breeders to better understand the biogeographical distribution, variability and historical development of the crop germplasm with which they are working, and to facilitate more efficient use of the available variability for the crop (Harlan 1992).

Because the conservation of Caricaceae germplasm must be based on an assessment of genetic variability within its home range, and because introduction of new germplasm is fundamental to commercial *C. papaya* breeding programs, a study with the following objectives was undertaken:

Objective 1.   To assess the genetic variability in cultivated and wild *C. papaya* germplasm and using this information to elucidate the likely region and process of domestication for *C. papaya*.

Objective 2.   To determine the genetic relationship between *C. papaya* and other *Carica* species.

The results of this study contribute significantly to the scientific understanding of the molecular systematics of Caricaceae, and provide a sound basis for future breeding and genetic resource conservation efforts involving this economically important plant family.

CHAPTER 2

LITERATURE REVIEW

Plant genetic resources conservation

Importance of plant genetic resources conservation

If American consumers wanted to live on food from crops native to the United States, they might be shocked to discover that their "independence diet" would be limited to sunflower seeds, wild rice, cranberries, blueberries, pecans and not much else. Most of the foods consumed by Americans are derived from exotic species (Harlan 1975). Similarly in Hawaii, all commercial crops such as sugarcane, pineapple, coffee, macadamia nut, papaya, avocado, mango, lychee, sweet potato, taro, anthurium and orchid were introduced by immigrants and visitors (Neal 1965). Worldwide, humans have utilized an estimated 3,000 species of plants for food and commercially exploited about 150 of these historically (Simpson and Conner-Ogorzaly 1986). Of this limited number, the combined production of the top four crops (wheat, rice, corn, potatoes) far exceeds the total production of all other crops (Food and Agricultural Organization 1994). The present trend in which fewer and fewer major crops were feeding more and more people was discussed by Harlan (1992).

Concomitant with the historical decline in the number of crop species cultivated is the reduction in the amount of genetic variability present within them (Harlan 1992). After the Second World War, rapid world population growth led to intensive, petroleum-based agriculture, which increased pressure on natural ecosystems and accelerated the reduction of genetic variability in domestic plants and animals. Simpson and Conner-Ogorzaly (1986) describe this reduction in the number of crops on which people depend and the loss of genetic variation within them as a vicious cycle. When newly developed superior crop varieties are distributed to farmers, the newer varieties often replace the lower yielding local varieties resulting in widespread propagation of a few selected genotypes. This erosion of genetic variability also happens in areas where a crop was first domesticated. Unfortunately, once these local varieties are no longer grown, they are lost forever. As depicted by the southern corn leaf blight, agricultural food production systems that are dependent on a limited number of selected genotypes are vulnerable to unforeseen disaster.

This alarming trend spurred the U.S. National Academy of Sciences to commission a survey on the genetic vulnerability of every major crop grown in the United States, which upon its completion revealed an extremely risky dependence on an increasingly narrow genetic base (National Academy of Sciences 1972). At the international level, Frankel and Bennett (1970) reported the recommendations of the 1967 United Nations Food and Agriculture Organization/International Biological Programme Conference regarding the steps that need to be taken to promote the

availability and conservation of genetic resources. These steps are: (1) to determine the location and nature of genetic resources in the field, e.g., the center of genetic diversity; (2) to survey material in existing collections; (3) to adequately classify, evaluate, and utilize genetic resources; (4) to conserve genetic resources; (5) to document collections scientifically and completely; and (6) to coordinate international guidance and administrative backing for genetic resource conservation.

In 1971, the International Board of Plant Genetic Resources (IBPGR), later renamed the International Plant Genetic Resources Institute (IPGRI), was established to facilitate international cooperation in conserving plant genetic resources. After ranking crops according to their importance to humans, institutes were established, if they did not already exist, for those crops with top priority and were instructed to collect and store as much of the germplasm in existing agricultural crops as possible. This involved sending researchers to areas in which the crops were first domesticated and/or areas in which wild relatives still persist (Simpson and Conner-Ogorzaly 1986).

Until recent decades, plant breeders who sought genetic variability for crop improvement simply had to go to the right places to find it in abundance. Today, the stores of wild and *in situ* germplasm have decreased as intensive agricultural methods have replaced more conservative or traditional systems, and as high-yielding cultivars (often developed in distant places) have displaced heterogeneous local varieties and mixtures. While the plant breeder commonly uses breeding stocks and working

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collections long established in a place, more and more frequently he or she faces the task of adapting an unadapted foreign crop to local conditions or even of developing a new crop from wild or primitive materials. Success in any such venture depends upon the availability and acquisition of a range of genetic stocks adequate to the purpose (Simmonds 1979).

Role of plant population genetics in conserving genetic resources

Population genetics serves to integrate molecular, population, and evolutionary biology and provides the basis for understanding environmental adaptations and the theoretical framework for crop improvement. The traditional theoretical and empirical methods of genetics and population genetics have melded with the new and powerful tools of molecular biology to provide an unparalleled view of genetic diversity and of the evolutionary mechanisms that shape genetic diversity (Brown et al. 1990).

Genetic diversity arises from the process of mutation, which guarantees a continuous input of new variants, and the equally important processes of environmental adaptation and random genetic drift, which shape the distribution of genetic diversity in time and space (Brown et al. 1990). The extent to which populations or species can adapt to environmental pressures is determined by the store of genetic variation existing in local populations and shared among networks of populations. In the same way, plant

breeders depend on genetic variation available within the gene pools of domesticated species and their close relatives as a resource for crop improvement.

Allozymes: tools for assessing genetic variability

The development of the starch gel electrophoresis (Smithies 1955a and b) and the histochemical staining of enzymes on gels (Hunter and Markert 1957), as well as the classic isozyme studies by Hubby and Lewontin (1966) and Lewontin and Hubby (1966), revolutionized population genetics, evolution, and systematics research. A major advance has been the development of isozyme electrophoresis to assess genetic variability quickly, reliably, and inexpensively. Isozymes are different molecular forms of an enzyme with the same substrate specificity and with different electrophoretic mobility that are coded by more than one locus (Markert and Moller 1959). The term "allozyme" designates the different molecular forms of an enzyme encoded by different alleles of the same gene locus. Often when the genetic basis of the multiple molecular forms is unknown, the term "isozyme" is used (Crawford 1990).

Applications and advantages of using isozyme techniques to survey genetic variation in animal and plant species have been reported by Peirce and Brewbaker (1973) and Brown and Weir (1983). One advantage is that the isozyme allelic expression is usually codominant and free of epistatic or environmental effects. A

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second advantage is that the specificity of each enzyme allows attribution of alleles to loci, and the comparability of loci in different populations or species. Another advantage is that the different alleles can be detected as a mobility difference that is independent of the functional role or the overall level of variation of the enzyme in question. The sampling of a particular locus does not depend on whether or not a gene is variable. Instead, it depends on its expression in a particular tissue, the suitability of extraction and availability of assays for zymograms. Furthermore, an array of enzymatic loci can be assayed conveniently on one individual, using small amounts of material with minimal preparation and expense (Brown and Weir 1983).

Hamrick and Godt (1990) reported that allozyme markers have been used successfully to investigate systematic problems or to measure levels of variation within and among populations. Such studies have contributed significantly to plant systematics, evolutionary ecology, population genetics, plant breeding, and the conservation of genetic resources. Studies of isozyme loci have revealed a patchy distribution of genetic variation within natural plant populations, where sometimes this heterogeneity is associated with environmental features and may be influenced by selection (Allard et al. 1972; Hamrick and Holden 1979), while in others it results from limited pollen or seed dispersal (Linhart et al. 1981).

Because it is a property of collections of interbreeding individuals, genetic diversity is a statistical concept (Brown et al. 1990). Weir (1990) developed the

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statistical concepts needed to make evolutionary inferences about populations from diversity statistics. Hamrick and Godt (1990), who applied diversity measures to the analysis of allozyme data from more than 450 plant species, explained that an understanding of the way genetic variation is partitioned among populations is of primary importance for the conservation of genetic diversity (and hence the evolutionary potential) of species. This understanding may be derived scientifically from allozyme data that are required to develop strategies for preserving genetic diversity.

In recent years, isozyme analysis has been used to develop genetic "fingerprints" of cultivars of fruit species such as cherimoya (Ellstrand and Lee 1987) and pineapple (Dewald et al. 1988). Isozyme analysis has also been used in assessing the breadth of genetic diversity in crops such as banana (Jarret and Litz 1986), lettuce (Kesseli and Michelmore 1986), and tomato (Rick et al. 1974). Crop species frequently present extreme morphological departures from their wild relatives, so that morphology is of limited utility in identifying phylogenetic relationships (Harlan 1992). In studies of the origin and evolution of crop plants, isozyme analysis provides a means of measuring evolutionary affinity (Doebley 1989).

Doebley (1989) mentioned four ways in which isozyme analysis can be used to study the origin and evolution of domesticated plants. One approach is to examine the isozyme variation found within the crop. It is expected that the variation in the

domesticate should not exceed that found in the presumed wild progenitor. Another approach is to compare the degree of similarity in variation in the crop and the progenitor using multivariate statistical analyses such as cluster and principal component analyses. Populations of the crop and progenitor will not be fully separated by these analyses if the wild taxon is indeed the progenitor of the crop. This has been demonstrated, for example, in peppers (Jensen et al. 1979) and squash (Decker and Wilson 1987). The third approach is to examine the allelic composition and level of polymorphism of the crop and its presumed wild progenitor. At the majority of their loci, the crop and its wild progenitor should share the same, most common alleles, but the crop should have only a subset of the alleles existing in the progenitor. Finally, Nei's (1972) genetic identity (I) can be used to determine whether a particular wild form is genetically similar enough to a crop to be considered a probable progenitor.

Gottlieb (1981) had suggested that conspecific populations usually have a mean I value of 0.90 or greater, and thus it can also be expected that the mean I value between crops and their wild progenitors will be 0.90 or greater (Doebley 1989). Examples of crops that have been examined using this technique include maize (Doebley et al. 1984), soybean (Kiang and Gorman 1983), and lettuce (Kesseli and Michelmore 1986).

Measures of genetic variation using isozymes

From isozyme banding patterns, it is possible to infer the number of gene loci for each enzyme, the number and type of alleles present at each locus, and therefore whether an organism is homozygous or heterozygous at a gene locus. The proper interpretation of patterns obtained from the staining of a particular enzyme depends on whether the active subunit composition of the enzyme is made up of one, two, or more polypeptides that combine to form the active enzyme, i.e., whether they are monomers, dimers, etc. (Crawford 1990). An enzyme is a monomer when it is comprised of one polypeptide chain and displays a single band per locus in a homozygous plant and two bands in a heterozygous plant (Acquaah 1992). A dimeric enzyme consists of two associated polypeptides and will produce three bands in a heterozygous individual. A tetrameric enzyme consists of four polypeptides and will have five bands in a heterozygous individual. Other factors that should be considered in interpreting enzymes genetically are the number of gene loci specifying different forms of the enzyme, and whether polypeptides encoded by different loci combine to form active enzymes.

Once the above factors have been determined, the allelic frequency at each locus for plants in a population or species can be estimated. The distribution of individual alleles among populations can also be ascertained. The allelic frequency data obtained

can address the question of how genetic variation is partitioned within and among populations or species.

Gottlieb (1977) pointed out that electrophoretic data are not used properly if bands in gels are simply compared in terms of similar and dissimilar mobilities. This approach would be biochemically faulty and nullify several of the important advantages of electrophoresis. Because allozymes are nearly always inherited as codominants, it is possible to distinguish between homozygous and heterozygous individuals for a given locus and between allozymes and isozymes. Thus, the exact number of genes included in the study can be quantified. This point is best illustrated in two plants where one is homozygous and the other is heterozygous for a monomeric enzyme. They would differ by one band if one would simply count the number of bands. If the same genetic situation were to exist in a tetrameric enzyme, the two plants would then be seen to differ by four bands. Spurious interpretation of systematic and phylogenetic data may result unless the genetic control of the enzymes is examined to confirm that they follow Mendelian inheritance.

Crawford (1990) discussed several ways to measure genetic variation in a population or species based on allelic frequency data. One way is to consider the percentage of polymorphic loci in a population or species. If the most common allele of a gene locus occurs in a frequency of less than some arbitrarily high value (0.99 or 0.95 are commonly employed), then that gene locus is said to be polymorphic. While

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this statistic is usually reported in isozyme surveys, it is at best, a rough guide to the level of genetic variation in a sample because of its dependence on sample size, and the number and kinds of enzymes sampled. Another way to measure variation is to observe the mean number of alleles per locus, i.e. allelic richness where alleles are counted equally irrespective of their biological importance. This value is also dependent on sample size, which may cause problems when comparing samples (Brown and Weir 1983).

Nei's (1973) gene diversity statistic is a useful measure of genetic variation that is commonly employed. It measures the evenness of allelic frequencies distribution in a population. In a random mating population, it is equivalent to the expected heterozygosity. In a non-random mating population like some domesticated crops, gene diversity may not be equivalent to the expected heterozygosity. Wright's F-statistical analysis (Wright 1965, 1978; Nei 1977) is sometimes used instead of Nei's gene diversity statistic (Hokanson et al. 1993). Wright's F-statistic, defined as the deviation of genotype frequencies from Hardy-Weinberg expected frequencies in a subdivided population, is equivalent to Nei's gene diversity statistic (Swofford and Selander 1989).

To assess variability within collections and species, the following statistics can be employed: (1) actual or observed heterozygosity (H_I), the proportion of loci heterozygous in an individual averaged over all individuals in a collection; (2) expected

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heterozygosity (H_S), the proportion of heterozygous loci one would find in a collection if the population were at Hardy-Weinberg equilibrium; and (3) gene diversity (H_T), the proportion of heterozygous loci one would find in a taxon if all of its populations formed a single panmictic unit that was at Hardy-Weinberg equilibrium (Doebley et al. 1984).

Genetic similarity and distance

Allelic frequency data also allow the pair-wise measurement of genetic similarity and distance. The advantage in having these two measures is that they condense a large amount of data into a form that can be easily visualized and interpreted.

Genetic identity of Nei (1972) is a common way of measuring similarity of allelic data. The genetic similarity between populations A and B at locus j is measured by the genetic identity, I_j ,

$$I_j = \sum a_i b_i / \sqrt{(a_i{}^2 b_i{}^2)} \tag{1}$$

where, a_i = frequencies of alleles in A; b_i = frequencies of alleles in B. The genetic identity value may range from 0 to 1 at a single locus for two populations. Two populations with no common allele would have a genetic identity value of zero. A

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genetic identity value of 1 indicates that the two populations have the same alleles in identical frequencies at all loci examined. Usually, more than one locus is included when comparing populations and arithmetic means of $\Sigma a_i b_i$, Σa_i^2, and Σb_i^2 over all gene loci are used to calculate the genetic identity, I, between the two populations.

Nei's (1972) genetic distance, D, between two populations or species is used to estimate the number of allelic substitutions per locus that have occurred during their separate evolution. Genetic distance is calculated as:

$$D = -\ln I \tag{2}$$

The genetic distance value may range from 0, which indicates there has been no allelic change, to infinity. Both Nei's genetic identity and genetic distance are used to express the genetic similarity (or divergence) among populations or taxa.

Rogers (1972) proposed another method for calculating genetic distance from allelic frequency. Rogers' distance, R, between populations A and B at a locus is given by:

$$R = \sqrt{0.5 \sum (P_{A_i} - P_{B_i})^2} \tag{3}$$

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where, n = number of alleles; P_{A_i} = frequency of ith allele in population A; and P_{B_i} = frequency of ith allele in population B. When two populations are genetically identical, the value of R is 0, but when the populations are fixed for different alleles, then R equals 1. The value of R for all loci in two populations is calculated by computing the arithmetic mean of the R values for each locus (Rogers 1972). Nei's and Rogers' estimates of genetic divergence are highly correlated in practice.

Phenetic analyses

After the allelic frequencies and genetic identities or distances have been determined for the plant populations, the data can then be analyzed and visualized by phenetic methods such as cluster and principal component analyses (Crawford 1990). These techniques are useful for determining relationships among populations of the same and different species. Principal component analysis allows visualization and subsequent interpretation of multivariate data, such as the allelic frequency data, by reducing the data set to a small number of unrelated groups of variables or their components that can be plotted along independent, linear axes (Broschat 1974; Iezzoni and Pritts 1991). The genetic identity or distance data can be subjected to cluster analysis, so that similarities among taxa by groupings based on their genetic relationships can be visualized (Wendel et al. 1992).

<u>Use of isozymic evidence in the elucidation of maize's wild progenitor</u>

The use of isozyme technique in the elucidation of a crop's wild progenitor is well-illustrated by a study on *Zea mays* L. subsp. *mays* (maize) and *Zea mays* subsp. *parviglumis* Iltis et Doebley (teosinte)/crop and progenitor complexes (Doebley et al. 1984). Twenty-one enzyme loci were assayed from 61 collections of maize and its wild relatives, the teosinte. The allele frequencies obtained for all the maize and teosinte populations were subjected to principal component analysis based on the variance-covariance matrix. This analysis revealed that maize and teosinte could not be distinguished by their isozymic constitution.

From the allelic frequency data, the degree of isozymic similarity between maize and teosinte was compared by calculating genetic identities, I, (Nei 1972) and a modified Roger's distance, R, (Wright 1978). Maize and its wild progenitor was found to share a genetic identity, $I > 0.9$, which is consistent with conspecific populations (Gottlieb 1981). The variability within collections (populations) and species was examined by calculating the actual heterozygosity (H_I), expected heterozygosity (H_S), and gene diversity (H_T). Based on these parameters, the levels of variation found in maize did not exceed those found in teosinte.

This isozymic evidence strengthened the hypothesis that the teosinte from the central portion of the Balsas River drainage in northern Guerrero in Mexico is most

similar to maize biochemically, and suggests that this teosinte is the most likely

ancestor of maize (Doebley et al. 1987).

Ethnobotany of *Carica papaya*

Taxonomy of Caricaceae

The Caricaceae has no known fossil record (Woodland 1991). Raven and

Axelrod (1974) classified Caricaceae, Cucurbitaceae, and Passifloraceae in the Order

Cistales while Woodland (1991) listed the three families in the Order Violales. All

members of the Caricaceae are diploid with $2n = 18$ (Darlington and Ammal 1945).

Woodland (1991) described the members of the genus *Carica* as small, herbaceous

trees generally exuding a milky latex. The palmately veined, lobed, or compound

leaves are arranged in an alternate pattern on the trunk and clustered at the stem apex.

The regular, hypogynous flowers can either be perfect or unisexual. The inflorescence

of a solitary flower is located in leaf axils or in cymes. There are five petals and

sepals. The sepals are connected into a lobed or toothed calyx. The ten stamens

consist of filaments that are distinct or connate at the base and adnate to the corolla

tube, and anthers opening by longitudinal slits. The compound pistils consist of five

united carpels with one or five locule(s), with many ovules attached to intruded parietal

or axile placentas. The fruit is a berry having many seeds covered with gelatinous

sarcotesta. Inside the seed is an endosperm and an embryo that is straight.

Badillo (1971) provided the most complete treatment on the taxonomy of the family Caricaceae. The Caricaceae consists of four genera and 32 species. Three of the genera, *Carica* (23 species), *Jacaratia* (six species) and *Jarilla* (one species), are neotropical in distribution. The African genus, *Cylicomorpha,* has two species. *Carica* is the only genus with domesticated species. Besides *Carica papaya*, the other edible species include *C. cauliflora* (tapachulo), *C. goudotiana* (payuelo), *Carica* x *heilbornii* n.m. *pentagona* (babaco), *C. monoica* ("col de monte" or mountain cabbage), *C. pubescens* (chamburo), and *C. stipulata* (siglalon).

Historical biogeography of *Carica papaya*

Storey (1976) stated that papaya probably originated in the lowlands of eastern Central America. From studies of floral anatomy, Storey (1967) suggested that the prototype of *C. papaya* probably had perfect flowers and small fruits (50-100 g) like those of the dioecious, small-fruited *C. papaya* found presently in the Carribean region. Today, this small-fruited, dioecious type, which was known earlier by various synonyms such as *C. cubensis*, *C. jamaicensis*, *C. portorricensis*, and *C. peltata* Hooker et Arnott but later classified as the same species as *C. papaya* (Badillo 1971), can be found growing wild in this region. Storey (1967) also indicated that the existence of present-day forms of *C. papaya* was probably due to the continuous selection and planting by humans.

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Of the few reviews on the archaeobotanical records of cultivated plants of New World origin, there was no mention of papaya being found (Smith 1965; Smith 1987). This is not surprising considering the fact that herbaceous species such as papaya do not preserve well in wet tropical habitats. Miksicek (1983) listed the remains of the root and carbonized seed of wild *C. papaya* found in the Pulltrouser archaeological site in Northern Belize. However, no explanation was given as to how these remains were determined to be from wild instead of domesticated *C. papaya* plants.

The earliest known reference to papaya in European literature is in the writings of Gonzalo Fernandez de Oviedo y Valdes's "Historia General y Natural de las Indias" circa 1525 (Patiño 1963). Oviedo, who was the Spanish overseer of mines in Hispaniola (present day Haiti and Dominican Republic) from 1513 to 1525, made no mention of the presence of the wild, small-fruited papaya in Nicaragua, although this did not mean it was absent in the area at the time (Oviedo y Valdes 1959a). The Mayans referred to this wild, small-fruited papaya as "chichput" (Roys 1931). "Chich" is a word for "bird" (Roys 1933), and "put" is the Mayan word for "papaya" (Scholes and Roys 1968); therefore, "chichput" means "bird papaya." Papaya is also listed with the common name "chichioalxochitl" (meaning flower of the breast) in a Mexican medicinal plant book (Hernandez 1943). As the species does not have a Sanskrit name, it is unlikely that it is an Asian domesticate (Candolle 1908).

The *C. papaya* described by Oviedo in 1525 was definitely of the domesticated type because he mentioned seeing a "certain fig tree" with fruit sizes that were comparable to "watermelons of Spain" (Oviedo 1959b). The fruits of this "fig" tree were attached to the trunk, had thin skin, thick flesh, and small black seeds in the middle of the fruit (Oviedo 1959a). Oviedo first saw these fruits in the land of the chief of Quebore in Nicaragua. A nobleman, Alonso de Valverde, who was in charge of the chief of Quebore, brought the "figs" to Darien to be planted (Oviedo 1959b). From Darien, these "figs" were introduced to Santo Domingo and other places of Tierra-Firme (Oviedo 1959b). According to the glossary in Oviedo (1959a), Tierra-Firme is the name given to the whole coast of the mainland south and west of Hispaniola. Tierra-Firme was divided into two regions— Nueva Andalucia which extended from the middle part of the Gulf of Uraba east to the Cabo de la Vela, and Castilla del Oro which extended from the middle part of the Gulf of Uraba to Cape Gracias a Dios. Castilla del Oro was further divided into Darien in the east, Panama in the center, and Veragua in the west.

Oviedo noted that in Hispaniola these "figs" were called "papaya," and in Tierra-Firme "higos del mastuerco" (Nasturtium Figs) (Mello and Spruce 1869). The common name "papaya" was believed to have originated from the Antilles (Tejera 1951 as cited in Patiño 1963; Henriquez Ureña 1938 as cited in Patiño 1963). Mello and Spruce (1867) stated that the word "papaya" originated with the Caribs; these researchers had heard Carib descendants on the Orinoco River and elsewhere refer to

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the plant as "papaya," "mapaya," and "mamaya." According to Oviedo (1959a), the Caribs were the bow-using people of Cartagena (Colombia) who lived along coastal areas and practiced cannibalism.

Oviedo also reported that in Nicaragua, papayas were called "olocoton" because there was a place in Nicaragua known as Olocoton province between the province of Nagrando and Honduras where these papayas were found (Oviedo 1959b). Olocoton is now the site of the old city of Leon in Nicaragua (Velasco 1971). According to Squier (1851), Oviedo indicated that the province of Nagrando was somewhere in the district between the northern extremity of Lake Managua and the Pacific in what was known as the Plain of Leon. The old city of Leon, sometimes called Leon de Nagrando (Squier 1851), was abandoned in 1610 (Stout 1859). The ruins of this city now lies 32 km from the present-day city of Leon (Mexico and Central American Handbook 1992).

Oviedo defined the geographic distribution of papaya as being "from the town of Acla to the Gulf of San Blas, and the port of Nombre de Dios, down the coast, in the land of Veragua, and on the islands of Corobaro" (Oviedo 1959a; Patiño 1963). Acla is a small town in the province of Darien on the north coast of Panama on the Caribbean side of the isthmus near the Gulf of San Blas (Alcedo 1967a; Oviedo 1959a). Nombre de Dios is a town near the mouth of the Chagres River in Panama and Corobaro islands are on the north coast of Veragua near the present Laguna Chiriqui in Panama (Oviedo 1959a).

There are several discrepancies in the spellings of the places mentioned by Oviedo in the various translations and excerpts. In the "Diccionario Geografico de Las Indias Occidentales," "Nagarando" instead of "Nagrando" was listed as the name of the Indian province in Nicaragua where the city of Leon was founded (Alcedo 1967b). Nagrando and Nagarando were probably different spellings of the same place. In Mello and Spruce (1867), Nagrando was spelled as "Nogrando." Another example is "Corobaro" in Oviedo (1959a), which was spelled as "Cerebaro" in Oviedo (1959b) and as "Zorobaro" in Patiño (1963). According to Squier (1851), Oviedo's chronicle was not published in the original or discovered until 1839 by Terneau Compans. This is perhaps one of the reasons for the discrepancies.

The explorers of Francisco Pizarro found papayas in Puerto Viejo on the dry coast of Ecuador in 1531 (Trujillo 1948 as cited by Prance 1984). Because of this, Gonzalez Suarez (1890 as cited by Patiño 1963) believed that the papaya was probably grown in Ecuador in prehispanic times. In 1560, in the interandean region of Ecuador, papaya was found in Ibarra (Jimenez de la Espada 1897 as cited by Patiño 1963). Papaya was known to occur in Venezuela in 1562 because a soldier was reportedly condemmed to death for disobeying Lope de Aguirre's order not to pick the fruits in the city of Valencia (Aguado 1919 as cited by Patiño 1963). In 1582, Zamora de los Alcaides is reported to have observed papaya grown on the eastern flanks of the Andes (Jimenez de la Espada 1897 as cited by Prance 1984).

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In 1583, papaya was found in Cali (Guillen Chaparro 1889 as cited by Patiño 1963). Both Patiño (1963) and Prance (1984) also believed that the papaya was well-distributed among many tribal groups in both South and Central America in Pre-Columbian times based on the early European records mentioned above, while Towle (1961) believed otherwise for Peru. Towle's (1961) ethnobotanical study of pre-Columbian Peru found that although papaya was sometimes cultivated in Peru, it was unknown in the wild state. Also, she mentioned that there was no positive proof that it was grown there in prehistoric times. She noted that the suggestion that some pottery reproductions utilized papaya as a model could also be attributed easily to other *Carica* species existing in the area, such as *C. candicans* Gray. In 1615, Vasquez de Espinosa's account of his stay in Cajamarca, Peru mentioned that stems of the papaya trees, which were abundant along the river banks, were used as rafts for crossing the Balsas river (Vasquez de Espinosa 1969).

According to Purseglove (1974), papaya was taken from Mexico to the Philippines after 1525, and from there spread rapidly to Malaysia and Indonesia. Papaya was mentioned by Friar Navarrete during his travels to Mindoro, Philippines in 1656-1657 (Cummins 1962). In 1734, *C. papaya* was very much a part of the rural life in the Philippines as depicted in a painting by a Tagalog artist Francisco Suarez (Cummins 1962). Papaya was noted in China and Zanzibar in the mid-eighteenth century (Candolle 1908). The earliest record of papaya in Polynesia was in the journal of Captain Domingo de Boenechea who sailed from Peru to Tahiti in 1772 (Corney

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1913). The crew of Captain Domingo de Boenechea showed the natives of Mehetia how to plant seeds of papaya and other species offered as a gesture of friendship and goodwill.

Papaya's introduction to Hawaii

The introduction of papaya to Hawaii is credited to a Spanish horticulturist, Don Marin, between the years 1800 and 1823. Those first introduced papayas were reported to be large-fruited types, but on October 7, 1911, Geritt P. Wilder introduced a small papaya (accession no. 2853) from Barbados and Jamaica (Yee et al. 1970). Unlike the larger variety, this small, pyriform papaya could be consumed as a single serving, and therefore was named 'Solo' in 1919. Solo papaya later replaced the large-fruited types and became the only commercially grown variety by 1936 (Yee et al. 1970).

'Kapoho Solo' papaya was selected on the island of Hawaii for its small, firm fruits suitable for export to distant markets (Morton 1987). Grown primarily on the eastern part of the island of Hawaii, where the annual rainfall averages more than 250 cm, this strain produces fairly smooth fruits ranging in weight from 400 to 800 g. The fruits tend to be exceptionally small when grown in dry areas.

'Sunrise Solo' papaya is an inbred reddish orange strain resulting from a cross between 'Line 9' or 'Pink Solo' with the yellow-fleshed farmer's selection, 'Kariya Solo' (Hamilton and Ito 1968). At the Hawaii Agricultural Experimental Station at Poamoho, Oahu, the weigh of these fruits average 425 to 600 g (Yee et al. 1970). 'Sunrise Solo' is an important cash crop in several parts of Brazil, such as in Espirito Santo, Bahia, near Manaus, and in the Bragantina zone east of Belem (Smith et al. 1992).

'Waimanalo Solo' (formerly 'Line 77') is an orange-yellow papaya whose fruits are round with a short neck. A result of crosses between the 'Betty' variety of Florida, 'Line 5', and 'Line 8', 'Waimanalo Solo' is a high-yielding, short-statured cultivar whose average height to first flower is 81 cm compared to 154 cm for 'Line 8'. With fruits ranging in weight from 450 g to 1.1 kg, 'Waimanalo Solo' is considered too large for export. Because of its preferred flavor, thick and firm flesh, and long storage life, 'Waimanalo Solo' has replaced most of the other commercial strains on Oahu for the fresh local market (Yee et al. 1970).

Uses of *Carica papaya*

The fruits of the domesticated papaya are grown mainly for fresh consumption as an after-dinner dessert or a breakfast fruit served with a squeeze of lime or lemon. The ripe flesh can be made into sauce for pies or preserved into jams. Papaya juice

makes excellent drinks and iced smoothies. In Thailand and Vietnam, green papaya is grated and served as a salad with a dressing made of vinegar, chili pepper, and fish sauce. In the Philippines, a type of chicken soup made with leaves of *Moringa oleifera* (horse-radish tree) also includes green papaya as an essential ingredient. Young leaves of papaya are cooked and eaten like spinach in the East Indies (Morton 1987). In Java, papaya flowers are also candied (Purseglove 1974). The red-fleshed varieties are especially rich in vitamin A, which is often deficient in the diets of tropical peoples (Ochse et al. 1961). Several entrepreneurs in Hawaii are marketing dried papaya as healthy snack foods. The soft fruits are also canned, crystallized, or blended to make nutritious juices or milkshakes. In some countries, immature fruits are stewed in cane juice to make a sauce or are boiled as a vegetable.

Local and export markets determine what type of papaya to grow. Papaya growers in Hawaii export hermaphroditic, pyriform fruits weighing about 450 g (Nakasone and Storey 1955), and sell fruits in the 500-800 g range for local consumption. Larger papaya fruits, e.g., up to 3 kg, are preferred in some tropical countries. Enhanced papain production is the emphasis of some breeding programs, while higher fruit quality is the goal of others (Giacometti 1987).

Folk remedies are prepared from papayas for both humans and livestock in tropical America as well as in regions of introduction, such as Africa, Southeast Asia, and the Pacific. The seeds are eaten to eliminate intestinal parasitic worms. In Ghana,

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the Ashanti use papaya for treating minor ailments such as headaches and stomachaches, as well as serious diseases such as gonorrhea (Irvine 1961). Papain derived from papaya is used to help digestion, treat slipped disks, tan leather, prevent shrinkage of wool, and keep beer clear during the brewing process (Cobley 1956).

Ethnobotany of other lesser known *Carica* species

In this section, information is presented for *Carica* species other than *C. papaya*. Eight such species and two hybrids that are utilized by humans and 13 species that remain undomesticated are described.

Carica pubescens Lenne et Koch (chamburo or "mountain papaya")

One of the "lost crops of the Incas," the natural distribution of *C. pubescens* (chamburo or mountain papaya) is from Panama to Chile and Argentina at elevations near the tree limit from 1,500 to 3,000 m (Badillo 1971). Found at such high elevations, *C. pubescens* is adapted to cool conditions and can tolerate light frost. While commonly grown throughout its Andean home range, it is not widely cultivated elsewhere (Smith et al. 1992). This species has either dioecious or andromonoecious (hermaphrodite) flowers, and is distinguished by having pubescent leaves and petioles. The ripe fruit reaches a maximum of 15-20 cm in length and about 130 g in weight with an interior cavity that is filled with spiky seeds. *Carica pubescens* is reported to

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be resistant to papaya ringspot virus (Horovitz and Jimenez 1967). It is propagated by seeds (National Research Council 1989).

Depending on the sweetness, mountain papaya fruits are sometimes eaten fresh, but are more typically cooked in syrup. The firm, yellow flesh of the fruit is suitable for stuffing with fruits, vegetables or other fillings. The pleasing fragrance and the clear juice yielded by the ripe fruits is excellent in pies, ice cream, marmalade, or sweets. Preserves are canned and marketed in Chile (National Research Council 1989).

Carica stipulata Badillo (siglalon)

Carica stipulata can be found in the central part of the province of Azuay and Loja in southern Ecuador between the elevations of 1,600-2,450 m (Badillo 1971). This spiny *Carica* species is dioecious and can grow up to 8 m tall. It bears fruits that have 10-11 ridges and weigh about 40-150 g with an interior cavity filled smooth, but sometimes corky seeds.

Like *C. pubescens*, *C. stipulata* fruits have a strong, pleasant aroma and are also cooked with sugar and consumed as sweets. The creamy flesh is often touted as the best *Carica* species for jams and sauces as well as for drinks. It is also the best source of papain that is important for clarifying beer (National Research Council 1989).

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Carica stipulata appears to be resistant to papaya ringspot virus (Horovitz and Jimenez 1967).

Carica goudotiana Solms (payuelo or papayuelo)

Found only at mid-elevations in Colombia, *C. goudotiana* grows in humid forests between 1,500 to 2,300 m (Badillo 1971). It has an upright habit that often branches at the base. A dioecious but highly variable species, it has flowers that are greenish white with red or green petioles. The five-angled fruits can range from shades of pale yellow to orange, red and dark purple. When mature, the fruits can be up to 20 cm in length and weigh up to 200 g. *C. goudotiana* seems to be susceptible to papaya ringspot virus (Horovitz and Jimenez 1967).

The flesh of the fruits is sometimes likened to that of a mildly acidic apple. The fruits are typically cooked before eating. Astringent fruits must be peeled and soaked overnight in water before being boiled with raw sugar and flavored with spices such as cinnamon (Luis Lopez, personal communication). Such spiced condiment is usually prepared at Christmas time and served with cheese in Colombia.

Carica cauliflora Jacq. (tapaculo)

The distribution of *C. cauliflora* is from southern Mexico to the northern part of South America, including the island of Trinidad, at elevations from sea level to 1,200 m (Badillo 1971). Fruits are yellow, ovoid, and about 7 cm in length. Seeds are covered with dense mucilaginous sarcotesta. The fruits are edible and are occasionally utilized like those of *C. goudotiana* and *C. pubescens*. *Carica cauliflora* appears resistant to papaya ringspot virus (Horovitz and Jimenez 1967).

Carica monoica Desf. (col de monte or "mountain cabbage")

Carica monoica can be found in Ecuador, eastern Peru and Bolivia at elevations between 600 and 1,700 m (Badillo 1971). A monoecious species, the plants can self-fertilize. Growing in regions of high rainfall and mild temperatures, it can attain a height of 1-3 m. The fruit has a hard skin that is brilliant orange. The flesh is deep yellow to orange in color with large horned seeds in the interior cavity.

The flesh of ripe, firm fruits can be stewed with lemon and sugar, candied, dried or frozen (National Research Council 1989). In addition, the young seedlings and mature leaves are eaten as vegetables and thus the name, "col de monte" or "mountain cabbage." *Carica monoica* is susceptible to papaya ringspot virus,

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however, hybrids with *C. pubescens* seem to be resistant to the virus (Horovitz and Jimenez 1967).

Carica microcarpa Jacq. (col de monte)

Of all the *Carica* species, *C. microcarpa* is the most variable morphologically and thus has been subdivided into several subspecies. *Carica microcarpa* Jacq. subsp. *microcarpa* Jacq. occurs in tropical and subtropical humid forests of Venezuela, Colombia, and Ecuador (Badillo 1971). Its ovoid fruits can be yellow or orange. *Carica microcarpa* subsp. *heterophylla* (Poepp. et Endl.) Badillo can be found in well-drained soils in tropical forests of Panama, southern Colombia, eastern Ecuador, Brazil (except the south), and Peru. Subspecies *heterophylla* also has ovoid, yellow fruits though it differs with subspecies *microcarpa* by leaf morphology. The distribution of *C. microcarpa* subsp. *baccata* (Heilborn) Badillo also includes the humid tropical regions of Ecuador, but it is distinguished by having red, ellipsoidal fruits. The leaves of all three subspecies are eaten as vegetables and thus the common name, "col de monte."

Carica pulchra Badillo (col de monte)

Carica pulchra Badillo is another species of *Carica* known commonly as "col de monte" or "mountain cabbage" because of its edible leaves. It is closely related to

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C. microcarpa Jacq. (Badillo 1971). The male flowers are olive in color, while the female flowers can be greenish-white to white in color. The undersides of the large, mature leaves are purplish. Fruits are smooth, orange to red, ellipsoidal, and about 4 cm long. It is known to occur only on the western slope of the Andes in Ecuador in the humid, subtropical forests between the elevations of 1,800-2,000 m.

Carica x heilbornii Badillo n.m. *pentagona* (Heilborn) (babaco)

Carica x heilbornii Badillo n.m. *pentagona* (Heilborn) (babaco) may be a natural hybrid between *C. stipulata* and *C. pubescens* (Badillo 1971). Known only from cultivation, no wild babaco populations have ever been observed. Babaco grows well in a moderately cool and dry climate. Presently cultivated in New Zealand, Australia, California, Colombia, and the Mediterranean region (Smith et al. 1992), babaco is the preferred hybrid for commercial production in mid-elevations to highlands. In Ecuador, it is grown in the Andean valleys for consumption as cooked fruits (Morton 1987). It has large, typically seedless fruits, some weighing 2 kg, that have a distinctive fragrance and flavorful taste reminiscent of strawberry with a hint of pineapple according to some reviewers. Babaco is harvested when it is green to yellow, and ripens to a bright yellow. The flesh is white to cream in color and juicy. The seedless fruits are readily eaten fresh (both skin and pulp may be consumed) or cooked.

Babaco is being exported as a fresh fruit from New Zealand to Japan and the United States (National Research Council 1989). With proper post-harvest handling, it has a shelf-life of approximately one month or more at 6°C. Also, it is especially successful as a greenhouse crop because the plant is small (1-2 m), can be propagated by cuttings or tissue culture, and needs no pollinators.

Carica x *heilbornii* Badillo n.m. *chrysopetala* (Heilborn) (toronchi)

Carica x *heilbornii* Badillo n.m. *chrysopetala* (Heilborn) or "toronchi" is a natural hybrid occurring up to about 2,500 m elevation near villages in southern Ecuador (Badillo 1971). Adapted to cool environments, it is frost-resistant and may grow vigorously to 5 m in height, although most selected types are shorter (2.5 m). Toronchi is one of the least seedy highland papayas. The mature fruit is typically 10-15 cm long and weighs up to 0.5 kg. When ripe, the fragrant, smooth-skinned fruit can be green to lemon-yellow in color. The white, juicy pulp has a medium papain content, and can be eaten fresh without peeling. If cooked, they are used in making sauces, jams, pies, and pickles, as well as for adding to cheesecake and dairy products such as yogurt. "Lemon Creme" is a vigorous and productive cultivar from New Zealand that bears lemon-scented fruits (National Research Council 1989).

Toronchi grows rapidly and bears high-quality fruits within 12 months. However, because toronchi fruits are delicate and must be handled more carefully than babaco, this hybrid does not ship well. While it functions as a sterile hybrid, pollination increases the production of fruits, which frequently contain viable seeds. Toronchi hybridizes readily with *C. stipulata* (siglalon) that results in many intermediate forms with different flavors and varying amounts of seed (National Research Council 1989).

Other wild *Carica* species

Wild *Carica* species described taxonomically by Badillo (1971) include *C. parviflora* (A.DC.) Solms, *C. augusti* Harms, *C. glandulosa* Pavon ex A.DC., *C. quercifolia* (St. Hil) Hieron, *C. aprica* Badillo, *C. candicans* A. gray, *C. chilensis* (Planch. ex A.DC.) Solms, *C. weberbaueri* Harms, *C. crassipetala* Badillo, *C. omnilingua* Badillo, *C. horovitziana* Badillo, *C. sprucei* Badillo, and *C. longiflora* Badillo. *Carica parviflora, C. quercifolia*, and *C. crassipetala* are potentially useful as ornamental plants. *Carica chilensis* is a rare and endangered species in Chile (Miguel Jordan, personal communication).

Disease resistance and conservation of *Carica* species

While *C. pubescens, C. stipulata,* and *C. cauliflora* appear to be resistant to papaya ringspot virus (Horovitz and Jimenez 1967), none of these wild species can be hybridized with papaya by conventional breeding methods (Litz 1986). Because wild material may eventually prove to be a source of resistance for some viruses and fungi, breeding research needs to address this constraint. In 1986, the Tropical Research and Education Center of the University of Florida developed a disease-tolerant *C. papaya* 'Cariflora', a variety from dioecious lines obtained from a commercial grove. 'Cariflora' can yield 35 metric tonnes per hectare per year and is recommended for Florida and lowland areas of the Caribbean (Conover et al. 1986). If the papaya ringspot virus pressure is severe, however, 'Cariflora' can succumb to the disease (Campbell 1986). At the University of Hawaii, a PRV-tolerant papaya (Line 356) has been developed recently (Zee 1985).

Root rot caused by *Phytopthora palmivora* in Hawaii and *P. parastica* in Brazil, root and trunk rot due to *Pythium* spp., and anthracnose caused by *Colletotrichum gloeosporioides* are the principal fungal diseases of papaya. *Carica monoica,*
C. goudotiana, and *C. cauliflora* have some degree of resistance to fungal diseases of leaf tissue caused by *Acrosporium caricae, Asperisporium caricae*, and *Cercospora caricae* (Smith et al. 1992).

For disease intervention and conservation efforts, Smith et al. (1992) suggest that at least some collections should be conducted from a coarse grid sampling of the papaya gene pool for ecogeographic variants. Collecting expeditions should be concentrated in Latin America, especially in papaya's area of origin. Africa, Asia, and the Pacific should also be explored for useful, unusual gene combinations. Collecting wild *Carica* species is also essential and their natural history needs further study. This is because wild species relatives of crops often harbor rich sources of disease resistance and arrays of morphological variation that are potentially useful in plant breeding (Marshall 1990).

CHAPTER 3

GERMPLASM COLLECTION OF *CARICA PAPAYA* AND RELATED SPECIES

Prior to 1992, the Department of Horticulture at the University of Hawaii and the United States Department of Agriculture (USDA) National Clonal Germplasm Repository maintained approximately 100 accessions of *C. papaya* and six accessions of related *Carica* species. Of the *C. papaya* accessions, most were cultivars and breeding lines from Hawaii and Asia. The virtual absence of *C. papaya* germplasm from its native area of origin in tropical America prompted two papaya collecting expeditions to Central and South America. The first expedition in March-April of 1992 covered southern Mexico, Belize, Guatemala, Honduras, and Costa Rica. The second expedition in June-July of 1993 included Venezuela, Colombia, Ecuador, and Panama.

METHODS

The choice of collecting locations was based on information obtained in the literature and from personal communications with other researchers familiar with the two regions. Most of the propagating material for the *C. papaya* and *Carica* species accessions was in the form of seeds extracted from mature fruits, although some stem cuttings were collected from *Carica* x *heilbornii* n.m. *pentagona* (babaco) and wild *Carica* species without fruit. The seeds were cleaned by removing the sarcotestae and dried before being sent via air mail to the USDA quarantine facilities in Honolulu.

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Whenever possible, fruits were collected from at least 30 individuals from as many

locations as possible of the different types of *C. papaya* and other *Carica* species in

markets, backyard gardens, and in the wild. If it was not possible to collect materials

personally, arrangements with collaborators were made to procure seeds and other

propagating materials for shipment later.

RESULTS

Types of *Carica papaya* collected

The *C. papaya* material collected can be divided into three types: (1) wild;

(2) domesticated; and (3) hybrid between wild and domesticated types (Fig. 3.1). The

domesticated papayas were usually collected from local markets, backyard gardens, and

orchards. The wild and the hybrid papayas were collected most often in hedgerows, in

abandoned fields, in rubbish heaps, and along roadsides, where they occur

spontaneously.

Wild *Carica papaya*

The wild *C. papaya* (also known by the synonym *C. peltata* Hooker et Arnott)

has small, almost spherical fruits with diameters of about 2.5 cm. The thin and hardly

edible flesh of the fruit is yellow-orange and never red as sometimes observed in

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Fig. 3.1. Photograph of domesticated, hybrid, and wild *Carica papaya*.

814   808

815

44
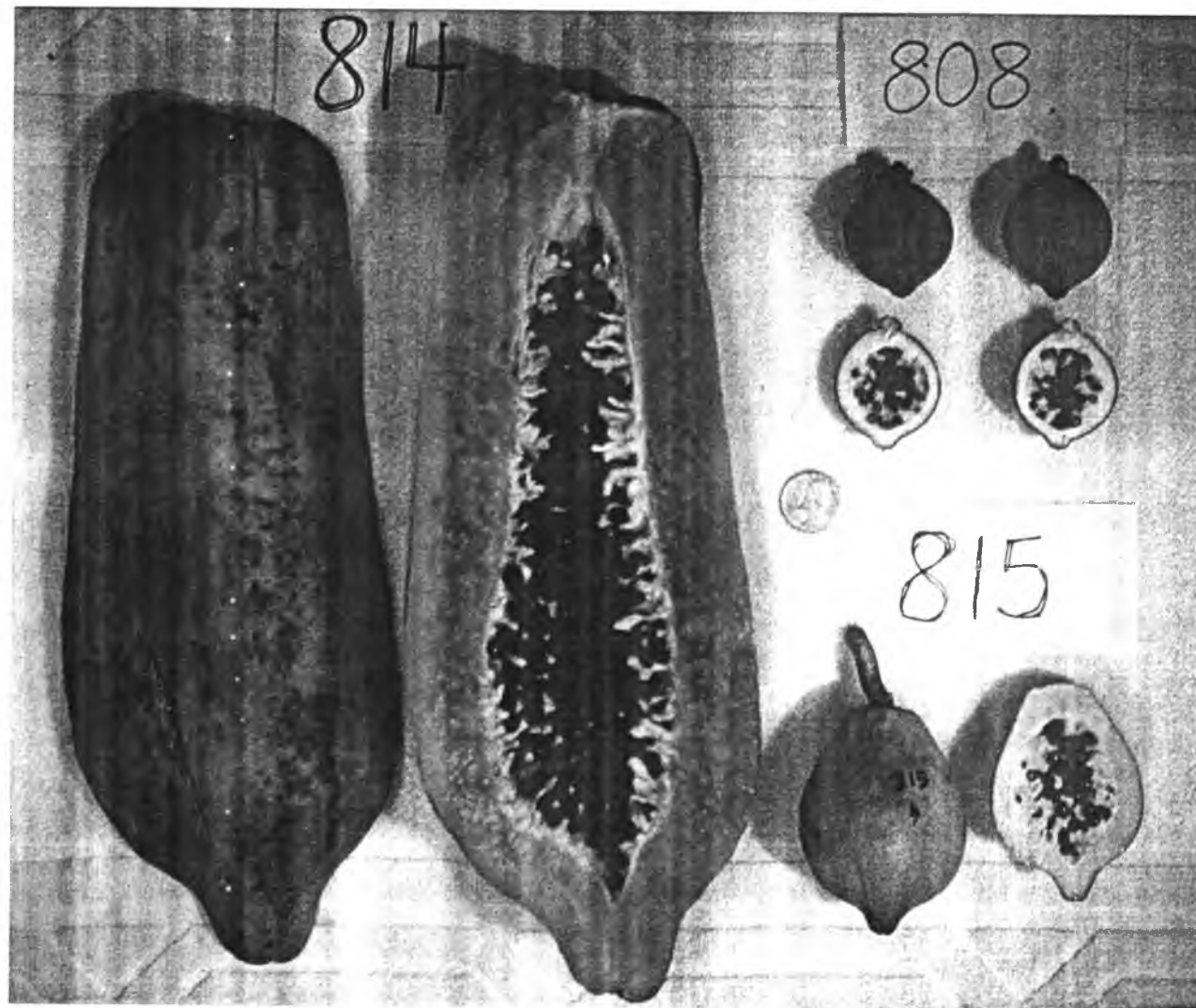
domesticated papayas (Fig. 3.1). The interior cavity of the fruit lacks air space and is completely packed with seeds. The fruit weight seldom exceeds 100 g (Appendix A). The leaf petioles are usually purple (Fig. 3.2), although some were found to have green or greenish-purple petioles. The flowers tend to be mostly yellow (Fig. 3.2) in contrast to the mostly cream-colored flowers of domesticated papayas. The fruiting nodes often bear multiple fruits (more than three) as depicted in Fig. 3.3, but individual wild plants with only one fruit per node were also encountered. The wild papaya appears to be dioecious as no hermaphrodites were found in any of the wild populations. The seeds of the wild papayas are distinctly smaller than the domesticated papayas and exhibit an apparent dormancy during germination.

The wild *C. papaya* described above thrives in open, disturbed habitats with calcareous soils from the Yucatan Peninsula in Mexico to Belize, and in the Peten region and the Rio Motagua valley of Guatemala. Wild *C. papaya* is often one of the first plant species to emerge in recently cleared forests and archaeological sites (Richard Adams, personal communication). During collecting trips for this dissertation research, wild papaya plants were usually observed to be associated with Mayan ruins, abandoned maize fields, and road sides as an opportunistic or pioneer species and were not observed in closed-canopy forest. Original populations of papaya probably exploited forest gaps and edges of rivers and lakes (Smith et al. 1992).

Fig. 3.2. Photograph of wild papaya flowers and petioles.

Fig. 3.3. Photograph of wild *Carica papaya* fruits in multiple clusters.
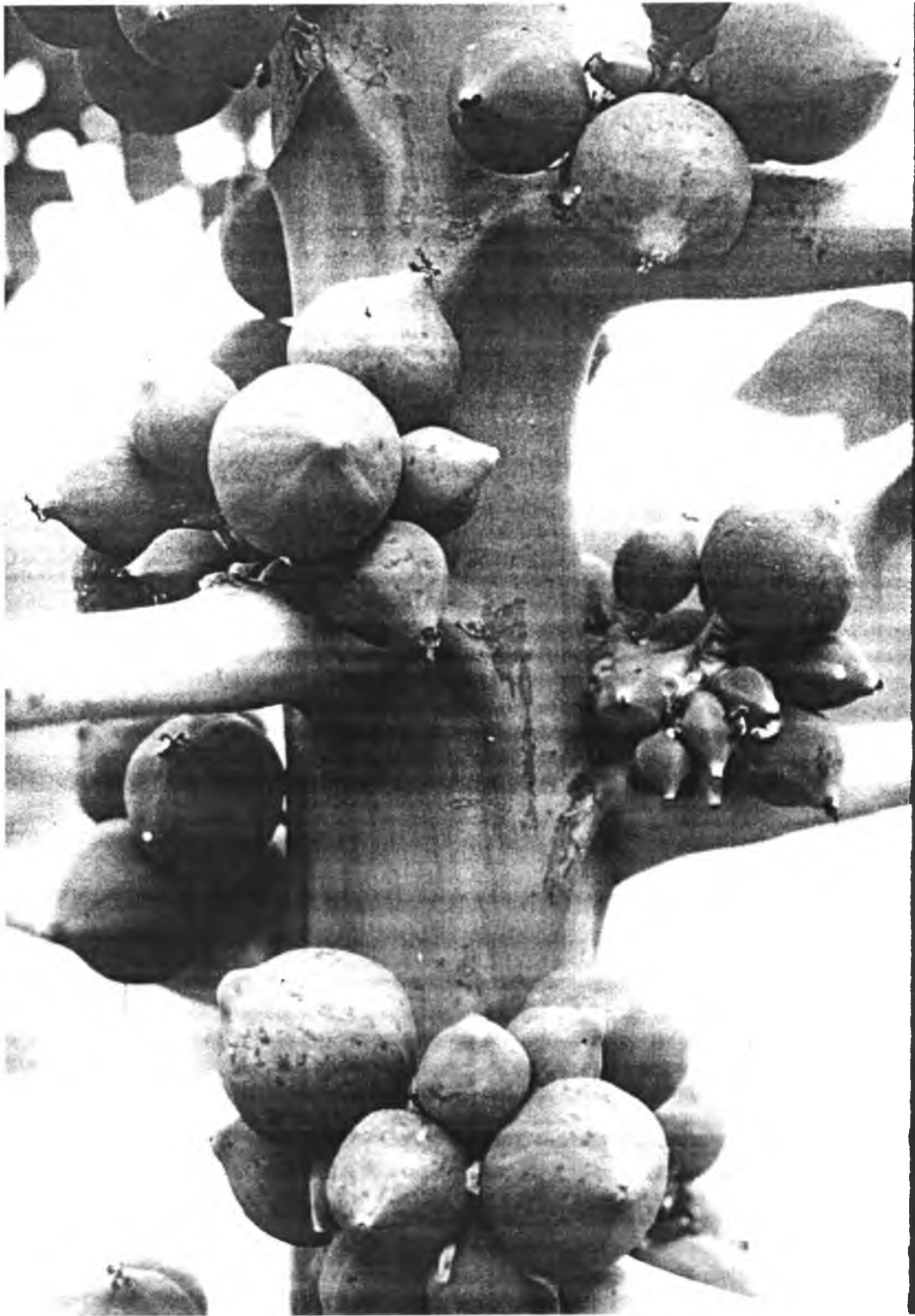
In contrast, the thick-fleshed domesticated papaya fruits can weigh from 1 to 10 kg (Appendix A). When ripe, the flesh color of domesticated papaya fruits ranges from yellow to orange and red. The flowers are usually white and the fruiting nodes seldom bear more than two fruits per node (Fig. 3.4). The larger seed size of the domesticates and lack of dormancy are consistent with trends found in other plants that have been domesticated (Evans 1993; Ladizinsky 1987). The domesticated papaya may be dioecious, gynodioecious, or polygamous, and the seeds collected were from both female and hermaphroditic plants. Symptoms of papaya ringspot virus (PRV) were observed in domesticates in Veracruz, Mexico; in wild "chichput" in Yucatan, Mexico; in commercial plantations near San Pedro Sula, Honduras; in backyard gardens near Maracay, Venezuela; and in commercial plantations in Pichincha, Ecuador. No signs of *Phytophthora* infection were observed in the papaya plantations or in the wild.

Hybrid *Carica papaya*

Often growing alongside the wild *C. papaya* are individuals with morphology intermediate between the wild and the domesticated papaya. The flesh of these hybrids is considerably thicker than the wild type, with colors ranging from yellow to red (Fig. 3.1). The fruit size is larger (usually 100 g to 1 kg) (Appendix A). The flower colors displayed are either white or yellow and the petiole color can be

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Fig. 3.4. Photograph of domesticated papaya flowers and petioles.

green to dark purple. While hybrid types can be found in the same areas as the wild type, their presence was also observed further south in Honduras, Costa Rica, Panama, and Venezuela where typically no wild type was encountered.

Carica papaya populations

Field expeditions in 1992 and 1993 resulted in the collection of seeds from 182 accessions of *C. papaya* from nine countries in Central and South America. Appendix A provides detailed information for all accessions. To facilitate the investigation of genetic variability in *C. papaya* germplasm, the accessions were classified as wild, domesticated, or hybrid, principally on the basis of fruit weight, and grouped into populations by similar geographic and ecological locations (Table 3.1 and Fig. 3.5).

Texcoco, Mexico, a town about 20 km from Mexico City at an altitude of 2000 m, is too high in elevation to grow papaya. All fruits collected in the markets there came from either the Pacific or Gulf coasts. In Veracruz, Mexico, no wild plants were observed or reported by the local people, although one small-fruited (150 g) plant was collected in Veracruz and classified as a hybrid type. The domesticated papayas found in Texcoco and Veracruz city markets consist of a yellow-fleshed, polygamous, dioecious variety known locally as 'Cera' (wax) and a red-fleshed, hermaphroditic type called 'Mamey' (Fig. 3.6). Most 'Cera' fruits were large (> 1,500 g), spheroidal to ovoid in shape, and had a strong, musky aroma. The thick, light-yellow flesh was not

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Table 3.1. *Carica papaya* populations, country of origin, location collected, and accession numbers

Type	Population	Country	Location	Accession Nos. (UH)
Domesticated	1. DVER	Mexico	Caribbean coast	800, 801, 804, 805
	2. DYUC	Mexico	Yucatan peninsula	814, 820
	3. DSAN	Belize	Cayo	825
	4. DRIO	Guatemala	Rio Motagua	878, 879, 880, 882
	5. DPAC	Guatemala	Pacific coast	883, 884, 885, 886, 891, 892, 894, 895, 896, 897
	6. DHON	Honduras	Honduras	899, 902, 903, 904, 910
	7. DCOS	Costa Rica	Costa Rica	916, 917, 918, 919, 923, 931, 932
	8. DVEN	Venezuela	Venezuela	1001, 1002, 1003, 1004, 1011, 1012
	9. DBUE	Colombia	Buenaventura area	1038, 1039, 1040, 1041, 1042, 1044, 1045, 1046, 1047, 1048, 1049, 1050, 1051, 1052
	10. DYOP	Colombia	Yopal	1067, 1068
	11. DDOM	Ecuador	Pichincha area	1075, 1076, 1077, 1079, 1080, 1081, 1082, 1083, 1109, 1110, 1111
	12. DNAP	Ecuador	Napo	1094, 1096, 1097, 1098
	13. DPAN	Panama	Panama City	1126, 1127, 1128
Hybrid	14. HVER	Mexico	Caribbean coast	806
	15. HSAN	Belize	Cayo	826, 832
	16. HPET	Guatemala	Peten	849, 851
	17. HRIO	Guatemala	Rio Motagua	863, 864, 865, 869, 870, 872, 873, 874, 875, 876
	18. HHON	Honduras	Honduras	898, 907, 908, 909, 911, 912, 914, 915
	19. HCOS	Costa Rica	Costa Rica	920, 925, 926, 927, 928, 929, 930
	20. HVEN	Venezuela	Venezuela	1006, 1008
Wild	21. WYUC	Mexico	Yucatan Peninsula	808, 812, 813
	22. WSAN	Belize	Cayo	827, 828, 829, 830, 835, 836, 837
	23. WPET	Guatemala	Peten	842, 843, 848, 852, 853, 854, 855, 857, 858, 859, 860, 861, 862
	24. WRIO	Guatemala	Rio Motagua	866, 867, 871
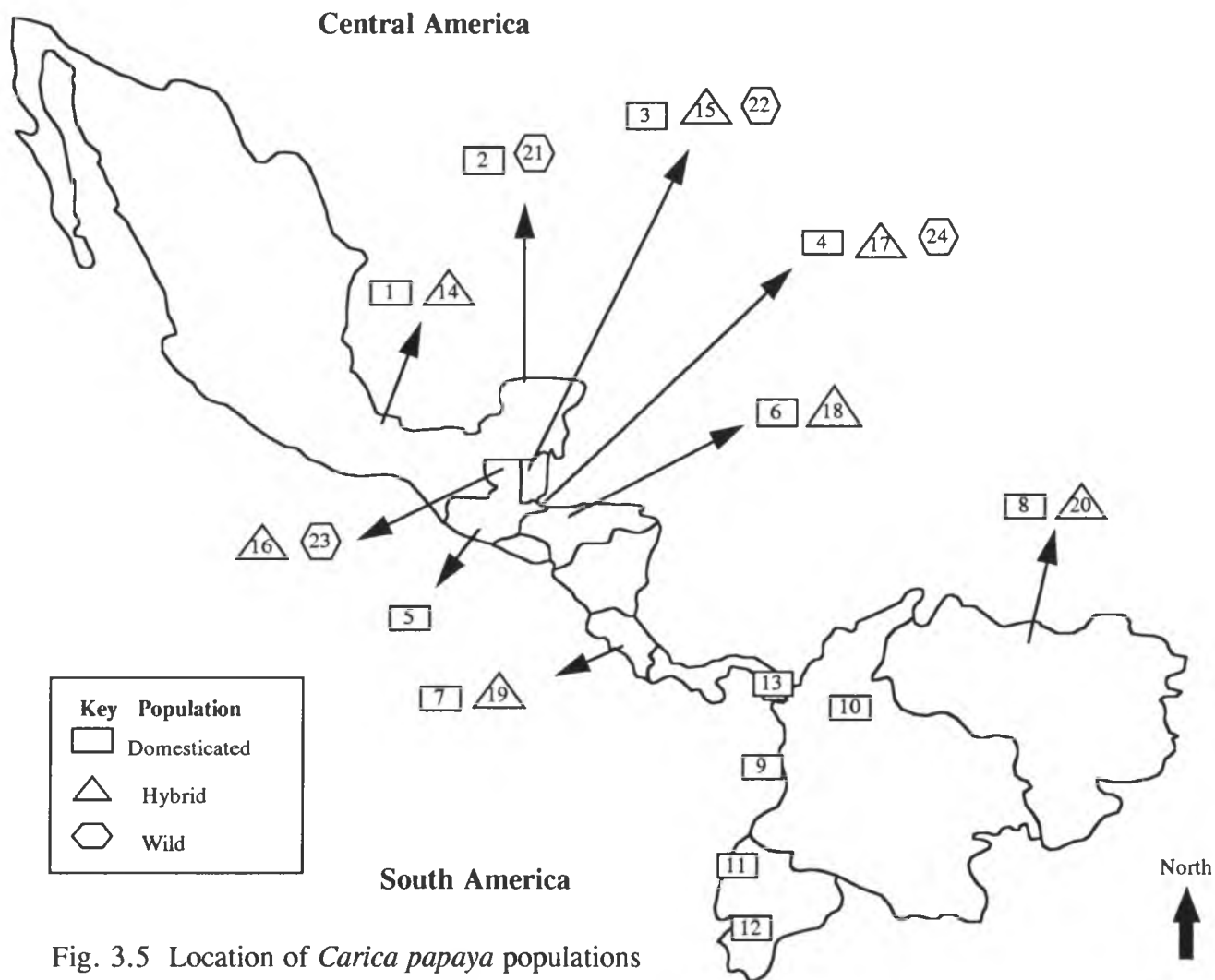
Fig. 3.5 Location of *Carica papaya* populations

Fig. 3.6. Domesticated *Carica papaya* from Veracruz, Mexico— yellow-fleshed 'Cera' and red-fleshed 'Mamey'.
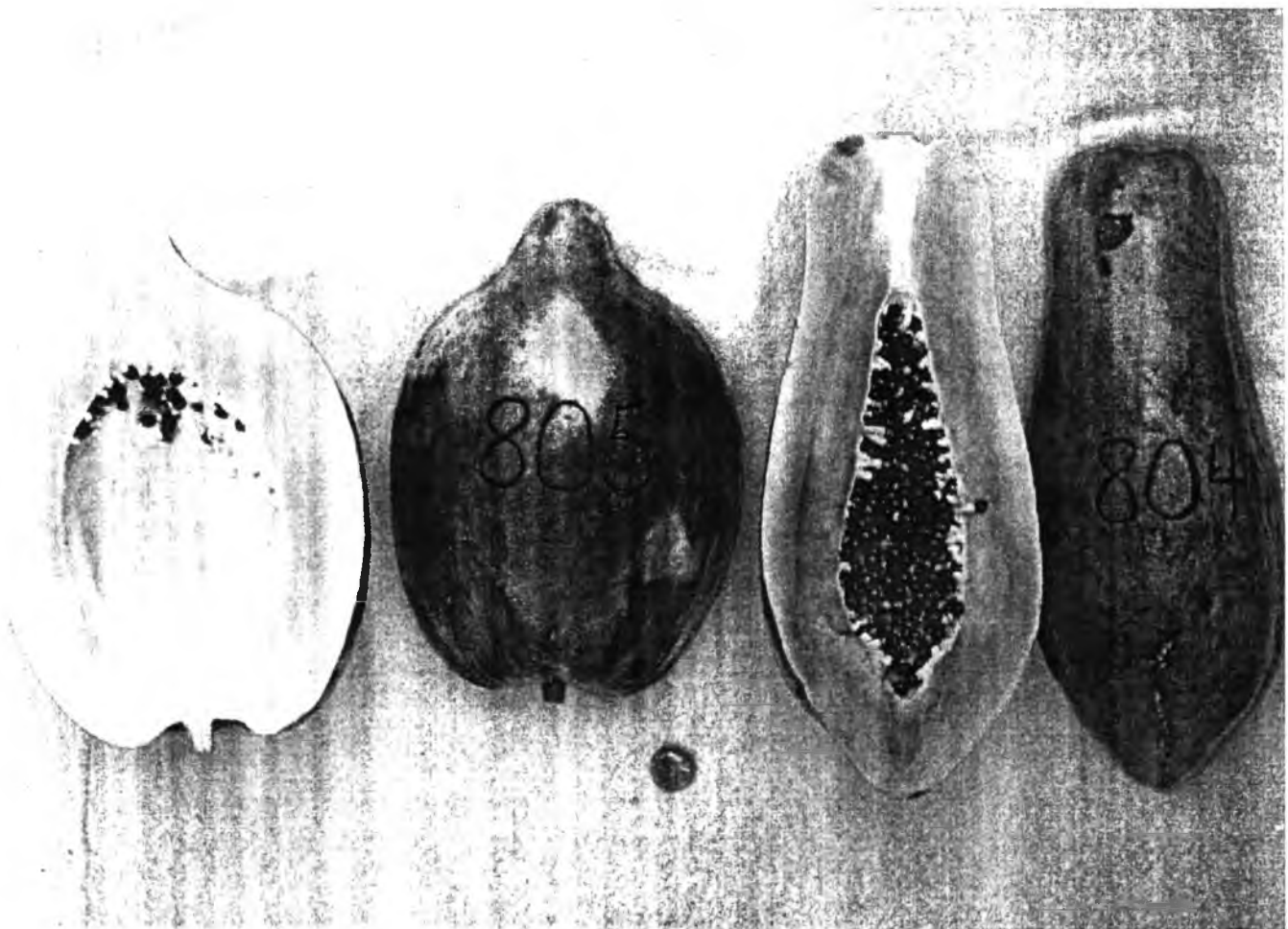
sweet (total soluble solids ranged from 7.7-9.7 percent). 'Cera' also has a thick-skinned fruit that does not bruise easily despite rough post-harvest handling (Raul Mosqueda, personal communication). According to the local vendors, the 'Mamey' papaya came originally from the Pacific coast of Mexico, although some fruits were grown in Tabasco province on the Gulf coast. 'Mamey' papayas sold in the markets also tend to be large (>2 kg), and have low sugar content (total soluble solids of 8.0-9.2 percent). The seed samples of domesticated and hybrid papayas obtained near Texcoco and Veracruz were designated as DVER and HVER, respectively. The papaya ringspot virus (PRV) disease is present in the papaya-growing areas in Veracruz province (Raul Mosqueda-Vasquez and Daniel Teliz-Ortiz, personal communications). In a commercial plantation of 'Cera' papaya in the town of Hatito, Veracruz province, PRV symptoms of mottling and chlorosis of the apical leaves was observed on most of the plants. No *Phytophthora* infection was observed on any papaya plant (either wild or domesticated).

In the Yucatan peninsula, domesticated (DYUC) and wild (WYUC) papaya samples were from areas in the vicinity of Merida south to Oxkutzcab (Table 3.1 and Fig. 3.1). Abundant wild plants growing in dry, calcareous soils were found along roadsides, in rubbish heaps, and at the Mayan ceremonial center in Uxmal. The fruits, which had very little flesh, varied from grape to golf ball size, weighed about 25-55 g, and were frequently observed to occur in multiple clusters at each node. Near the town of Loltun, wild papaya plants (UH accession nos. 816 and 817) showed the

58

characteristic PRV symptoms of mottled leaf and "ringspots" on the fruit. The people of the Yucatan area refer to this wild papaya as "papaya de los pajaros" (bird papaya) or by its Mayan name "chichput" (little bird papaya). Apparently, the seeds of these wild papayas are eaten and dispersed by birds.

The domesticated papayas in the markets of the Yucatan tend to be of the red-fleshed 'Mamey' type. There was evidence of hybridization between the wild and the domesticated papayas in the Yucatan. Individuals with fruits intermediate in size (like a tennis ball) between the wild and the domesticated (from 115-125 g) were found at garbage dumps and in hedgerows of a backyard garden. These hybrids can be spheroidal in shape or obovate with a pronounced stylar end.

The Belizean papaya accessions were mostly from areas around San Ignacio, Cayo District. The wild papaya (WSAN) thrived along newly opened dirt roads in this region. However, domesticates and hybrids tended to be rare. The wild papaya fruits ranged in shape and size from that of a grape to a ping-pong ball. The fruit cavity was packed full of seeds. Some plants along the Yalbac Road had fruits infested with insect larvae. The thin, yellow flesh of the wild fruit was soft and succulent when ripe and had a musky odor. One hybrid individual (UH accession no. 826) had fruits that were spheroidal with distinct ridges. The other hybrid individual (UH accession no. 832) was found among a cultivated patch of papaya plants in a banana field. UH accession no. 832 had obovate fruits with a pronounced stylar end, musky aroma, fruit cavity full

of seeds. Only one domesticated papaya (DSAN) was obtained, and this came from a robust tree in a dooryard garden. This individual plant had a fruit with red-orange flesh and an elongated shape with a pronounced stylar end. The leaf petiole was, however, dark purple like most wild papayas.

In Guatemala, the papaya accessions were collected from three major areas, the Peten region in the north, the Rio Motagua valley in the south, and the Pacific coast area that includes Suchitepequez and Retalhuleu provinces in the west. In the Peten region, mostly wild (WPET), two hybrid (HPET), and two domesticated papayas (DPET) were found (Fig. 3.7). The wild populations had small (15-100 g), yellow-fleshed, spheroidal fruits arranged in multiple clusters on each node. Like the wild Yucatan fruits, the wild Peten fruits were thin-fleshed and full of seeds. The flowers of the wild plants were consistently yellow, and the leaf petioles varied from light to dark purple. The two hybrid accessions were also yellow-fleshed, but with fruit sizes intermediate (250-350 g) between the wild and the domesticated papayas. The fruit cavity was partially compact, i.e., contained an air space. These hybrids also had light purple petioles. No flowers were present.

Two domesticated accessions were collected from the Peten area. Although one accession (UH no. 846) had a small-sized fruit (50 g), it was classified as a domesticated type for various reasons. First of all, it was a hermaphrodite plant in a backyard garden in Santa Elena with elongated fruits, unlike the wild papayas that were

60

Fig. 3.7. *Carica papaya* accessions from Peten, Guatemala.
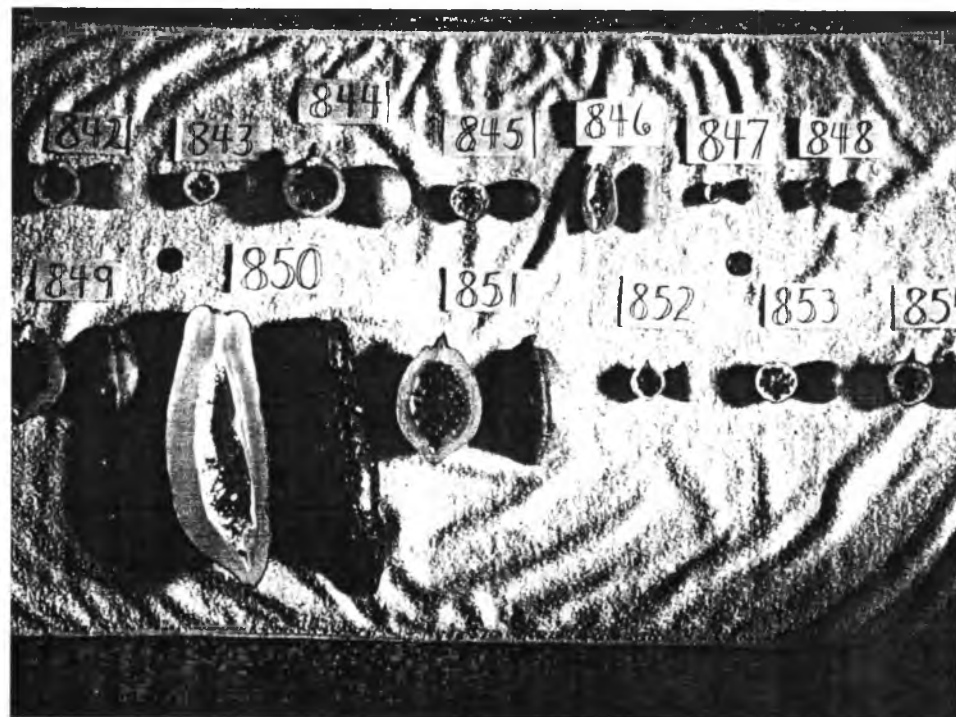
dioecious and usually with spheroid-shaped fruits. The fruit cavity contained a large air space that was not packed with seeds as is typical of wild fruits. Furthermore, the fruit flesh was red while the wild ones tended to have yellow flesh. Unfortunately, the few seeds that were present in the fruit cavity did not germinate. The other domesticated accession obtained (UH no. 850) was a large, red-fleshed type, although no seeds were available for analysis. No PRV or insect larvae-infested fruit was observed in the Peten.

In the Rio Motagua valley, all three types of papaya were found (Figs. 3.8 and 3.9), and thus were designated DRIO, HRIO, and WRIO for the domesticated, hybrid, and wild type, respectively. Except for three domesticated samples, the remaining Rio Motagua accessions had yellow-fleshed fruits. There were fewer wild papayas and more hybrids compared to the Peten. A trend of increasing fruit size was evident as we traveled from the Peten in the northern part of Guatemala and the San Ignacio, Belize area (about the same latitude as the Peten) to the Rio Motagua valley in the south, where the spontaneous papaya populations displayed more hybrid features. Insect larval infestation of the wild and domesticated fruits was observed in the Rio Motagua. In the province of Zacapa in the town of Doña Maria, a species of fruit fly (*Toxotrypana curvicauda*) was observed on the fruit of a domesticated papaya tree.

To the west, only domesticated papayas (DPAC) were collected from the Pacific coast of Guatemala with the assistance of personnel from the Universidad de

63

Fig. 3.8. *Carica papaya* accessions from Rio Motagua, Guatemala.

863 864 865 866 867

868 869 870 871 872

65

Fig. 3.9. *Carica papaya* accessions from Rio Motagua, Guatemala.

873 874 875 876

877 878

67
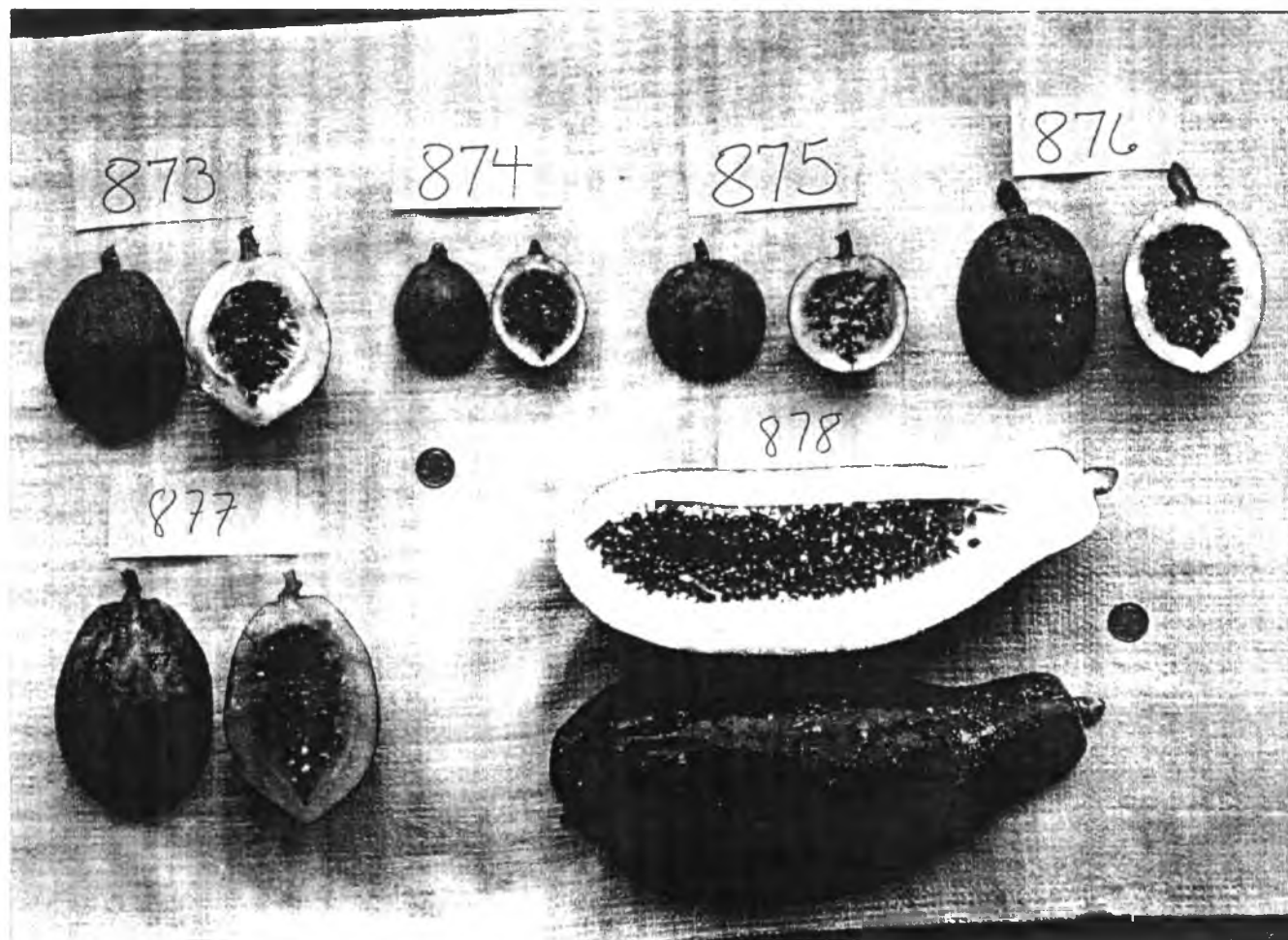
San Carlos (USC), Guatemala City, Guatemala. It was not known if wild or hybrid papaya existed there although the USC collectors did say that "small-fruited" types were present on the Pacific side. The domesticated papaya fruits from the Pacific coast of Guatemala were uniformly red-fleshed (Fig. 3.10) unlike those of the east coast in Rio Motagua where most were yellow-fleshed. The Pacific coast papayas also contained high total soluble solids (average 11.7 percent). Most of the Pacific coast papayas were larger than 1,300 g, with two exceptions that weighed 500-600 g.

In Honduras, although two wild populations were observed, neither had viable seeds for analysis because the fruits collected were immature. Again, the further south we traveled from the Peten/San Ignacio area, the less frequently were wild papaya populations encountered. Most of the Honduran materials consisted of hybrid and domesticated papaya populations (Fig. 3.11). Several hybrids (HHON) were observed in the province of Cortes (La Lima and La Entrada) and Atlantida (Metalia and Las Mangas). The flesh color of the San Pedro Sula domesticated papayas (DHON) tended to be more of a salmon shade rather than the typical orange-red color associated with domesticated papayas from other regions. Domesticates from the markets in San Pedro Sula were also among the largest (>5 kg) found during either expedition (Appendix A). Symptoms of PRV were observed in commercial plantations near San Pedro Sula.

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Fig. 3.10. *Carica papaya* accessions from Pacific coast, Guatemala.
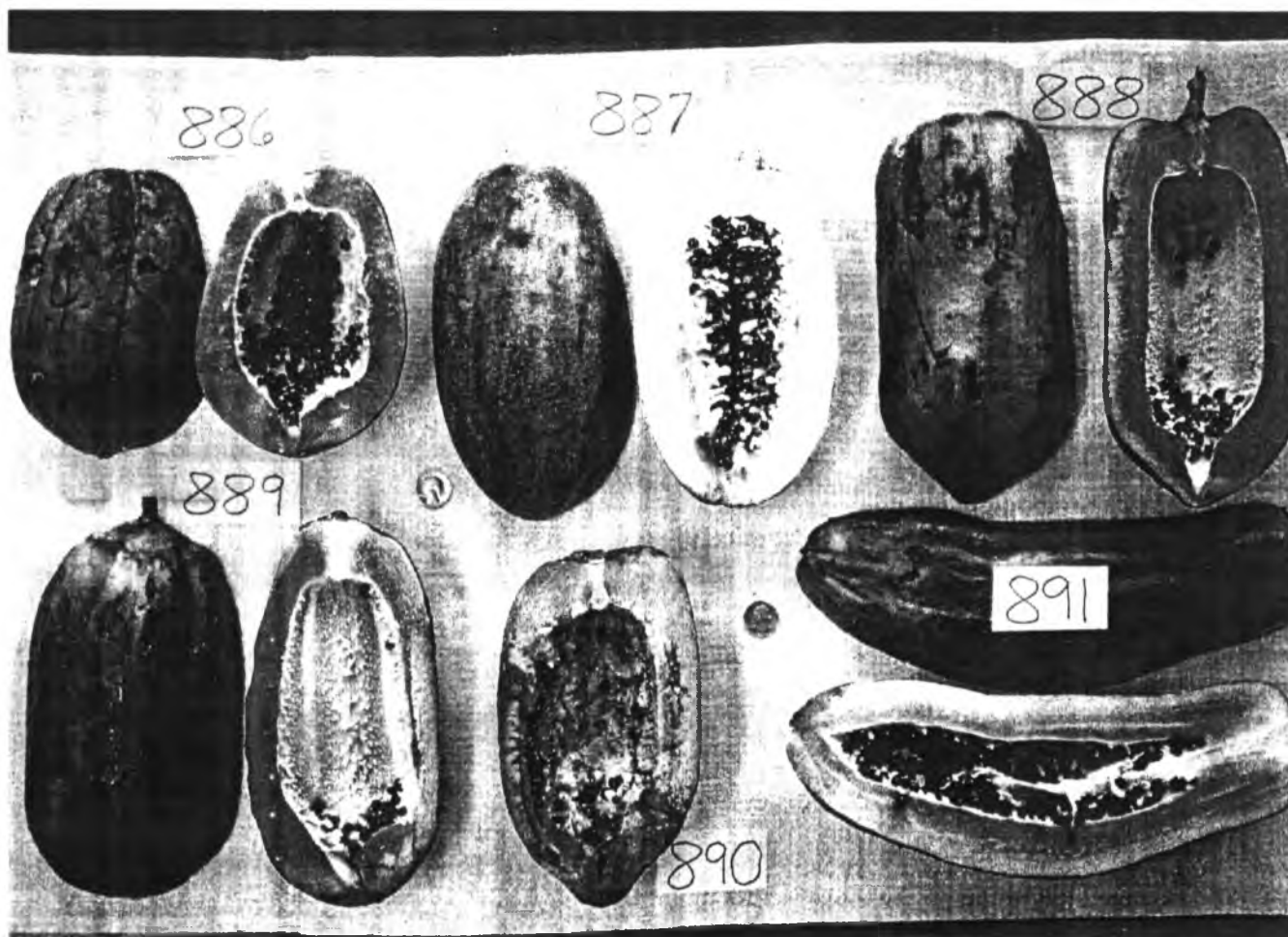
Fig. 3.11. *Carica papaya* accessions from Honduras.

906   907

908   909

72
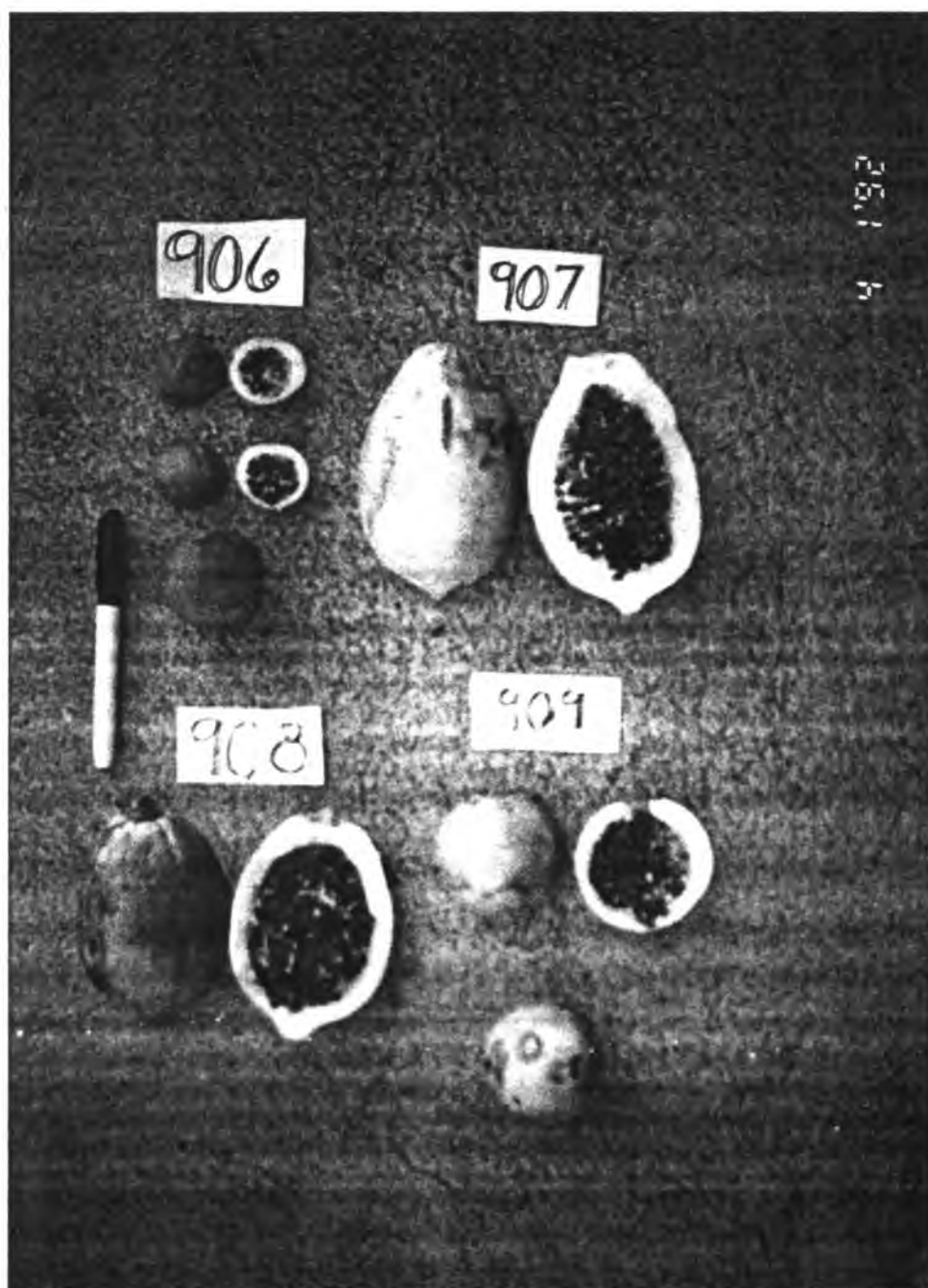
No small-fruited wild populations were found in Costa Rica. Several hybrid populations (HCOS) were found in Potrero Grande in the valley of the Rio General on the southwest coast, and at the campus of Escuela Agricultura de Region Tropical Humedos (E.A.R.T.H.) at El Brujo, and at Rio Frio (gift of Dr. Jorge Leon) on the East coast. The hybrids were mostly females with exceptionally thick ovary walls, and all (except UH accession no. 925, which was too immature to determine the fruit color) had yellow-fleshed fruits. One plant collected from a dooryard garden near Potrero Grande had a large fruit (2.4 kg), although its overall morphology was more like the other hybrids than Costa Rican domesticates. The domesticated papayas (DCOS) were from markets in Orotina, Coopebarro, Buenos Aires, and San Isidro General. Except for one accession (UH no. 931), which had yellow-fleshed and bullet-shaped fruits, the domesticated papayas found here had a musky smell, an elongated fruit shape, and flesh that was red or salmon pink. Hermaphrodites predominated among domesticates. Figure 3.12 depicts some of the papaya fruits collected in Costa Rica.

The domesticated papayas from Venezuela (DVEN) consist of accessions obtained in Caracas, Maracay, Palo Negro, and Guacamaya. Fruits obtained in Maracay (UH accession no. 1003), Palo Negro (UH accession no. 1011) and Guacamaya (UH accession no. 1012) had PRV ringspots. A few hybrid populations were found (HVEN) along the sandy Caribbean coast near the town of Mirimito and along the roads in Rancho Grande National Park. The hybrid plant in Mirimito (UH accession no. 1006) had a very high sugar content (19.2 percent total soluble solids).

73

Fig. 3.12. *Carica papaya* accessions from Costa Rica.
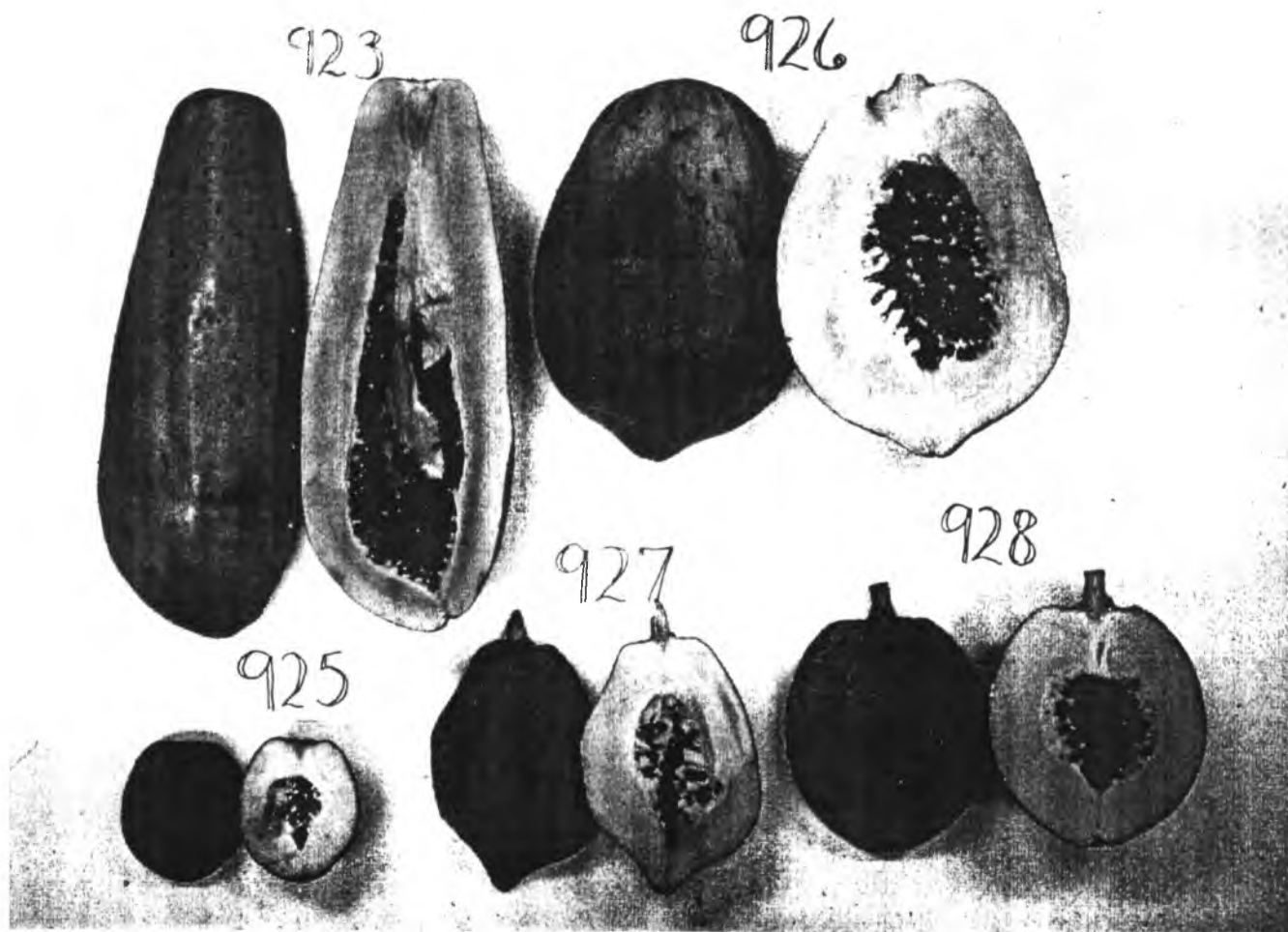
Unlike the other Venezuelan hybrids, which were growing spontaneously along the roadside, UH accession no. 1006 was collected as a cultivated, dooryard garden plant. No wild small-fruited papayas ("papaya de los pajaros" or "chichput") were found in Venezuela. Dr. Victor Manuel Badillo, renowned expert on Caricaceae at the Universidad Central in Maracay, indicated that the papaya that most closely resembled the wild type of papaya would be those that grew spontaneously along the road from Boca de Tocuyo to Mirimito such as UH accession no. 1006. He described that these fruits were larger, however, than the small-sized fruits of chichput in Central America. None of the local folks expressed having seen or heard of the small-fruited, wild papayas when shown photographs of the chichput from the Yucatan region.

In Colombia, most of the papayas, which were of the domesticated type (DBUE), were from the Buenaventura area on the Pacific coast (Fig. 3.13). Known as the Choco, this region is humid, swampy, and malaria-infested; the annual rainfall exceeds 250 cm. Therefore, the Choco region may be a source of *Phytophthora*-resistant papaya germplasm. Throughout Colombia, no *Phytophthora* infection was observed on any of the fruits or trees found. The UH accession nos. 1038 and 1039 that were obtained from the markets near Buenaventura were actually grown near Cali according to the local vendors. UH accession no. 1039 had ringspot symptoms on the fruit skin. UH accession no. 1043 was introduced originally from Venezuela according to the owner of the tree. Two domesticated papaya (DYOP) accessions were also obtained on the eastern slope of the Andes in Yopal. No hybrid or wild papayas were

Fig. 3.13. *Carica papaya* accessions from Colombia.

1044

1045

1046

1047

1048
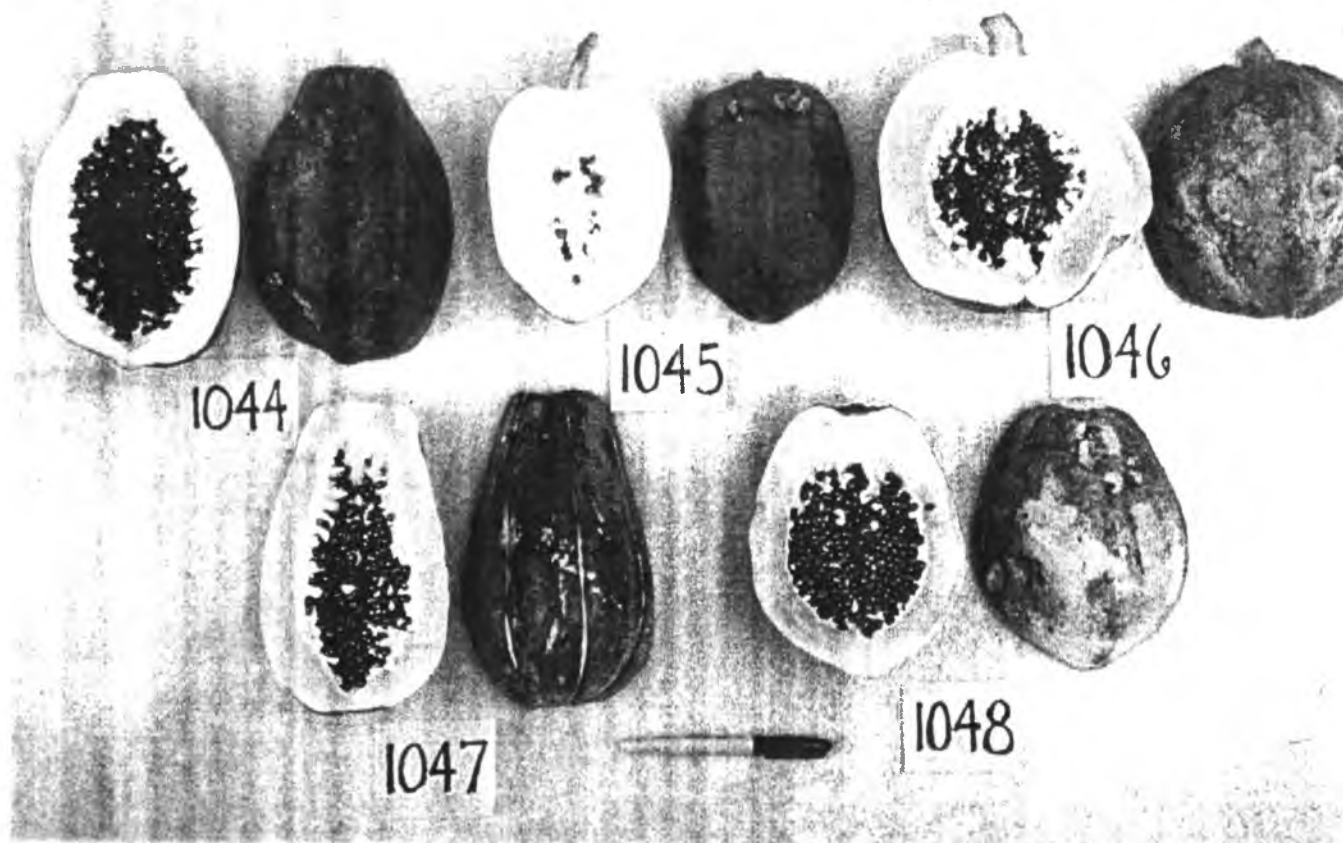
found. Discussions with Dr. Victor Manuel Patiño also confirmed that the wild, small-fruited papaya might not be found in Colombia. Like in Venezuela, photographs of the wild, small-fruited chichput did not elicit any recognition by any of the local people.

The domesticated papayas from Ecuador were collected from two major areas, on the Pacific coastal plain near Santo Domingo in the Province of Pichincha (DDOM) and on the Amazonian side of the Andes near Tena in Napo province (DNAP) (Table 3.1). In both provinces, several domesticated papaya plants had long peduncles (about 10-30 cm) (Fig. 3.14), while others had dark purple petioles typical of the wild papayas found in Central America. Most plants had fruits with yellow flesh. In a commercial papaya plantation in Pichincha, Ecuador, various plants were observed with PRV symptoms such as watery lesions on the leaf petioles and chlorotic leaf apex. No signs of *Phytophthora* infection were seen on any papaya plants in Ecuador. No wild or hybrid types of papaya were collected in Ecuador. Although we talked to people and showed photographs of the Central American wild type, no one could show or tell us of similar types nearby.

The Panamanian accessions consist of both hybrid and domesticated papayas, but none of the hybrid seeds germinated, and thus were not available for allozyme analysis. Therefore, the Panamanian population, which is represented by a sample of three fruits from a single vendor in Panama City, consists of the domesticated type only (DPAN) (Table 3.1).

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Fig. 3.14. *Carica papaya* from Ecuador.

Carica **species collected**

In addition to *C. papaya*, 80 accessions of other *Carica* species were collected. Appendix B summarizes the individual accessions by *Carica* species, location, and type of propagating material collected. Seed samples collected from *Carica* species did not germinate. A list of the accessions that were subjected to allozyme analysis (Chapter 5) is presented in Table 3.2. Colombia and Ecuador have the largest number of different *Carica* species. The Andean mountain range, which runs north to south through both countries, has created considerable variability of topographic, climatic, and vegetation zones. The steep slopes and deep valleys are a mosaic of diverse microhabitats and physical barriers that set the ecological stage for the differentiation of the genus.

Seeds extracted from *C. cauliflora* fruits were collected in Panama, Venezuela, and Colombia. In Venezuela, while some plants were found in the coastal range north of Valencia, none had mature fruits. The *C. caulifora* plant at Rancho Grande Park north of Maracay had white flowers, green petioles, and yellow, ellipsoidal fruits with pointed blossom ends. At Juan Maria Cespedes Botanical Garden, Tulua, Valle de Cauca, Colombia, the *C. cauliflora* plants found had white flowers, ellipsoidal fruits with grooved carpel sutures. In Panama, some individuals had fruits with pronounced carpel sutures while others had no grooves. All of these fruits had white flesh and a yellow exocarp when ripe (Fig. 3.15). Not all of the *C. cauliflora* accessions from

82

Table 3.2.   *Carica* species accession numbers.

Species	Germplasm Collection	Accession Numbers
C. cauliflora	UH	1007, 1015, 1121, 1124
C. crassipetala	UH	1018
C. goudotiana	UH	1016, 1017, 1021, 1022, 1023, 1025, 1026, 1027, 1028, 1030, 1031, 1032, 1034, 1035, 1036, 1037, 1057
C. glandulosa	NCGR	9424
C. microcarpa *subspecies microcarpa (1)*	UH	1069
C. microcarpa *subspecies microcarpa (2)*	UH	1009
C. microcarpa *subspecies baccata*	UH	1072
C. microcarpa *subspecies heterophylla*	UH	1100
C. microcarpa *subspecies (?)*	UH	1118
C. monoica	UH	1129
C. parviflora	NCGR	HCAR 179
C. pubescens	UH	1020, 1062, 1063, 1065, 1066
C. quercifolia	NCGR	HCAR 226
C. sphaerocarpa	UH	1054, 1055
C. stipulata	NCGR	HCAR 177
C. x *heilbornii* n.m. *pentagona*	UH	1103, 1117

Fig. 3.15. *Carica cauliflora* fruit.

1015
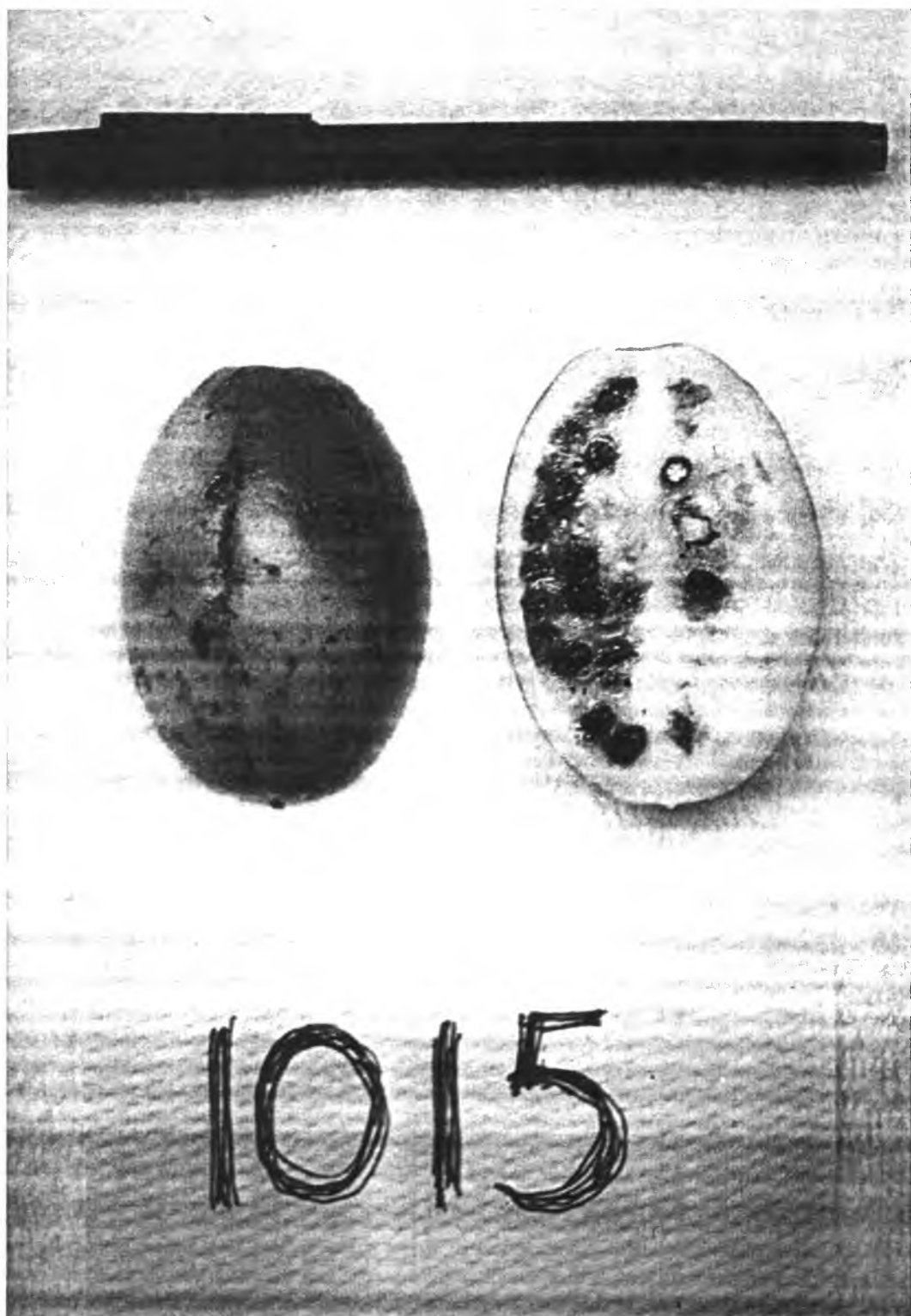
Panama germinated, and thus some were unavailable for study. Unlike *C. papaya*,
C. cauliflora is shade tolerant and can be found in understories of other plants.

Germplasm of the exclusively Colombian species, *C. goudotiana*, was collected
in backyard gardens in Santa Rosa de Cabal (Risaralda province), La Cumbre and
Pavitas (Valle de Cauca province), and Boquia (Quindio province) (Appendix B).
Carica goudotiana appears to be a species that has been domesticated and the fruits
were edible as described in Chapters 2 on pages 33 and 34. Fruit weights ranged from
100 to 200 g. *Carica goudotiana* exhibited variable fruit morphology. The color of
the ripe fruit exocarp can range from light yellow in some individuals to pinkish purple
in others (Fig. 3.16). The white-fleshed fruits can be spheroidal, ellipsoidal, obovate,
elongated, or spindle-shaped. No male plants were observed in domesticated
situations. Wild or feral plants were seen only at the Juan Maria Cespedes Botanical
Garden, Tulua, Valle de Cauca, but these were not flowering or fruiting.

Carica crassipetala was noted by the late Dr. Harold St. John, former
botany professor at the University of Hawaii, to occur near Termales, Risaralda,
Colombia in the 1930's (Badillo 1971). In 1993, one individual of this species
(UH accession no. 1018) was found by thermal springs at the base of a waterfall on the
property of the Hotel Termales (Appendix B). Another individual was found on the
south side of the Rio San Ramon about 1 km above the Hotel Termales. Both
individuals were female with bright orange fruits that were strongly five-lobed and

Fig. 3.16. *Carica goudotiana* fruit.

1030

Fig. 3.17. *Carica crassipetala.*

90

weighing 65-100 g. The flowers were white (Fig. 3.17) and somewhat succulent.
Carica crassipetala is an understory tree in shady, humid rainforest. Seeds were viable
as propagating material.

Carica sphaerocarpa is another species that appears to occur exclusively in
Colombia (Appendix B). Three individuals of this species were found in a farmer's
sugarcane field near the town of La Elsa in the Valle de Cauca province at elevation
680 m. This area was surrounded by dense, wet rainforest. The fruits are remarkably
similar to sweet orange in terms of size, color, and skin texture, except with a pointed
stylar end (Fig. 3.18). Weighing about 150 g, the fruit has five locules and a thick
white ovary wall. Seeds were viable as propagating material. It is not known whether
the fruits of this species are utilized like *C. goudotiana*.

Carica pubescens is another domesticated species occurring in backyard
gardens of Panama, Venezuela, Colombia, and Ecuador (Badillo 1971). The 10
Colombian accessions were from Boquia (province of Quindio), Tocancipa Villapinzon
(province of Cundinamarca), and Parroquia Vieja and the Rancherios district (province
of Boyaca) (Appendix B). In Ecuador, the species was found in Cuyuja, Baeza, and
Santa Elena de Los Huacamayos (all of Napo province) and in Ulvilla, Salasaca, and
Panatu (all of Tungurahua province) (Appendix B). In both countries, the fruits were
mostly ellipsoidal to spindle-shaped, strongly lobed (Fig. 3.19), and had an average
weight of about 150 g. The Colombian accession had fruits with yellow exocarp while

91

Fig. 3.18. *Carica sphaerocarpa* fruits.

1054

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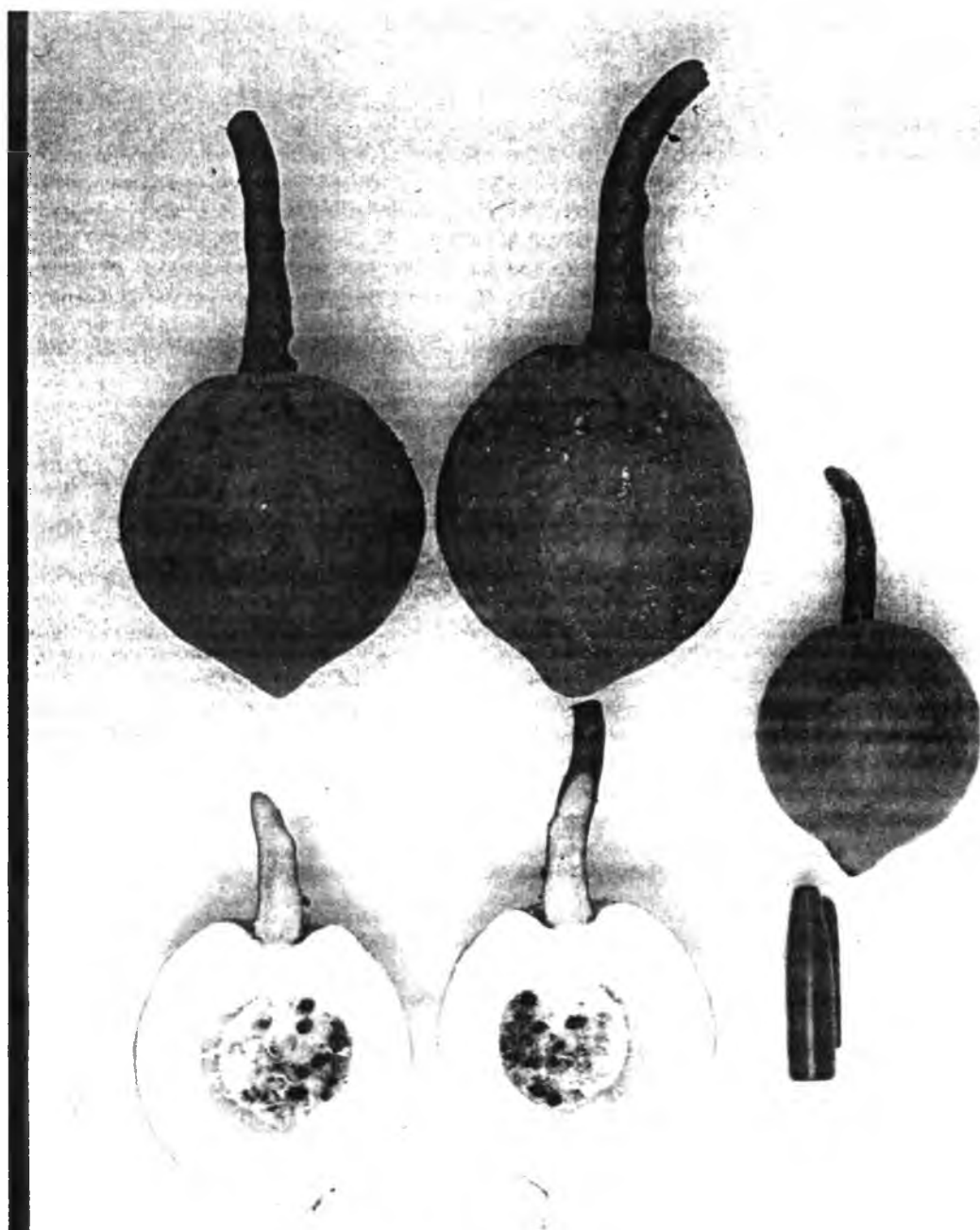
Fig. 3.19. *Carica pubescens* fruits (UH Acc. Nos. 1086-1093) as compared to *Carica papaya* fruit (UH Acc. No. 1094).
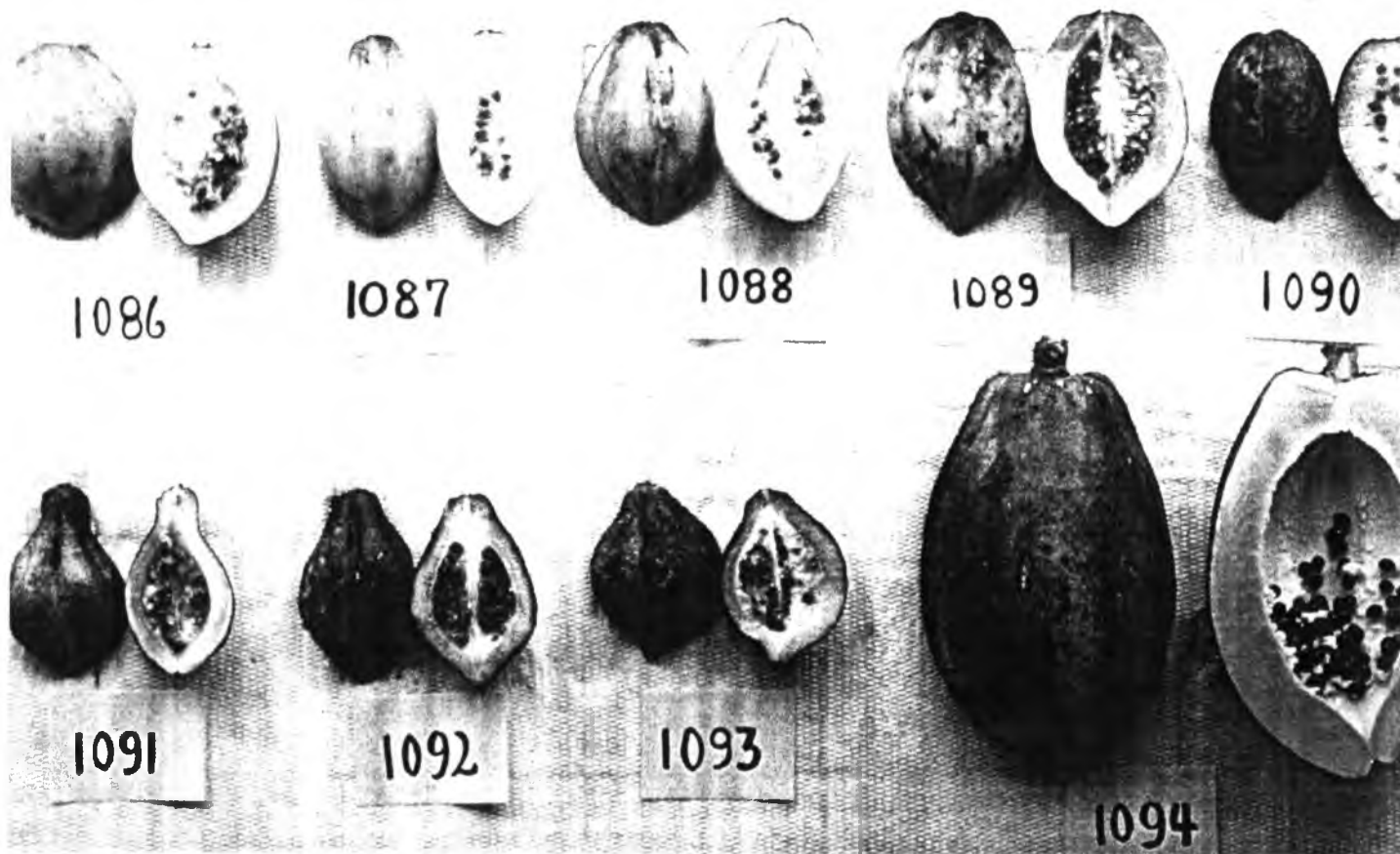
in Ecuador they were greenish-yellow. Perhaps the greenish-yellow exocarp was an indication that the Ecuadoran fruits were immature at the time of the collection because none of the seeds from Ecuador germinated, while all of the *C. pubescens* seeds from the Colombian accessions were viable. Thus, none of the Ecuadoran accessions were available for allozyme studies. No wild *C. pubescens* individuals were observed. The *C. pubescens* found in both Colombia and Ecuador were all domesticates and included female and hermaphrodite plants. No *C. pubescens* were found in Panama or Venezuela during the trip.

Morphologically, *Carica microcarpa* is one of the most variable *Carica* species, and Badillo (1971) has divided it into several subspecies. Seeds of *C. microcarpa* ssp. *microcarpa* were collected at an elevation of 800 m on a road to Chorioni from Maracay in the province of Aragua, Venezuela. This plant occurred in wet, rainforest undergrowth. The fruits were small (about 5 g) compared to the other *Carica* species observed. The deep orange fruits were spheroidal in shape with pointed tips, and occurred in clusters on the trunk. In Colombia, along Sogamosa-Pajarito road between the town of Huerte Vieja and Quebrada Negra (Boyaca province), seeds of another individual of *C. microcarpa* ssp. *microcarpa* were collected. Also known locally as "papaya montañero," this individual had fruits with exocarp that was bright orange, like *C. sphaerocarpa*. This Colombian subspecies *microcarpa* had fruits that were larger (average weight of 20 g), strongly ridged, and shaped like an apiculate sphere. In Ecuador, *Carica microcarpa* subspecies *baccata* was found at the elevation of 220 m

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in forest understory at the Rio Palenque Preserve, near the town of Patricia Pilar in the province of Pichincha. The fruits of *C. microcarpa* subspecies *baccata* were spheroidal to slightly ellipsoidal in shape with bright red exocarp (Fig. 3.20), and small (average weight of 7 g) like those of *C. microcarpa* subspecies *microcarpa* found in Venezuela. Seeds from five individuals were collected, but only one accession germinated. Stem cuttings were collected from *C. microcarpa* subspecies *heterophylla* and *C. microcarpa* of an unknown subspecies in Mera, province of Pasteza, Ecuador.

Carica stipulata was found in a dry valley with cactus in Rio de Rircay, Azuay province of Ecuador. The flowers were yellow and the fruits were elliptical shape (Fig. 3.21) weighing approximately 100 g. The plants were probably five years old, had sharp stipules, and no leaves. Unfortunately, none of the seeds collected would germinate. The *C. stipulata* sample used in the subsequent allozyme study presented in Chapter 5 was from the NCGR collection.

Carica pulchra was found along a creek bank near Chiriboga, Pichincha province in Ecuador (Appendix B). Stem cuttings were collected because only male plants were found. The flowers were observed to be greenish-yellow. Petioles were green, and the undersides of the leaves had a distinctive purplish tinge (Fig. 3.22).

Numerous natural hybrids occur in Ecuador. Local farmers in the area have propagated and perpetuated those that bore promising fruits. Some hybrids such as

Fig. 3.20. *Carica microcarpa* fruits.

Fig. 3.21. *Carica stipulata* fruits (UH Acc. Nos. 1107, 1108) as compared to *Carica papaya* fruits (UH Acc. Nos. 1109,, 1110, 1111).
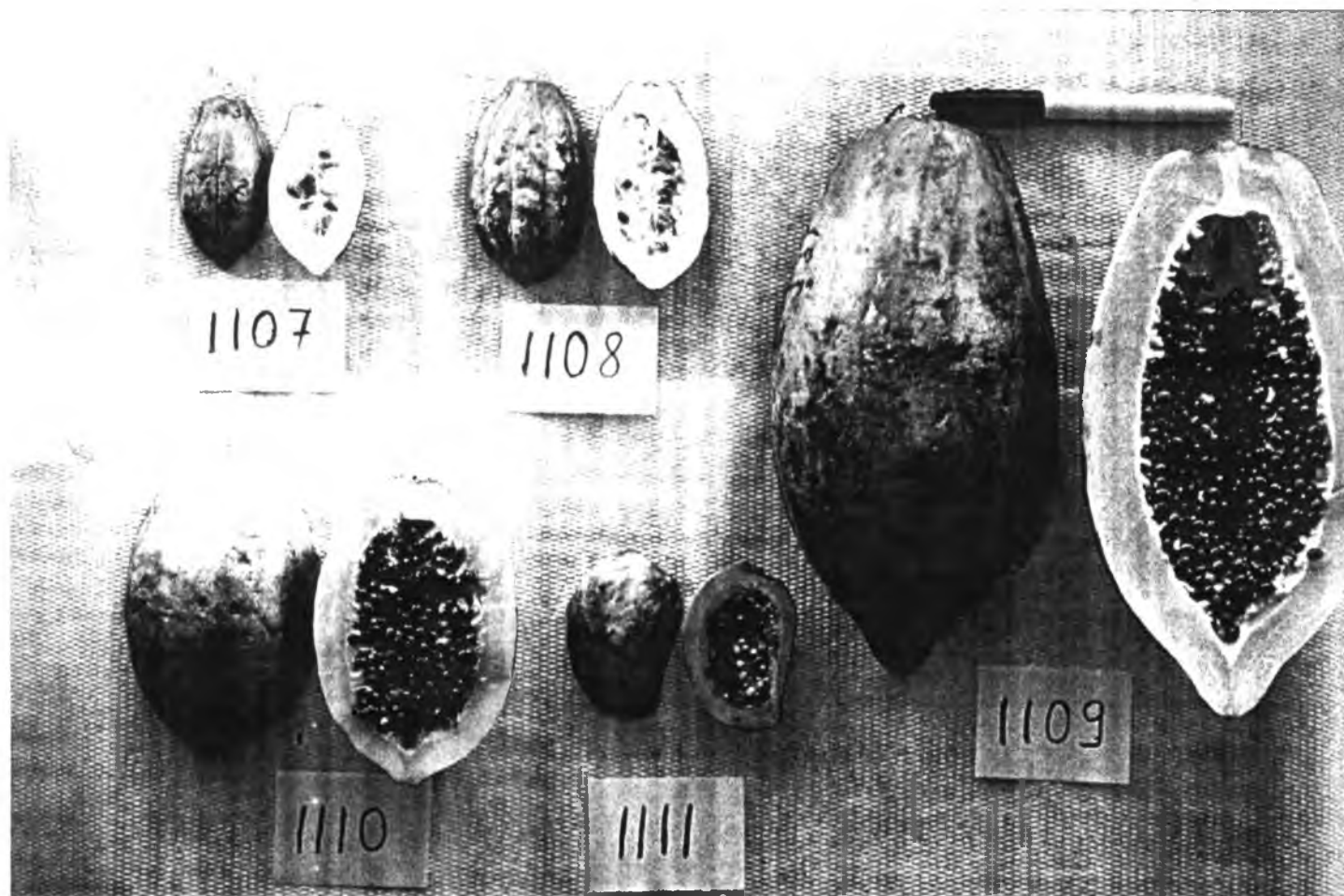
Fig. 3.22. Underside of the leaf of *Carica pulchra*.

Carica x *heilbornii* n.m. *pentagona* (babaco) are sterile and exist only in cultivation.

Stem cuttings of babaco (UH accession nos. 1114-1116) were collected because it is not

propagated by seeds. Unfortunately, the babaco samples collected showed viral disease

symptoms (leaf chlorosis), and therefore were destroyed. One hybrid with the common

name of "chamburo" (UH accession nos. 1102-1104) was found in Compud,

Chimbarazo province of Ecuador, and another called "higacho" (UH accession no.

1117) was found in San Javier, Tungurahua province of Ecuador.

Although *C. monoica* and *C. parviflora* were reported to occur in Ecuador

(Badillo 1971), neither species was encountered or collected during the expedition to

Ecuador. The *C. parviflora* and *C. quercifolia* samples used in the allozyme study in

Chapter 5 were obtained from the NCGR collection. Seeds of *C. monoica* and

C. glandulosa were received from Brazil as gifts from CENARGEN, EMBRAPA, in

1994 and were subsequently included in the allozyme study in Chapter 5.

CHAPTER 4

GENETIC VARIABILITY IN *CARICA PAPAYA*

The center of diversity of a crop is the area to which the major proportion of the genetic diversity in the crop is confined geographically (Vavilov 1951). If the center of diversity of the crop can be delimited to a particular geographical region, this fact, in addition to other supporting evidence such as the distribution of wild populations, can be used to interpret the center of origin of the crop and the probable area of its domestication.

While the center of greatest diversity of a crop usually coincides with the area where the crop was domesticated, it is not often the location where the crop is most grown commercially at present (Smith et al. 1992). For example, the most important commercial cash crop of Colombia and Brazil is *Coffea arabica* (coffee), which is a native of Africa. Oil palm, a native of West Africa, and rubber, which came originally from the Amazon in Brazil, are the largest crops in Malaysia. *Carica papaya*, an important crop in Hawaii's economy ranking fourth after sugarcane, pineapple, and macadamia, is native to the American tropics.

Commercial plantations established outside the natural range of a crop have an advantage in productivity due to the absence of the native pests and diseases, at least initially (Anderson 1954). When they do arrive, disease and pest problems are often

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compounded by the fact that domesticated crops possess only a portion of the genetic variation, including resistance factors, that can be found in the home range (Doebley 1989; Ladizinsky 1985). Thus, the limited genetic variability in the crop may make it vulnerable eventually to incoming pests and diseases.

Papaya is no exception. A better understanding of papaya germplasm resources may help to overcome these problems and to plan and implement conservation strategies to preserve genetic resources. Before any conservation strategies can be accomplished, it would be prudent to first determine the area of greatest diversity for *C. papaya*. An objective of this study is to describe the genetic diversity at the molecular level within *C. papaya* and to identify the biogeographical area of greatest diversity for the species. Results are interpreted to suggest the probable pattern and general region of papaya domestication.

MATERIALS AND METHODS

Carica papaya germplasm

Carica papaya seeds were collected in 1992-93 from 182 individual plants distributed throughout the range of the species in Central and South America (Fig. 3.5). The germplasm, which was maintained at the Department of Horticulture, University of Hawaii (UH), consisted of both wild and domesticated *C. papaya* types

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(Appendix A). From the papaya germplasm collection, 131 accessions were grouped into 24 populations according to their geographic origin and whether they were of the wild, domesticated, or hybrid (between the wild and domesticated) types, as described in Chapter 3 (Table 3.1 and Fig. 3.5). Seeds from each population were germinated, and seedlings were maintained in a greenhouse on the UH campus at Manoa or in the field at the UH Poamoho Agricultural Experiment Station on the north shore of the island of Oahu. Leaf samples from seedlings of each population were collected for subsequent isozyme analysis by starch gel electrophoresis. The number of individual seedling plants sampled per population ranged from 7 to 100, with a mean of 36 individuals.

Enzyme electrophoresis

The isozyme extraction technique involved grinding approximately 1 cm^2 of leaf tissue with 5-6 drops of cold extraction buffer (Bousquet et al. 1987) in a small tube or tray kept on ice. Whatman filter paper wicks (1 x 0.5 cm) were used to absorb the crude extracts and were quickly inserted into 12% starch gels (Sigma Chemical Co.), previously prepared in histidine-citrate buffer pH 6.5 (Cardy et al. 1983) and cooled to 4°C. The gel buffer consisted of 0.016 M histidine (free base) and 0.002 M citric acid (anhydrous) and the tray buffer consisted of 0.065 M histidine and 0.007 M citric acid. Of the six buffer systems tested, the histidine-citrate buffer provided the best, most consistent enzyme resolution and was used subsequently for starch gel electrophoresis

Table 4.1.   Enzymes resolved in *Carica papaya*.

Enzyme	EC number	Locus	Subunit structure
Aconitase	EC 4.2.1.3	*Aco-1*	Monomer
		Aco-2	Monomer
Isocitrate dehydrogenase	EC 1.1.1.42	*Idh*	Dimer
Malate dehydrogenase	EC 1.1.1.37	*Mdh-1*	Dimer
		Mdh-2	Dimer
Phosphoglucoisomerase	EC 5.3.1.9	*Pgi-2*	Dimer
Phosphoglucomutase	EC 2.7.5.1	*Pgm-1*	Monomer
		Pgm-2	Monomer
Shikimate dehydrogenase	EC 1.1.1.25	*Skd*	Monomer
Triose-phosphate isomerase	EC 5.3.1.1	*Tpi-1*	Dimer
		Tpi-2	Dimer
Uridine diphosphoglucose pyrophosphorylase	EC 2.7.7.9	*Ugp*	Monomer
6-phosphogluconate dehydrogenase	EC 1.1.1.44	*6-Pgd*	Dimer

Table 4.2.   Other enzymes attempted in *Carica papaya* that remained unresolved
             due to lack of activity, poor resolution, or inconsistency.

Enzyme	EC number	Buffer used*
Acid phosphatase	EC 3.1.3.2	HC, LB, SB, TB, TC
Alcohol dehydrogenase	EC 1.1.1.1	HC, TC, MC
Aldolase	EC 4.1.2.13	HC, TC,
Alkaline phosphatase	EC 3.1.3.1	LB, SB, TB
Catalase	EC 1.11.1.6	SB, TC
Diaphorase	EC 1.6.2.2	HC, MC, TC
Esterase	EC 3.1.1.1	LB, SB, TB,
Fructose-1,6-diphosphatase	EC 3.1.3.11	HC, MC, TC
Formaldehyde dehydrogenase	EC 1.2.1.1	HC, MC, TC
Fumarase	EC 4.2.1.2	HC, MC, TC
Glutamate dehydrogenase	EC 1.4.1.2	HC, MC, TC
Glutamate oxaloacetate transaminase	EC 2.6.1.1	HC, LB, SB, TB, TC
Glucose-6-phosphate dehydrogenase	EC 1.1.1.49	SB
Hexokinase	EC 2.7.1.1	HC, MC, TC
Leucine aminopeptidase	EC 3.4.11.-	TC
Malic enzyme	EC 1.1.1.40	HC, MC, TC
Mannose-6-phosphate isomerase	EC 5.3.1.8	HC, MC, TC
Peroxidase	EC 1.11.1.7	HC, LB, MC, SB, TB,TC
Superoxide dismutase	EC1.15.1.1	HC

*HC=Histidine Citrate; LB=Lithium Borate; MC=Morpholine Citrate;
 TB=Tris Borate-EDTA; TC=Tris Citrate; SB=Sodium Borate.

(Tables 4.1 and 4.2). The gels were electrophoresed at 4°C and at 200 volts (constant voltage). At the completion of the electrophoresis, which typically required five hours of running time, the gels were sliced horizontally into 1-mm-thick slabs and stained for different anodically migrating enzymes. Staining protocols and recipes were those of Arulsekar and Parfitt (1986), Marty et al. (1984), and Shaw and Prasad (1970).

Appendix C shows some of the typical banding patterns of each enzyme system stained. Banding patterns as a result of staining were observed and recorded (Appendix D). When an enzyme was encoded by more than one gene, the locus with the fastest anodic mobility was designated as 1, the next most anodic as 2, and so on. At each locus, the allele coding for the most cathodic electromorph was designated as A, the next most cathodic band as B, and so forth. Based on this scoring procedure, a total of 29 alleles in 13 loci were detected in nine enzyme systems. By defining a polymorphic locus as one at which the frequency of the most common allele is less than 0.99, nine out of 13 loci qualified as polymorphic. The genetic control of variation at eight of the nine polymorphic loci was discerned by analyzing segregation ratios in progenies of crosses between parents expressing different allelomorphs: two alleles for *Aco-1*, two for *Aco-2*, two for *Pgi-2*, two for *Pgm-1*, two for *Tpi-1*, three for *Tpi-2*, two for *Ugp*, and two for *Skd* (Table 4.3). Chi-square values were calculated to test the goodness-of-fit to expected ratios using Yates corrections for continuity (Little and Hills 1978). Four out of five loci that were not examined by segregation analysis (*Idh*, *Mdh-1*, *Mdh-2*, and *6-Pgd*) were not variable in all populations examined in this study.

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Data analysis

For each population, allele frequencies were calculated for 13 isozyme loci

(Table 4.4). The genetic relationships between populations were determined by

calculating the unbiased genetic identity, I, (Nei, 1972) for all possible pairwise

comparisons (Table 4.5). All computations were completed using the computer

program BIOSYS-1 (Swofford and Selander 1989). The genetic relationships between

populations were portrayed in a dendrogram by subjecting the genetic identity matrix to

cluster analysis. Cluster analysis was performed with the UPGMA algorithm included

in the BIOSYS-1 program. The cophenetic correlation coefficient (Rolf and Sokal

1981) between cophenetic matrix and Nei's genetic identity matrix was also computed

using BIOSYS-1 to test the congruity of the genetic identity matrix and the

dendrogram.

The allele frequencies were subjected to various statistical analyses to measure

intrapopulational variability. As reviewed in Crawford (1990), mean number of alleles

per locus, percentage of polymorphic loci, and observed and expected levels of

heterozygosity were the measures of intrapopulational variability used in this study

(Table 4.6). Values for direct or observed mean heterozygosities were obtained by

summing the number of heterozygous individuals at each locus in the population,

dividing this number by the total number of individuals in the population, and

averaging these values over all loci. Mean estimated heterozygosity values for each

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locus were calculated based on Hardy-Weinberg expectations by inserting allele frequencies into a Hardy-Weinberg equation derived for the number of alleles at that locus. The values obtained were then averaged over the number of loci within the population. These computations were calculated using BIOSYS-1. The mean expected and observed heterozygosity values were also calculated separately for populations composed of seedling progenies from domesticated (fruits $> 1,000$ g) hermaphrodite plants, domesticated female plants, and wild (fruits < 100 g) female plants (Table 4.7).

Wright's fixation index, F, (Wright 1965), which is defined as $(H_{exp} - H_{obs})/H_{exp}$, where H_{exp} and H_{obs} are expected and observed heterozygosities, respectively, was calculated for each of the three above-mentioned composite populations. F is interpreted as the proportional increase or reduction in heterozygosity as compared to panmictic expectations. The value of F varies from -1.0 to 1.0, with positive values indicating a deficit of heterozygotes and negative values indicating a surplus of heterozygotes. These values were used to examine the question of whether the selection and development of hermaphroditism from wild dioecious populations was crucial to the domestication of papaya.

In addition, principal component analysis (PCA) was also used to determine relationships among populations. Allele frequencies for all populations made up the input data matrix. In this analysis, each individual allele frequency in the population represents a character whose value may range from 0 to 1. From this matrix, a

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variance-covariance matrix was calculated from which principal components were obtained that represent least-square lines through the multidimensional space defined by all alleles. PCA computations were expedited by the microcomputer program NTSYS (Exeter Publishing Ltd., Setauket, NY).

RESULTS

Electrophoretic phenotypes and their genetic control

Of the 28 enzyme systems assayed, only nine gave consistent banding patterns (Tables 4.1 and 4.2). A total of 13 loci, which are described below, were detected in the nine enzyme systems. Four out of 13 loci were found to be monomorphic.

Aconitase (ACO- E.C. 4.2.1.3) is a monomeric enzyme with two polymorphic loci in papaya. *Aco-1*, the most anodic locus, has two alleles (A and B) and three zymotypes (Fig. 4.1). Both alleles A and B of *Aco-1* segregated in a Mendelian ratio (Table 4.3). *Aco-2*, the slower migrating locus, has four alleles and ten zymotypes (Fig. 4.1). Alleles B and D segregated in a Mendelian ratio, but no controlled cross was available to investigate if alleles A and C in *Aco-2* also followed a Mendelian pattern of inheritance.
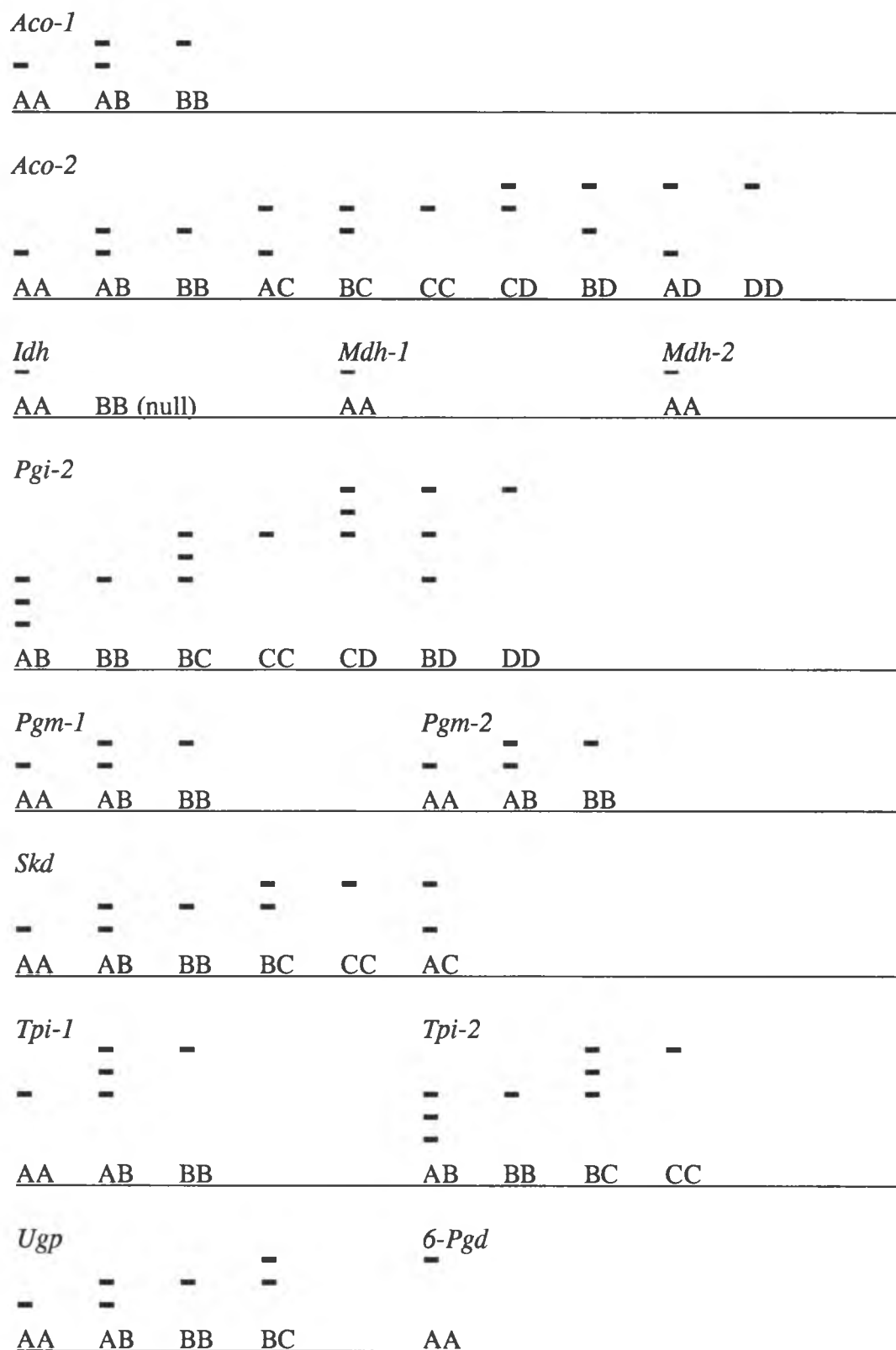
Fig. 4.1. Electrophoretic phenotypes observed in *Carica papaya*.

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Table 4.3. Goodness-of-fit tests for single-locus segregation ratios at eight loci.

Enzyme locus	Cross	Genotype of parents	Progeny genotypes	Expected ratios	Chi-square	Probability
Aco-1	M210-3 x M210-4	BB x AB	AB:27 BB:17	1:1	1.841	0.25-0.10
Aco-1	M269-5 x M269-4	AA x AB	AA:28 AB:25	1:1	0.075	0.95-0.90
Aco-2	M269-5 x M269-4	BD x BB	BB:24 BD:29	1:1	0.302	0.75-0.50
Pgi-2	M182-2 x M182-1	BC x BC	BB:7 BC:24 CC:10	1:2:1	1.634	0.50-0.25
Pgm-1	M182-2 x M182-1	AB x AB	AA:6 AB:27 BB:8	1:2:1	4.315	0.25-0.10
Pgm-1	M212-5 x M212-4	AB x AB	AA:7 AB:29 BB:10	1:2:1	3.522	0.25-0.10
Pgm-1	M210-3 x M210-4	AB x AB	AA:10 AB:23 BB:10	1:2:1	0.209	0.98-0.90
Skd	M210-3 x M210-4	BC x AB	AB:12 BB:14 BC:7 AC:10	1:1:1:1	2.488	0.50-0.25
Tpi-1	M182-2 x M182-1	AB x BB	AB:17 BB:24	1:1	0.878	0.50-0.25
Tpi-2	M212-5 x M212-4	BC x BC	BB:5 BC:19 CC:6	1:2:1	2.200	0.50-0.25
Tpi-2	M269-5 x M269-4	BC x BB	BB:22 BC:31	1:1	1.207	0.50-0.25
Ugp	M210-3 x M210-4	BB x BC	BB:23 BC:20	1:1	0.093	0.95-0.90
Ugp	M212-5 x M212-4	BC x BB	BB:24 BC:22	1:1	0.022	0.95-0.90

Isocitric dehydrogenase (IDH- E.C. 1.1.1.42) is a dimeric enzyme. Only one allele, A, was observed in all of the papaya accessions surveyed in this study. Although a null allele was known to occur in the UH cultivar, 'Waimanalo,' also known as 'Line 77' (Morshidi, unpublished data), this cultivar was not part of this study. No segregation analysis was conducted for IDH.

Malate dehydrogenase (MDH- E.C. 1.1.1.37) is another dimeric enzyme in papaya. Two loci were detected, but they were found to be monomorphic in papaya. A shadow band was found to be associated with the second locus in MDH (*Mdh-2*) (Fig. 4.1). No segregation analysis was conducted for MDH.

Although two zones of activity were detected in phosphoglucose isomerase (PGI- E.C. 5.3.1.9), only the slower migrating locus (*Pgi-2*) was resolved and scored. This enzyme is dimeric and has four alleles and seven electromorphs in papaya (Fig. 4.1). Alleles B and C were found to segregate in the expected Mendelian ratio of 1:2:1 (Table 4.3). No controlled cross was available for alleles A and D.

Phosphoglucomutase (PGM- E.C. 2.7.5.1) is a monomeric enzyme. Two zones of activity (*Pgm-1* and *Pgm-2*) were detected on gels stained for PGM (Fig. 4.1). The two alleles observed in the *Pgm-1* locus were inherited in a Mendelian manner (Table 4.3). No controlled cross was available to conduct a similar analysis for the two alleles in the *Pgm-2* locus.

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Phosphogluconate dehydrogenase, (PGD or 6-PGD- E.C. 1.1.1.44) is a dimeric enzyme that is monomorphic in papaya. Because 6-PGD was found to be monomorphic in papaya, no segregation analysis was conducted for 6-PGD.

Shikimate dehydrogenase (SKD- E.C. 1.1.1.25) is a monomeric enzyme that exhibited one zone of activity. Three alleles and six zymotypes were detected in papaya (Fig. 4.1). All three alleles observed (A, B, and C) behaved in a Mendelian fashion (Table 4.3).

Triosephosphate isomerase (TPI- E.C. 5.3.1.1) displayed two zones of activity. The faster-migrating locus, *Tpi-1*, has two alleles (A and B) and three zymotypes (Fig. 4.1). The slower-migrating locus, *Tpi-2*, has three alleles (A, B, and C) and four zymotypes (Fig. 4.1). In *Tpi-2*, alleles B and C appeared to segregate in a Mendelian ratio (Table 4.3), while the inheritance of allele A was untested. A shadow band appeared to be associated with the *Tpi-2* locus.

Uridine diphosphoglucose pyrophosphorylase (UGP- E.C. 2.7.7.9) is a monomeric enzyme with only one distinct zone of activity. Three alleles and four different zymotypes were detected (Fig. 4.1). Both B and C alleles segregated with the expected Mendelian ratio (Table 4.3). No cross was available to determine the inheritance of allele A.

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Of the nine enzyme systems studied, seven (no allelic variation was found at MDH or 6-PGD) were represented by more than one allele. This study revealed that the electromorphs observed can be interpreted genetically and that they are inherited in a Mendelian fashion. Because controlled crosses were not available to test certain allelic variation at *Aco-2* (A and C), *Pgi-1* (A and D), *Pgm-2* (A and B), *Tpi-2* (A), and *Ugp* (A), the interpretation of these loci and alleles remains putative.

Cluster analysis

The observed allele frequencies for 13 loci encoding nine enzyme systems for 24 populations of *C. papaya* from Central and South America are presented in Table 4.4. From the allele frequencies, the genetic differentiation among populations was analyzed by computing pair-wise, unbiased genetic identities (*I*) among populations (Nei 1972) as well as modified Rogers' genetic distances (Wright 1978). The genetic identity and distance coefficients from Central and South American populations are presented in Table 4.5. The pair-wise identities among populations range from 0.821 to 0.997, with an overall mean of 0.926.

The genetic identity matrix among all pair-wise comparisons presented in Table 4.5 was subjected to a cluster analysis with the UPGMA algorithm. The cophenetic correlation coefficient between the cophenetic matrix and Nei's genetic

Table 4.4. Allele frequencies in *Carica papaya* populations.

Locus	Allele	Population							
		1	2	3	4	5	6	7	8
	(N)	39	62	16	36	29	23	78	35
Aco-1	A	0.410	0.258	0.188	0.444	0.810	0.500	0.596	0.686
	B	0.590	0.742	0.812	0.556	0.190	0.500	0.404	0.314
Aco-2	A	0.590	0.161	0.219		0.638			
	B	0.385	0.831	0.531	0.889	0.207	0.913	0.635	0.757
	C	0.025	0.008	0.250	0.111	0.103	0.087	0.321	0.243
	D					0.052		0.045	
Idh	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-1	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-2	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Pgi-2	A								
	B	0.949	0.532	0.531	0.028	0.310	0.283	0.853	0.257
	C	0.051	0.468	0.469	0.972	0.690	0.717	0.147	0.743
	D								
Pgm-1	A	0.769	0.565	0.375	0.028	0.638	0.130	0.801	0.643
	B	0.231	0.435	0.625	0.972	0.362	0.870	0.199	0.357
Pgm-2	A	0.064			0.014	0.397	0.217		
	B	0.936	1.000	1.000	0.986	0.603	0.783	1.000	1.000
Skd	A			0.031					
	B	1.000	1.000	0.969	0.986	1.000	1.000	0.994	1.000
	C				0.014			0.006	
Tpi-1	A		0.274	0.031					
	B	1.000	0.726	0.969	1.000	1.000	1.000	1.000	1.000
Tpi-2	A								
	B	1.000	1.000	1.000	0.694	0.914	0.935	0.622	0.814
	C				0.306	0.086	0.065	0.378	0.186
Ugp	A				0.083				
	B	1.000	1.000	1.000	0.917	1.000	1.000	1.000	1.000
	C								
6-Pgd	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Note: Blanks indicate zero values.

Table 4.4.   (Continued) Allele frequencies in *Carica papaya* populations.

		Population							
Locus	Allele	9	10	11	12	13	14	15	16
	(N)	30	42	100	30	30	7	22	50
Aco-1	A	0.900	1.000	0.755	0.917	0.967	0.500	0.205	0.260
	B	0.100		0.245	0.083	0.033	0.500	0.795	0.740
Aco-2	A							0.386	0.040
	B	0.367	0.226	0.130	0.267	0.967	0.714	0.091	0.360
	C	0.633	0.774	0.870	0.733		0.286	0.523	0.600
	D					0.033			
Idh	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-1	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-2	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Pgi-2	A								
	B	0.900	0.286	0.925	0.617	1.000	0.500	0.682	0.530
	C	0.100	0.714	0.075	0.383		0.500	0.318	0.470
	D								
Pgm-1	A	0.800	0.524	0.715	1.000	0.967		0.341	0.010
	B	0.200	0.476	0.285		0.033	1.000	0.659	0.990
Pgm-2	A								
	B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Skd	A							0.045	0.060
	B	1.000	1.000	1.000	1.000	1.000	1.000	0.455	0.920
	C							0.500	0.020
Tpi-1	A							0.432	
	B	1.000	1.000	1.000	1.000	1.000	1.000	0.568	1.000
Tpi-2	A								
	B	0.900	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	C	0.100							
Ugp	A	0.033							
	B	0.967	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	C								
6-Pgd	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Note: Blanks indicate zero values.

Table 4.4. (Continued) Allele frequencies in *Carica papaya* populations.

Locus	Allele	Population							
		17	18	19	20	21	22	23	24
	(N)	37	26	58	33	8	28	45	7
Aco-1	A	0.770	0.692	0.397	0.561	0.438	0.554	0.411	0.929
	B	0.230	0.308	0.603	0.439	0.562	0.446	0.589	0.071
Aco-2	A		0.096			0.063	0.125	0.222	
	B	0.176	0.250	0.371	0.167	0.313	0.196	0.144	
	C	0.810	0.654	0.629	0.833	0.624	0.679	0.634	0.857
	D	0.014							0.143
Idh	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-1	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-2	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Pgi-2	A	0.014							
	B	0.662	0.712	0.379	0.606	0.938	0.964	0.989	1.000
	C	0.324	0.288	0.121	0.394	0.062	0.036	0.011	
	D			0.500					
Pgm-1	A	0.284	0.115	0.147	0.667	0.125	0.018	0.089	0.214
	B	0.716	0.885	0.853	0.333	0.875	0.982	0.911	0.786
Pgm-2	A		0.038						
	B	1.000	0.962	1.000	1.000	1.000	1.000	1.000	1.000
Skd	A					0.125	0.214	0.189	
	B	0.905	1.000	0.974	1.000	0.875	0.518	0.667	0.929
	C	0.095		0.026			0.268	0.144	0.071
Tpi-1	A					0.375	0.089	0.056	
	B	1.000	1.000	1.000	1.000	0.625	0.911	0.944	1.000
Tpi-2	A								0.071
	B	0.986	0.981	0.966	1.000	1.000	1.000	0.967	0.929
	C	0.014	0.019	0.034				0.033	
Ugp	A			0.310					
	B	0.973	1.000	0.690	1.000	1.000	1.000	0.956	1.000
	C	0.027						0.044	
6-Pgd	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Note: Blanks indicate zero values.

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Table 4.5. Genetic identity and distance estimates for *Carica papaya* from different geographical areas.

Population	1	2	3	4	5	6	7	8
1 DVER	*****	.956	.960	.844	.938	.896	.962	.924
2 DYUC	.198	*****	.988	.933	.918	.961	.949	.964
3 DSAN	.194	.117	*****	.947	.928	.970	.946	.960
4 DRIO	.373	.244	.222	*****	.893	.986	.880	.956
5 DPAC	.236	.265	.252	.307	*****	.927	.917	.952
6 DHON	.304	.187	.172	.119	.254	*****	.913	.969
7 DCOS	.184	.210	.220	.325	.267	.277	*****	.962
8 DVEN	.260	.179	.192	.202	.206	.172	.183	*****
9 DBUE	.218	.278	.270	.381	.263	.321	.141	.223
10 DYOP	.318	.301	.271	.299	.223	.267	.262	.182
11 DDOM	.230	.295	.262	.397	.285	.338	.188	.261
12 DNAP	.257	.296	.292	.393	.249	.341	.195	.212
13 DPAN	.232	.275	.320	.412	.313	.338	.183	.251
14 HVER	.287	.198	.147	.166	.285	.109	.267	.204
15 HSAN	.270	.249	.213	.352	.322	.318	.308	.320
16 HPET	.291	.229	.134	.224	.308	.191	.287	.254
17 HRIO	.272	.277	.218	.301	.261	.254	.232	.228
18 HHON	.262	.260	.194	.275	.260	.222	.243	.237
19 HCOS	.296	.260	.196	.272	.318	.241	.278	.267
20 HVEN	.228	.241	.195	.326	.246	.278	.189	.200
21 WYUC	.263	.239	.201	.327	.331	.273	.262	.298
22 WSAN	.292	.305	.242	.348	.342	.298	.293	.326
23 WPET	.254	.281	.208	.343	.328	.293	.272	.318
24 WRIO	.303	.351	.299	.391	.322	.338	.271	.318

Notes: Above diagonal– Nei's (1978) coefficients of unbiased genetic identity; below diagonal– modified Rogers' distances (Wright 1978).

Table 4.5. (Continued) Genetic identity and distance estimates for *Carica papaya* from different geographical areas.

Population	9	10	11	12	13	14	15	16
1 DVER	.948	.888	.942	.929	.945	.912	.917	.905
2 DYUC	.913	.898	.903	.903	.921	.960	.928	.941
3 DSAN	.920	.920	.926	.908	.894	.983	.951	.983
4 DRIO	.839	.902	.826	.831	.821	.974	.857	.945
5 DPAC	.923	.946	.910	.933	.897	.912	.875	.891
6 DHON	.886	.922	.874	.873	.880	.993	.883	.960
7 DCOS	.979	.923	.961	.959	.967	.923	.887	.906
8 DVEN	.946	.965	.925	.952	.935	.958	.879	.927
9 DBUE	*****	.959	.993	.990	.967	.911	.883	.898
10 DYOP	.195	*****	.957	.972	.897	.936	.878	.924
11 DDOM	.086	.199	*****	.982	.933	.911	.906	.918
12 DNAP	.104	.163	.130	*****	.948	.887	.869	.879
13 DPAN	.183	.314	.255	.226	*****	.884	.823	.837
14 HVER	.290	.249	.291	.327	.337	*****	.918	.990
15 HSAN	.320	.328	.291	.342	.405	.277	*****	.946
16 HPET	.302	.263	.273	.333	.393	.117	.223	*****
17 HRIO	.173	.144	.143	.207	.312	.191	.250	.176
18 HHON	.209	.187	.185	.256	.324	.146	.251	.138
19 HCOS	.281	.268	.261	.316	.372	.187	.266	.161
20 HVEN	.144	.157	.105	.138	.288	.242	.252	.211
21 WYUC	.254	.287	.224	.312	.346	.198	.190	.166
22 WSAN	.271	.292	.239	.330	.371	.219	.200	.181
23 WPET	.262	.298	.225	.322	.365	.213	.189	.160
24 WRIO	.190	.225	.156	.252	.330	.266	.302	.252

Notes: Above diagonal– Nei's (1978) coefficients of unbiased genetic identity; below diagonal– modified Rogers' distances (Wright 1978).

Table 4.5. (Continued) Genetic identity and distance estimates for *Carica papaya* from different geographical areas.

Population	17	18	19	20	21	22	23	24
1 DVER	.917	.924	.899	.942	.927	.904	.927	.902
2 DYUC	.912	.923	.921	.934	.939	.893	.908	.865
3 DSAN	.948	.961	.958	.960	.961	.936	.953	.905
4 DRIO	.898	.916	.916	.881	.883	.864	.867	.835
5 DPAC	.922	.923	.879	.932	.875	.863	.874	.887
6 DHON	.928	.946	.934	.914	.920	.900	.902	.877
7 DCOS	.939	.933	.909	.960	.925	.901	.914	.922
8 DVEN	.942	.937	.917	.956	.902	.878	.883	.891
9 DBUE	.968	.953	.911	.979	.933	.919	.923	.964
10 DYOP	.978	.963	.919	.974	.912	.905	.900	.948
11 DDOM	.979	.963	.924	.989	.950	.938	.944	.977
12 DNAP	.954	.929	.889	.981	.897	.880	.885	.935
13 DPAN	.898	.890	.851	.914	.877	.854	.858	.889
14 HVER	.964	.982	.966	.939	.966	.951	.953	.930
15 HSAN	.929	.930	.916	.928	.965	.957	.961	.902
16 HPET	.966	.980	.972	.951	.975	.964	.972	.933
17 HRIO	*****	.997	.959	.984	.972	.972	.970	.990
18 HHON	.072	*****	.967	.971	.983	.978	.979	.986
19 HCOS	.191	.174	*****	.945	.957	.945	.953	.933
20 HVEN	.126	.166	.219	*****	.952	.935	.945	.959
21 WYUC	.173	.146	.204	.216	*****	.988	.992	.967
22 WSAN	.163	.147	.220	.241	.130	*****	.997	.973
23 WPET	.167	.142	.202	.221	.115	.066	*****	.969
24 WRIO	.114	.132	.251	.202	.196	.169	.179	*****

Notes: Above diagonal– Nei's (1978) coefficients of unbiased genetic identity; below diagonal– modified Rogers' distances (Wright 1978).

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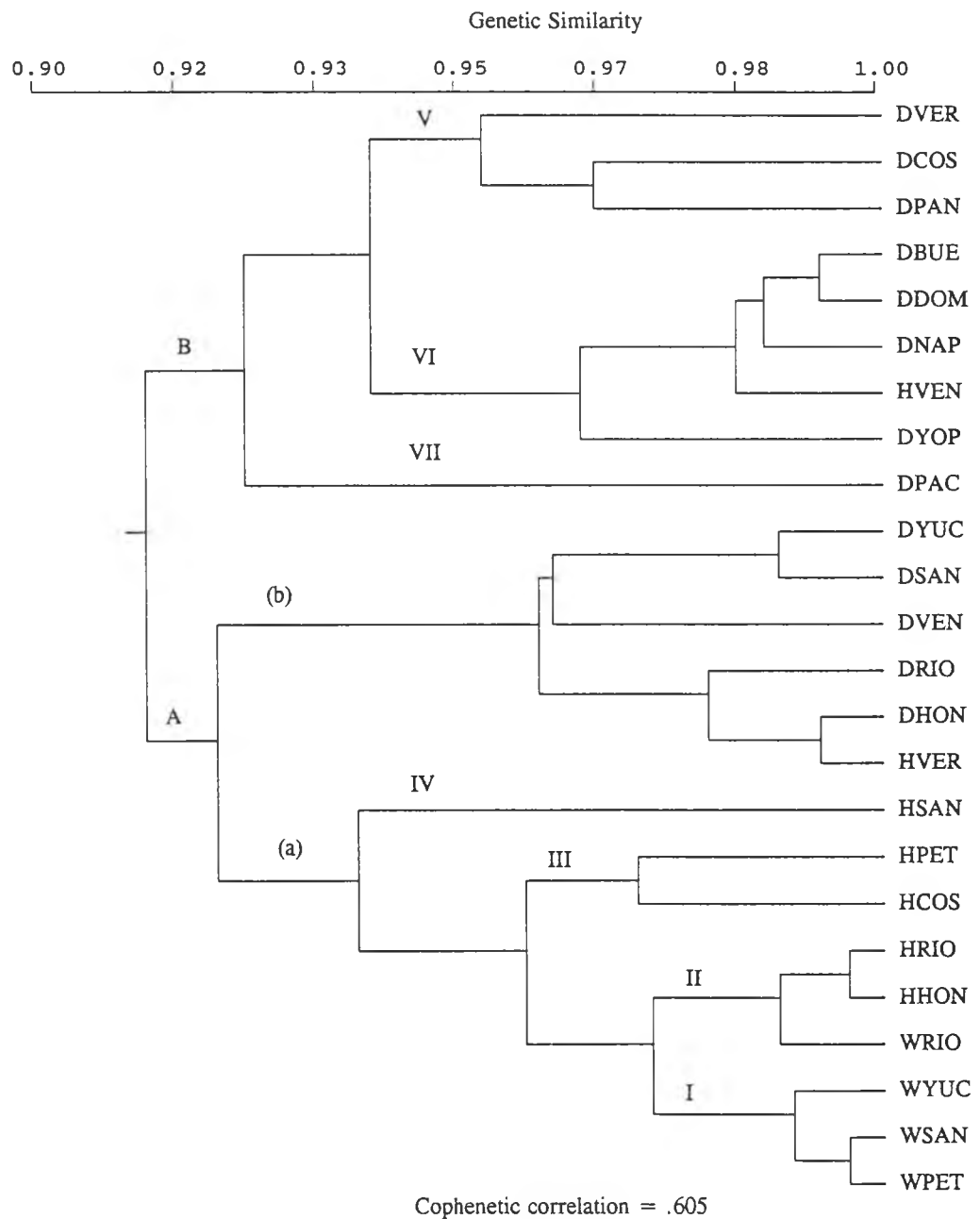
Fig. 4.2. Genetic relationships among different *Carica papaya* populations.

identity matrix was found to be 0.605. The cluster analysis results are presented as a dendrogram in Fig. 4.2. The cluster analysis revealed two major groupings: major group A of mainly Central American populations, and major group B of mostly South American populations. Major group A includes two clusters: group (a) which consists of the wild and hybrid populations of Central America; and group (b) which consists of mostly domesticated populations of Central America. Group (a) was further subdivided into four clusters. Cluster I was made up of wild populations from the Yucatan, San Ignacio (Belize), and the Peten (WYUC, WSAN, and WPET) that are most closely related to each other and which have genetic identities greater than 0.98. The wild population of Rio Motagua, Guatemala (WRIO), fell into cluster II with the hybrid population in the same area (HRIO) and the hybrids in nearby Honduras (HHON). However, these two clusters still shared a very high genetic identity of greater than 0.97. The wild and hybrid populations of clusters I and II are related closely to the various hybrids found in the same area (HPET, HCOS, and HSAN) that are grouped in clusters III and IV, respectively. Group (a) is most closely related to group (b) at an identity of greater than 0.92. Group (b) consists mostly of Central American domesticates (DYUC, DSAN, DRIO, DHON), one Central American hybrid (HVER), and one South American domesticate (DVEN).

The second major group B consists of mostly domesticates from South America, with a few domesticates from Central America and a hybrid from Venezuela. In this major group B, cluster V was made up of Central American domesticated papaya

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populations (DVER, DCOS, and DPAN). Cluster VI consisted primarily of South American domesticates (DBUE, DDOM, DNAP, and DYOP) and a hybrid papaya population (HVEN). Cluster VII is a domesticated papaya population from the Pacific coast of Guatemala (DPAC).

Principal component analysis

Based on the allele frequency data summarized in Table 4.4, principal component analysis (PCA) was used to establish correlations between populations and to visualize the relationships of populations in a 3-dimensional graph. The first three principal components accounted for 33.5 percent, 28.0 percent, and 15.2 percent of the variance, respectively. These three orthogonal vectors for the *C. papaya* populations are plotted in Fig. 4.3. On the basis of domestication status (wild to domesticated) and geographic location (Central America to South America), five PCA groups were apparent. Group I consists of wild papaya populations (WPET, WYUC, WSAN, and WRIO). Cluster analysis grouped the WRIO population with the hybrid populations of Rio Motagua and Honduras (Fig. 4.2). WRIO's average fruit size is at the top range although within the size limit of the wild fruits. In the PCA, WRIO could be classified in either the wild or the hybrid group, but was included in PCA group I because its average fruit weight was within the size limit of the wild fruit (Chapter 3 and Appendix A). Group II contains hybrid papaya populations of Central America (HPET, HSAN, HCOS, HHON, HRIO, and HVER). Group III features Central American

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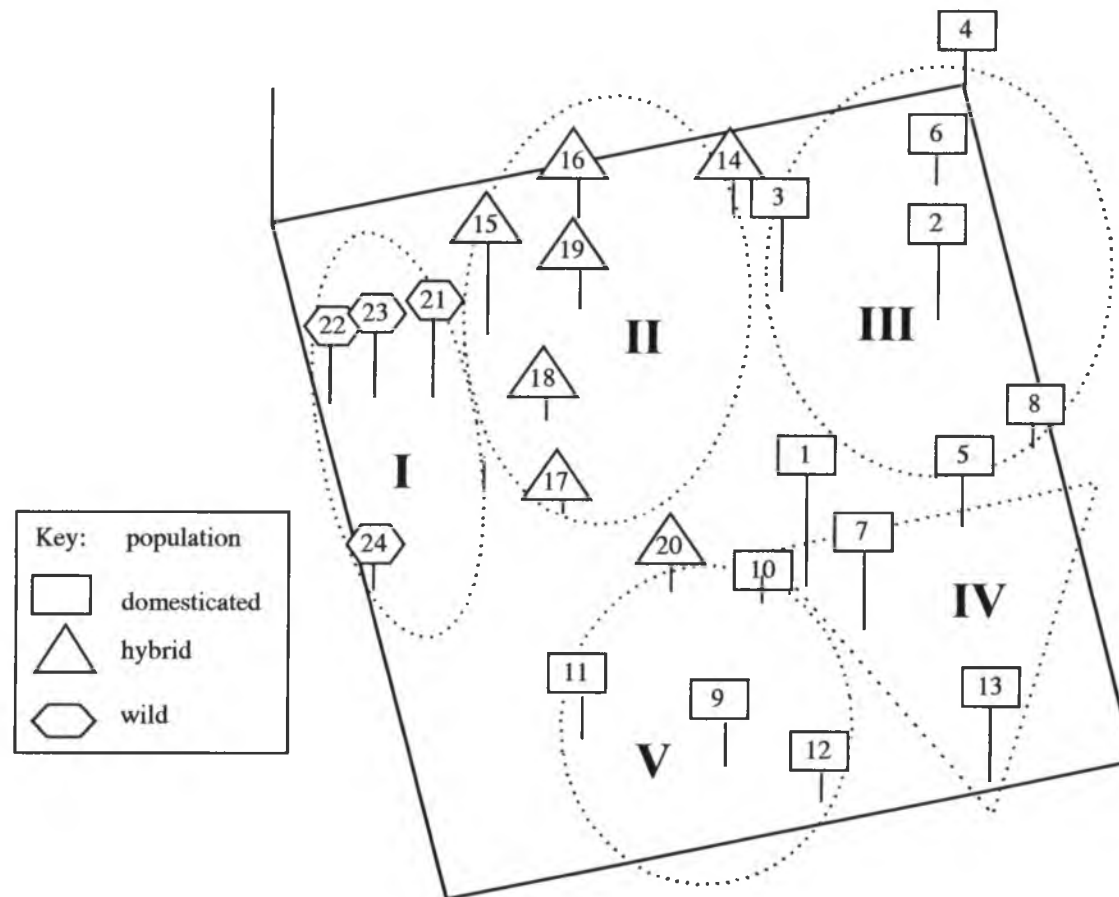
Fig. 4.3. Principal component analysis of *Carica papaya* populations.

domesticated populations (DSAN, DRIO, DHON, and DYUC), which occur in the

same areas as most of the wild and hybrid papaya populations in groups I and II above.

Domesticated population 8 (DVEN) from Venezuela clusters with group III and may

represent material introduced recently from a more northerly region. Group IV

consists of populations from Central America lacking wild papayas, but which may

have hybrid populations present (DVER, DPAC, DPAN, and DCOS). Group V has

South American domesticated (DYOP, DBUE, DNAP, and DDOM) and hybrid

(HVEN) populations. Although WRIO was grouped with the remaining wild

populations of Central America, it also has genetic identity values close to those of the

populations in group V. Similarly, HRIO (in group II) has close genetic relationships

with populations of group V. The five population groupings that emerged from the

PCA agree basically with the results obtained through the cluster analysis.

Intrapopulational genetic variability

The degree of genetic variability within each of the 24 populations was assessed

by examining the mean number of alleles per locus (A), the percentage of polymorphic

loci (PLP) per population, and the mean expected heterozygosity (H_{exp}) (Table 4.6).

The mean number of alleles per locus varied from 1.2 (DYOP, DPAN, and HVER) to

1.8 (WPET), with an overall mean of 1.5. The PLP per population varied from 23.1

percent in DYOP, DPAN, and HVER to 61.5 percent in DRIO and WPET, with an

overall mean of 41.4 percent.

Table 4.6. Genetic variability at 13 loci in 24 populations of *Carica papaya* in Central and South America.

Population	Sample Size		Mean no. of alleles per locus (A)	Percentage of polymorphic loci[1] (PLP)	Mean observed heterozygosity (H_{OBS})	Mean expected heterozygosity[2] (H_{EXP})
	Parent Accession	Seedling Progeny				
1 DVER	4	39	1.5 (0.2)[3]	38.5	0.022 (0.012)[3]	0.122 (0.054)[3]
2 DYUC	2	62	1.5 (0.2)	38.5	0.093 (0.045)	0.159 (0.060)
3 DSAN	1	16	1.5 (0.2)	46.2	0.240 (0.105)	0.159 (0.066)
4 DRIO	4	36	1.6 (0.1)	61.5	0.064 (0.031)	0.112 (0.047)
5 DPAC	10	29	1.6 (0.2)	46.2	0.143 (0.050)	0.186 (0.063)
6 DHON	5	23	1.5 (0.1)	46.2	0.070 (0.027)	0.138 (0.051)
7 DCOS	7	78	1.5 (0.2)	46.2	0.124 (0.050)	0.157 (0.059)
8 DVEN	6	35	1.4 (0.1)	38.5	0.112 (0.043)	0.152 (0.059)
9 DBUE	14	30	1.5 (0.1)	46.2	0.072 (0.032)	0.109 (0.042)
10 DYOP	2	42	1.2 (0.1)	23.1	0.112 (0.060)	0.098 (0.052)
11 DDOM	11	100	1.3 (0.1)	30.8	0.079 (0.042)	0.088 (0.042)
12 DNAP	4	30	1.2 (0.1)	23.1	0.097 (0.057)	0.080 (0.046)
13 DPAN	3	30	1.2 (0.1)	23.1	0.015 (0.008)	0.015 (0.008)
14 HVER	1	7	1.2 (0.1)	23.1	0.154 (0.088)	0.117 (0.062)
15 HSAN	2	22	1.6 (0.2)	46.2	0.252 (0.087)	0.221 (0.071)
16 HPET	2	50	1.5 (0.2)	38.5	0.138 (0.065)	0.121 (0.057)
17 HRIO	10	37	1.7 (0.2)	53.8	0.106 (0.042)	0.139 (0.050)
18 HHON	8	26	1.5 (0.2)	46.2	0.130 (0.054)	0.130 (0.054)
19 HCOS	7	58	1.6 (0.2)	53.8	0.168 (0.063)	0.181 (0.064)
20 HVEN	2	33	1.3 (0.1)	30.8	0.154 (0.062)	0.132 (0.059)
21 WYUC	3	8	1.5 (0.2)	46.2	0.154 (0.062)	0.166 (0.061)
22 WSAN	7	28	1.6 (0.2)	46.2	0.135 (0.060)	0.146 (0.064)
23 WPET	13	45	1.8 (0.2)	61.5	0.137 (0.051)	0.155 (0.058)
24 WRIO	3	7	1.4 (0.1)	38.5	0.044 (0.019)	0.081 (0.034)
Overall Mean	5.4	36.3	1.5	41.4	0.117	0.132

[1] A locus is considered polymorphic if the frequency of the most common allele does not exceed a value of 0.99.

[2] Unbiased estimate based on Hardy-Weinberg expected value (Nei 1978).

[3] Standard errors are given in parentheses.

Two measures of mean heterozygosity were determined, the mean expected or panmictic heterozygosity (H_{exp}) adjusted for small sample sizes (Nei 1978) and the mean observed or direct count heterozygosity (H_{obs}) (Table 4.6). The mean observed heterozygosity for the 24 populations ranged from 0.015 (DPAN) to 0.252 (HSAN), with an overall mean of 0.117. The mean expected heterozygosity based upon Hardy-Weinberg equilibrium ranged from 0.015 (DPAN) to 0.221 (HSAN), with an overall mean of 0.132.

Correlation analyses were conducted using Minitab Version 10.1 (Minitab Inc, State College, PA 16801-3008) to determine if a statistically significant relationship exists between sample size and genetic variability parameters, A and PLP, obtained for the 24 populations listed in Table 4.6. Sample size parameters analyzed were the number of accessions contributing to seedlings sampled, and the number of seedlings sampled (Table 4.6). Significant correlations ($P < .05$) were observed between number of accessions and A ($r = 0.469$) and between number of accessions and PLP ($r = 0.461$). No significant correlation was found between the number of seedlings sampled and A ($r = 0.046$) or PLP ($r = 0.020$).

The wild populations of Yucatan (WYUC), Peten (WPET), San Ignacio (WSAN), and Rio Motagua (WRIO) (PCA group I) have the highest values in two out of three intrapopulational variability measures, where A ranges from 1.4 to 1.8 (mean 1.57), PLP ranges from 38.5 to 61.5 (mean 48.1), and H_{exp} ranges from 0.081 to

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0.166 (mean 0.137) (Tables 4.6 and 4.7). The wild population of Rio Motagua (WRIO) has much lower values for all variability measures than the other three wild populations in PCA group I.

The second highest variability exists in Central American hybrid populations (PCA group II), where A ranges from 1.2 to 1.7 (mean 1.52), PLP ranges from 23.1 to 53.8 (mean 43.6), and H_{exp} ranges from 0.117 to 0.221 (mean 0.152) (Tables 4.6 and 4.7).

The domesticated populations of PCA group III which came from northern regions of Central America where wild papayas exists, have the third highest variability, where A ranges from 1.4 to 1.6 (mean 1.50), PLP ranges from 38.5 to 61.5 (mean 46.2), and H_{exp} ranges from 0.112 to 0.159 (mean 0.144) (Tables 4.6 and 4.7).

The PCA group IV, which consists of a hybrid and domesticates from regions in Central America lacking wild populations has the fourth highest variability, where A ranges from 1.2 to 1.5 (mean 1.45), PLP ranges from 23.1 to 46.2 (mean 38.5), and H_{exp} ranges from 0.015 to 0.186 (mean 0.120) (Tables 4.6 and 4.7).

The lowest variability values among all populations studied exist in PCA group V, which includes hybrids and domesticates from South America. The

intrapopulational variability measure, A, ranges from 1.2 to 1.5 (mean 1.32), PLP

ranges from 23.1 to 46.2 (32.3), and H_{exp} ranges from 0.08 to 0.152 (mean 0.105)

(Tables 4.6 and 4.7).

Because the correlation coefficients between the number of accessions and the

the genetic variability parameters A and PLP of the 24 populations (Table 4.6) were

found to be significant, correlation analyses using Minitab were also conducted between

the mean number of accessions and the mean A and PLP of the five PCA groupings

presented above (Table 4.7). No significant correlation was found between the mean

number of accessions in each PCA group and the mean genetic variability parameters A

(r=-0.329) or PLP (r=-0.475) of each group.

Mean expected and observed heterozygosities were also presented for

domesticated-hermaphrodite, domesticated-female, and wild-female populations (Table

4.8). The deficit of heterozygotes (Wright's fixation, F, index of 0.657) was highest in

the domesticated-hermaphrodite populations, followed by the domesticated-female

populations (F = 0.298). The wild-female populations had the lowest F value (0.139),

which indicates that it had the greatest number of heterozygotes of the three population

categories. Both domesticated-hermaphrodite and domesticated-female populations also

had a highly significant deficiency of heterozygotes as compared to Hardy-Weinberg

expectations.

Table 4.7. Genetic variability at 13 loci in five PCA Groups of *Carica papaya* in Central and South America.

Group (Mean)	Sample Size		A	PLP	Hexp
	Accession	Seedling			
PCA I (Pop. #21,22,23,24)	6.5	22.0	1.575	48.1	0.137
PCA II (Pop.#14,15,16,17,18,19)	5.0	33.3	1.517	43.6	0.152
PCA III (Pop. #2,3,4,6,8)	3.6	34.4	1.500	46.2	0.144
PCA IV (Pop. #1,5,7,13)	6.0	44.0	1.450	38.5	0.120
PCA V (Pop.#9,10,11,12,20)	6.6	47.0	1.300	30.8	0.101

Table 4.8. Comparison of inbreeding and heterozygosity of different papaya sex types.

Population[1]	Sample size	F Wright's Fixation Index	Mean observed heterozygosity	Mean expected heterozygosity[2]
Hermaphrodite (domesticated)	229.0	0.657 **	0.061 (0.021)	0.178 (0.063)
Female (domesticated)	194.0	0.298 **	0.113 (0.040)	0.161 (0.056)
Female (wild)	88.0	0.139	0.130 (0.048)	0.151 (0.058)

** Highly significant ($P < 0.01$).
[1]Domesticated fruits > 1000 g; wild fruits < 100 g.
[2]Unbiased estimate (Nei 1978) (standard error in parentheses).

Geographic patterns of genetic diversity in *Carica papaya* populations

A total of 29 alleles were found from the survey in Central and South America (Table 4.4). In addition to a single allele at *Idh*, *Mdh-1*, *Mdh-2*, and *6-Pgd*, the two regions share the following 13 common and widespread alleles: *Aco-1A*, *Aco-1B*, *Aco-2B*, *Aco-2C*, *Pgi-2B*, *Pgi-2C*, *Pgm-1A*, *Pgm-1B*, *Pgm-2B*, *Skd-B*, *Tpi-1B*, *Tpi-2B*, and *Ugp-B*. Of the remaining 12 alleles that are less widespread, 10 are found only in Central America, occurring mostly in the San Ignacio (Belize), Rio Motagua, and Peten (Guatemala) areas. Two less widespread alleles occurred in both Central and South America: *Ugp-A* was present in Guatemala (DRIO), Costa Rica (HCOS), and Colombia (DBUE) and *Tpi-2C* occurred in eight Central American populations, as well as in Colombia (DBUE) and Venezuela (DVEN). Alleles for which discernable patterns of distribution are evident are described below.

The allele A at locus *Aco-1* is one of the most common alleles found in papaya (Table 4.4 and Fig. 4.4). Its predominance in the South American populations is indicated by its fixed or nearly fixed frequencies in Colombia, Ecuador, and Venezuela. The two Central American populations with high frequencies of *Aco-1A* are the wild population in Rio Motagua, Guatemala (WRIO at 0.929) and the domesticated Pacific coast population of Guatemala (DPAC at 0.810). With these two exceptions, the frequencies of this allele seem to decrease northwards from Costa Rica to Mexico. The domesticated population of San Ignacio, Belize (DSAN) has the lowest
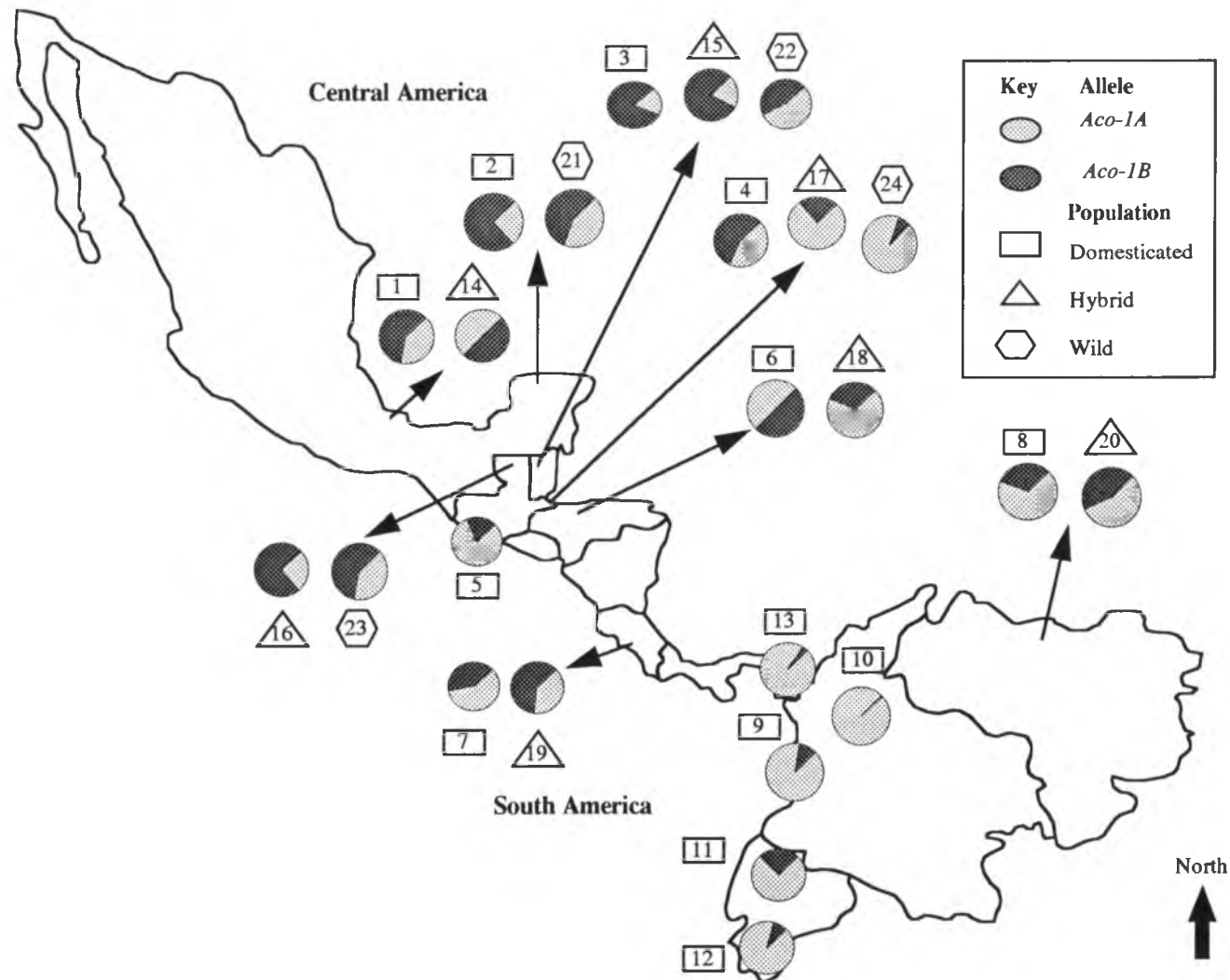
Fig. 4.4. Frequencies of *Aco-1* alleles in *Carica papaya* populations.

frequency of *Aco-1A* at 0.188. The other allele at this locus, *Aco-1B*, followed the opposite trend as expected.

Aco-2A is present in 10 populations of Central America, with frequencies ranging from 0.638 in DPAC to 0.04 in HPET (Table 4.4 and Fig. 4.5). Intermediate frequencies were found in domesticated, hybrid, and wild populations from Veracruz, Mexico to Peten, Guatemala. This allele was not encountered south of Honduras, and was notably absent immediately north of this limit in all populations in the Rio Motagua valley, Guatemala.

Aco-2B was found in all populations except WRIO (Table 4.4). The frequencies range from 0.967 (DPAN) to 0.091 (HSAN). *Aco-2B* existed in high frequencies in all domesticated populations of Central America, especially in Yucatan, Rio Motagua (Guatemala), Honduras, and Panama, as well as in Venezuela. Slightly lower frequencies were found in the remaining domesticated populations of South America. The hybrid and wild populations of Central America had the lowest frequencies of *Aco-2B* found among all populations examined.

Aco-2C is present in all the populations studied except DPAN (Table 4.4). The range in allele frequency was from 0.870 (DDOM) to 0.008 (DYUC). The frequencies of *Aco-2C* appeared to increase from north to south with the lowest frequencies in the domesticated populations of Central America and the highest frequencies in the

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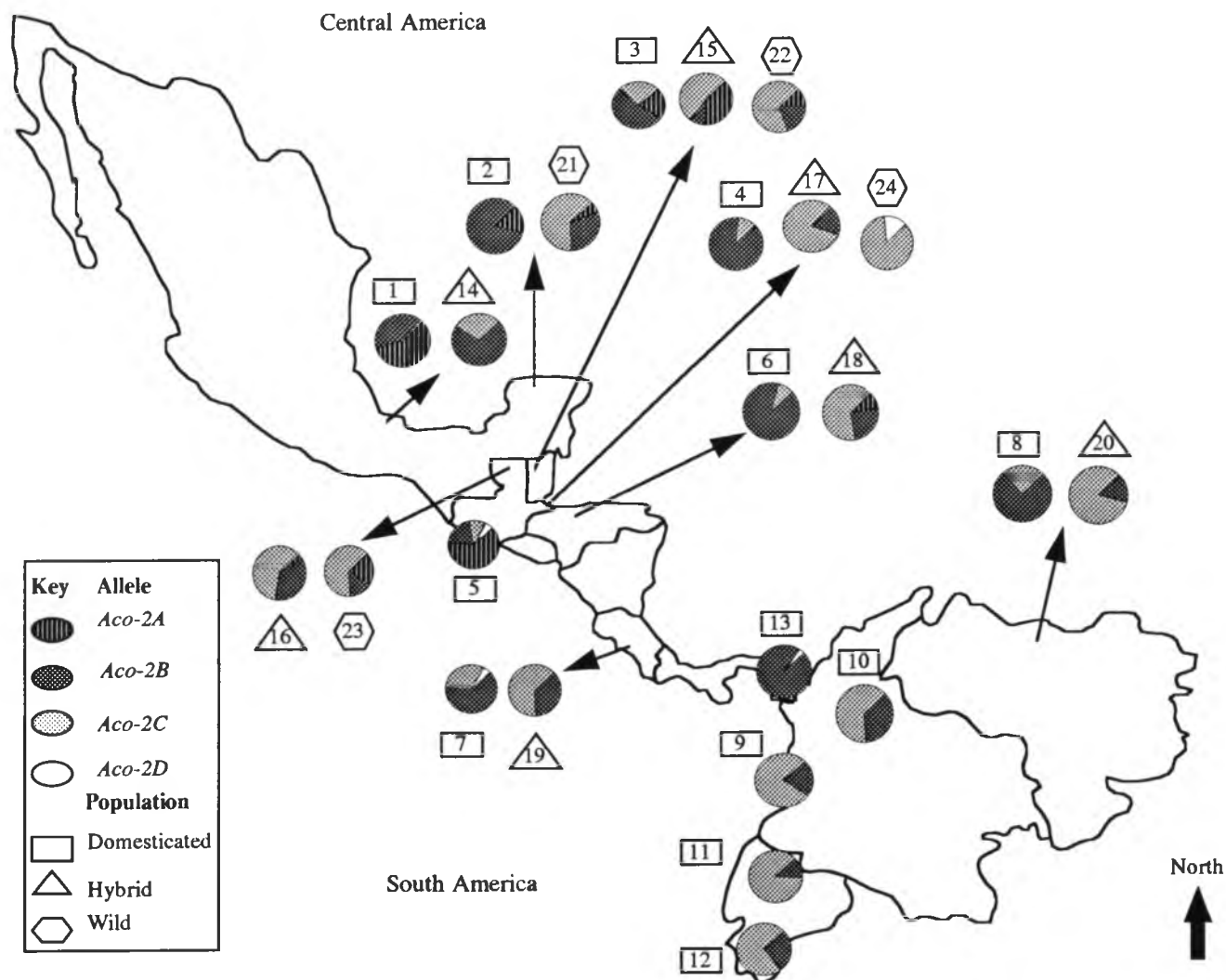
Fig. 4.5. Frequencies of *Aco-2* alleles in *Carica papaya* populations.

domesticated populations of South America. Intermediate frequencies were present in the wild and hybrid populations.

Pgi-2C was present in all except the wild Rio Motagua (WRIO) population (Table 4.4 and Fig. 4.6). The allele frequencies ranged from 0.972 (DRIO) to 0.011 (WPET). A trend in allele frequencies of *Pgi-2C* was observed to be highest in the domesticated (range of 0.972 to 0.075), intermediate in the hybrid (range of 0.5 to 0.121), and lowest in the wild populations (range of 0.076 to 0.011). No trend was observed from Central America to South America.

At *Pgm-1*, allele A is present in all of the papaya populations except HVER (Table 4.4 and Fig. 4.7). The range in frequency was from 1.00 in the domesticated population in Ecuador to 0.01 in the hybrid population of Peten. *Pgm-1A* also occurs with the highest frequencies in the domesticated populations of both regions. The lowest average frequencies were found in the wild populations and intermediate frequencies were found in the hybrid populations. In addition, *Pgm-1A* appeared to increase in frequency from north to south within the domesticated populations. Because *Pgm-1B* is the only other allele at this locus, its trend is opposite that of *Pgm-1A* as expected. *Pgm-1B* is predominant in the wild populations, intermediate in hybrid populations, and least frequent in the domesticated populations.
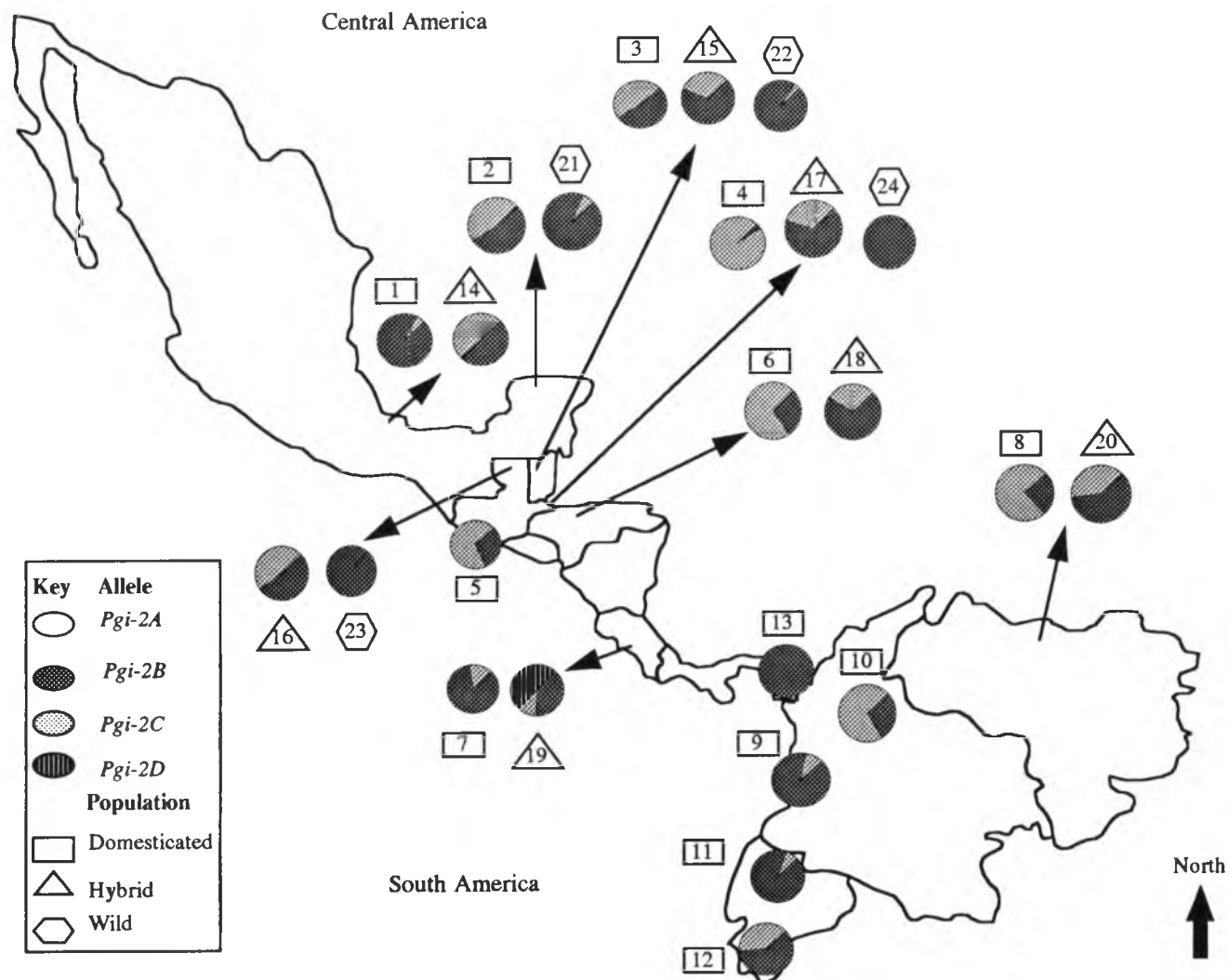
Fig. 4.6. Frequencies of *Pgi-2* alleles in *Carica papaya* populations.
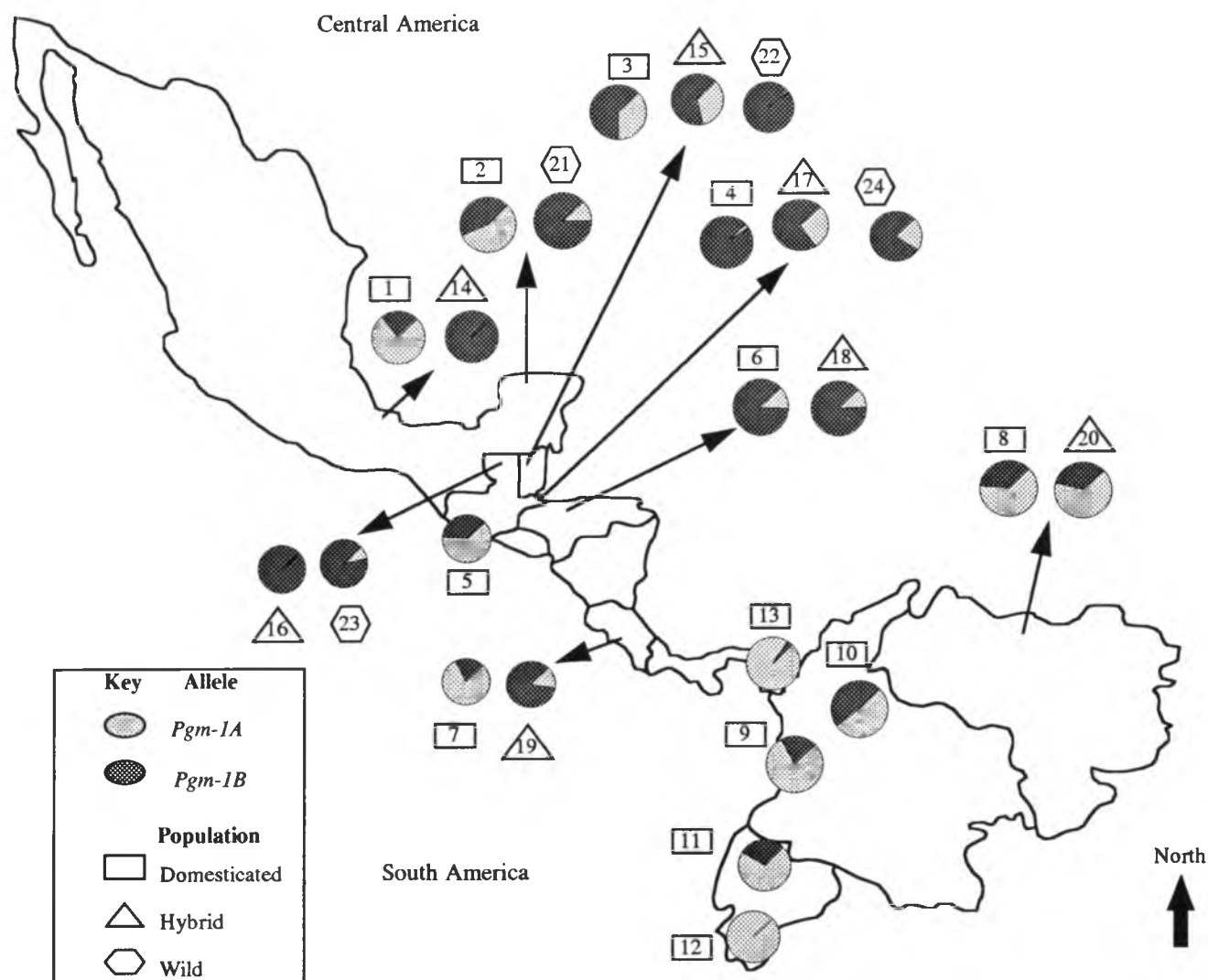
Fig. 4.7. Frequencies of *Pgm-1* alleles in *Carica papaya* populations.

Skd-A occurs at a range of 0.214 (WSAN) to 0.031 (DSAN) (Table 4.4 and Fig. 4.8). *Skd-A* is found only in the domesticated, hybrid, and wild populations of the Peten and San Ignacio. A gradient was noticeable with the highest *Skd-A* frequencies in the wild populations to intermediate frequencies in the hybrid populations, and lowest frequencies in the domesticated populations. *Skd-C* is present only in the domesticated, hybrid, and wild Central American populations of Rio Motagua, San Ignacio, Peten, and Costa Rica with a range in frequencies from 0.268 (WSAN) to 0.006 (DCOS). *Skd-C* followed the same trend in allele frequencies as that observed for *Skd-A*.

Tpi-1A is limited to the populations of Yucatan, San Ignacio, and Peten (Table 4.4 and Fig. 4.9), yet is common in those populations (frequency > 0.05) (Marshall and Brown 1975). *Tpi-2C* has a similar pattern as *Pgm-2A*. *Tpi-2C* was present in the domesticated and hybrid populations of Rio Motagua (Guatemala), Honduras, Costa Rica; the domesticated populations of Pacific coast (Guatemala), Venezuela, and Buenaventura (Colombia); and the wild population of Peten. The range in frequencies was from 0.378 (DCOS) to 0.014 (HRIO). Higher allele frequencies occurred in the domesticated populations than in hybrid or wild populations. *Tpi-2C* is one of two less widespread alleles found in both Central and South America. The other, *Ugp-A*, occurs in only three areas— in the domesticated populations of Rio Motagua, Guatemala (DRIO), Buenaventura, Colombia (DBUE), and in the hybrid population of Costa Rica (HCOS).

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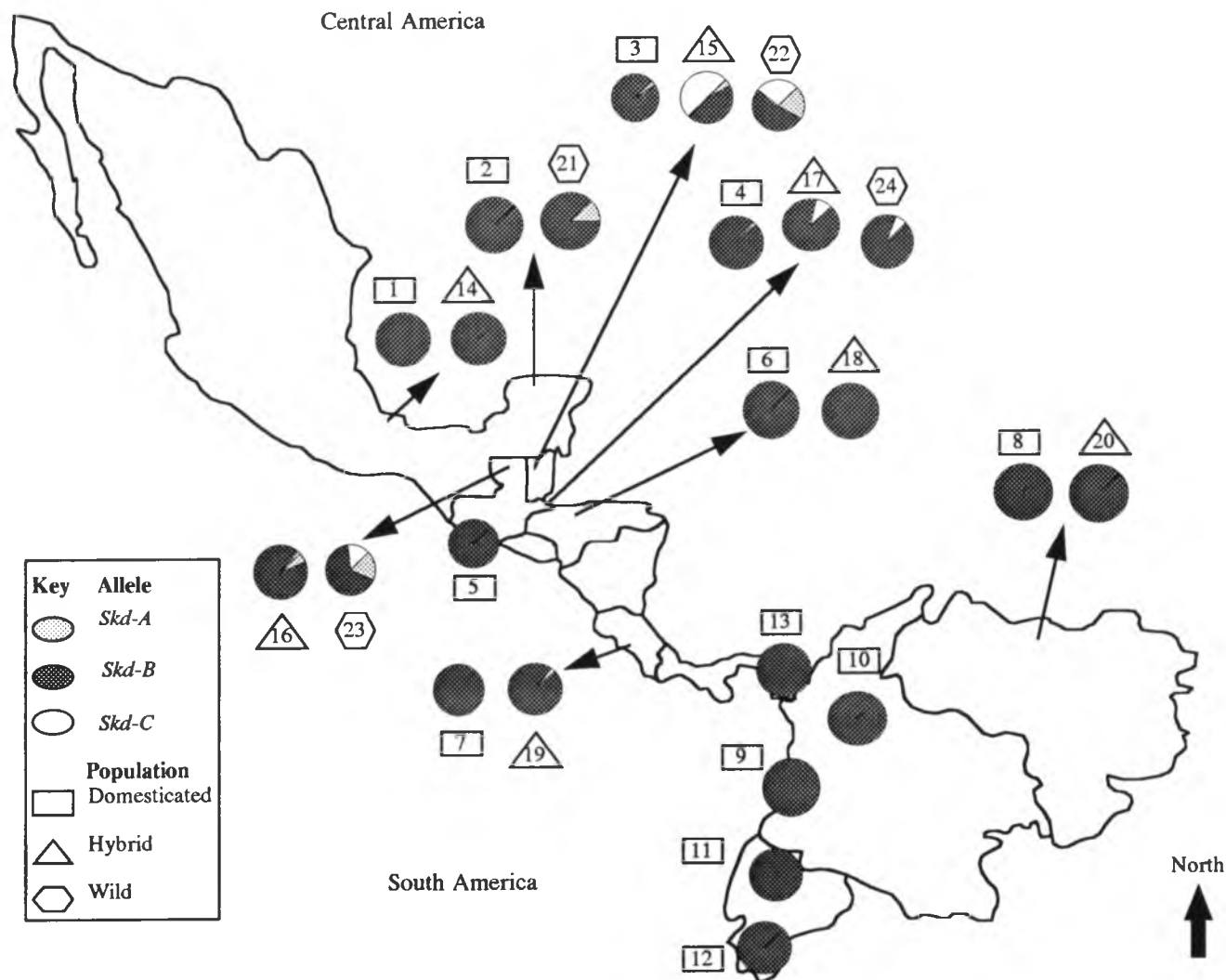
Fig. 4.8. Frequencies of *Skd* alleles in *Carica papaya* populations.
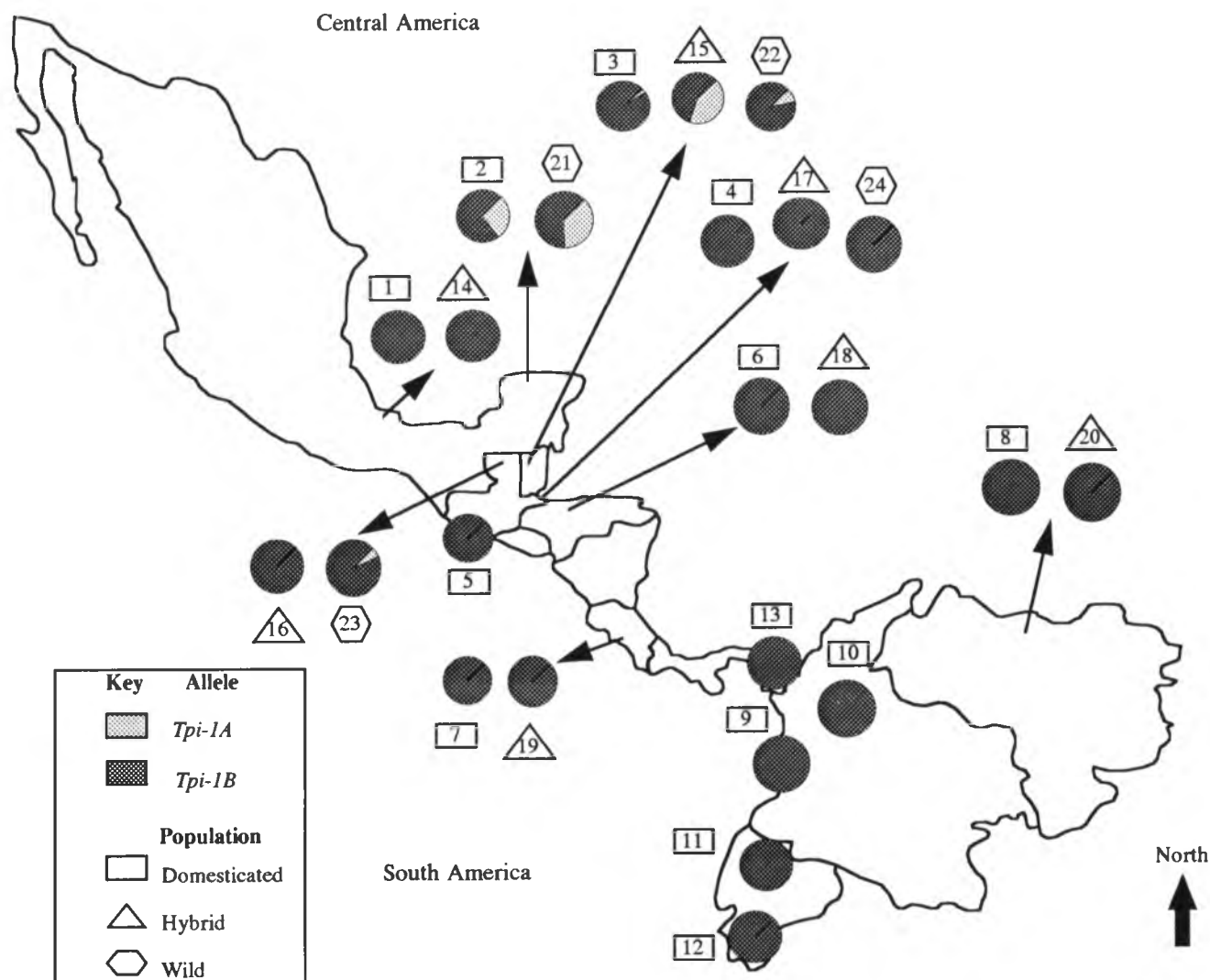
Fig. 4.8. Frequencies of *Skd* alleles in *Carica papaya* populations.

DISCUSSION

Carica papaya center of diversity

The center of origin of *C. papaya* has been a longstanding scientific issue as reported in the literature. Central America has been suggested as the center of origin of *C. papaya* by Storey (1976), and Vavilov (1951), while South America has been proposed as the most likely region by Badillo (1971), Brucher (1989), and Prance (1984). The isozyme distributional patterns and genetic affinities of the wild and domesticated papaya populations obtained in this study are used to determine the center of diversity of papaya. This information, along with available historical evidence, is interpreted to attempt resolution of the center of origin of the domesticated *C. papaya*.

High values for genetic identities indicate moderate variation in papaya, and taken together with a mean genetic identity value of $I > 0.9$, suggest that all of the populations examined are conspecific (Gottlieb 1977). This supports Badillo's (1971) designation of the wild papaya populations, previously designated as *C. peltata,* as the same species as *C. papaya*.

As observed in Fig. 4.3 and Table 4.6, the greatest diversity of all populations studied exists in the wild populations of Yucatan, Peten, San Ignacio, and Rio Motagua (PCA group I) based on the intrapopulational variability measures (A, PLP, and H_{exp}).

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These results suggest that the center of diversity for *C. papaya* is the Yucatan-Peten-San Ignacio-Rio Motagua area where the wild populations exist.

PCA group II represents the hybrid group that occurs in the same Yucatan-Peten-San Ignacio-Rio Motagua area as the wild and domesticated groups I and III of Central America. Based on the same measures, PCA group II has the second highest genetic variability and is intermediate between group I (wild) and group III (domesticated). The high variability of group II is a probable result of intercrossing between group I and group III.

PCA group III, which represents the domesticated populations existing in the same area as the wild and hybrids of groups I and II of Central America, has less variability than either of the other two groups. This is because domesticated populations are usually derived from a subset of the wild population. During the domestication process, human selection acting on the domesticated populations probably caused further narrowing of the genepool of the domesticated populations (Doebley 1984). However, when compared with the other domesticated groups (PCA groups IV and V), which are not sympatric with the wild and hybrid populations, group III has the highest variability. This evidence provides further support for the Yucatan-Peten-San Ignacio-Rio Motagua area in Central America as the center of diversity for *C. papaya* because both the domesticated papaya populations and the wild papaya populations that exist in the area have the highest variabilities.

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The question of whether sample size might be a factor in influencing the level of genetic variabilities in the *C. papaya* populations emerged when significant correlations were found between number of accessions and two genetic variability parameters (A and PLP). However, when the populations were assigned according to the PCA groupings, no significant correlations were found between the mean number of accessions and mean A or PLP. This demonstrates that the pattern of genetic variability in the papaya populations is not an artifact of sample size, as the first correlation had suggested. Rather, the level of genetic variability present in *C. papaya* populations appears to be influenced by the domestication status (wild, hybrid, or domesticated) and geographic location (Central or South America) as indicated by the PCA groupings. Furthermore, because wild populations exhibited the largest genetic variability from the fewest number of accessions and seedling progenies sampled, sample size is sufficient to provide valid results.

Genetic variability tends to decrease the further away the population is located from the wild populations of group I. In South America, where no wild *C. papaya* populations were found (Chapter 3), the intrapopulational variability measures (A, PLP, H_{exp}) of the domesticated *C. papaya* populations are the lowest of all populations studied. This indicates that this area of South America is not likely the center of diversity or the region of domestication of papaya. In addition to the existence of the wild *C. papaya* populations in Central America, the majority of the different alleles encountered were in Central America rather than in South America (Table 4.4). While

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no alleles were unique to any of the South American populations, 10 out of a total of

29 alleles were found exclusively in Central American populations. Most of the 10

alleles occur in the Yucatan-Peten-San Ignacio-Rio Motagua area, which strengthens

the probability that this area is the center of diversity of papaya. This area also

corresponds roughly with the ancient Mayan empire.

Patterns of allelic frequency distribution and probable origin of domesticates

From the allelic frequency data (Table 4.4), several generalizations can be made

about the allelic distribution in papaya populations. The common alleles that are

localized to a particular area, such as *Aco-2D*, *Pgi-2D*, *Pgm-2A*, *Skd-A*, *Tpi-1A*,

Tpi-2A, and *Ugp-A,* are presumably adaptive and selectively maintained in populations

(Marshall and Brown 1975). They might be of particular interest to plant breeders

because they represent adaptations to local variations in the biotic or abiotic

environment (Marshall and Brown 1975). This is not to say that the widespread

common alleles as well as monomorphic alleles are not of importance to the

populations. The fact that they are widespread suggests that they are essential to the

adaptedness and high productivity of the populations in nearly all genetic backgrounds

and environments (Allard 1992). Some alleles at a locus seem to increase in frequency

from north to south or vice versa and from domesticated to wild or vice versa. The

patterns of allelic frequency distributions in relation to the five PCA groupings

(Fig. 4.3) are discussed below.

As discussed in the previous section, the center of diversity of *C. papaya* is roughly in the region extending from the Yucatan peninsula through Belize, the Peten and eastern Guatemala, where the wild populations exist. The domestication of papaya probably occurred somewhere in this region. This is supported by the higher variability observed in the domesticated populations PCA group III found in this area when compared to the other domesticated groups (PCA groups IV and V) found in Central America and South America.

The domesticated populations of PCA group III could have been derived from the wild populations of PCA group I. As indicated by the genetic identities in Table 4.5 and by the grouping of major group A of the cluster analysis (Fig. 4.2), populations belonging to PCA groups I, II, and III are more closely related to each other than to the remaining populations studied. The frequencies of certain alleles revealed the influence of wild populations in the domesticated papaya populations found in PCA group III. For example, allele B at *Pgm-1* locus is most prevalent in the wild (PCA group I), the hybrid populations (PCA group II), and in the domesticated populations of PCA group III. The frequency of *Pgm-1B* decreases the further away the populations are located from the Peten, San Ignacio, Rio Motagua, and Honduras, where most of PCA groups I, II, and III are found. *Skd-A* and *Tpi-1A* are localized in the Yucatan-Peten-San Ignacio area and have higher frequencies in the wild than in domesticated populations. It is possible that *Skd-A* and *Tpi-1A* could have arisen in the wild populations and then spread to the crop populations that occur sympatrically with

the wild populations. *Aco-2A* is localized in the domesticated papaya populations of Mexico (Veracruz and Yucatan), Belize, and the Pacific coast of Guatemala. Where wild populations exist, lower frequencies are detected in both the wild and hybrid populations in these areas. This suggests that the presence of the *Aco-2A* allele in the wild, hybrid, and domesticated populations is the result of long-term hybridization involving all populations.

Aco-2B is a widespread allele of the domesticated populations in both Central and South America that varies from north to south and as well as from domesticated to wild. This allele may have arisen in the domesticated populations of Central America and spread south to the domesticated populations of South America. However, the populations with lowest frequencies of this allele are the wild and hybrid populations of Central America. This may be due to *Aco-2B* not being adaptive in the wild and hybrid populations.

In PCA group IV, the higher genetic identities that this group shares with members of PCA group III indicate that group IV is closely related genetically to group III. The higher genetic variability that exists in group III compared to group IV suggests that it is more likely that group IV was derived from group III rather than the reverse. Genetic drift probably played an important role in reducing genetic variation during the movement of the crop from the area of origin. This is because in disseminating a crop to new area, humans usually take a limited sample of the crop's

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genepool from the original population, and as a result, the further away the crop is from the area of origin, the less the genetic variability (Hancock 1992). From the Yucatan-Peten-San Ignacio-Rio Motagua area, it appears that domesticated papayas might have been brought to Veracruz, the Pacific coast of Guatemala, Costa Rica, and Panama.

As alluded to earlier in the results, the wild population of Rio Motagua (WRIO) has considerably lower genetic variability than the other three wild populations found in the Yucatan (WYUC), San Ignacio (WSAN), and Peten (WPET). Having fruits at the upper size range of those found in the other three areas also indicates that WRIO probably has had some influence from domesticated populations. Cluster analysis results suggest that WRIO is closely allied to the hybrid populations of Rio Motagua and Honduras. Slight differences in allelic compositions such as *Aco-2B*, *Skd-A*, *Tpi-1A* (absent in WRIO; present in WYUC, WSAN, and WPET) and *Aco-2D* and *Tpi-2A* (present in WRIO; absent in WYUC, WSAN, and WPET) also suggest that the wild Rio Motagua population is removed slightly from the other three wild populations in Central America.

The genetic identity values (Table 4.5) indicate that WRIO is more closely related to the domesticated populations of South America than to the domesticated populations of Central America. The closest Central American population to WRIO is DCOS (the domesticated Costa Rica population). The genetic identities of the South

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American populations indicate that they are closely related to DCOS, WRIO, and HRIO (the hybrid population of Rio Motagua) from among the Central American populations. Furthermore, WRIO and DPAC (domesticated population of Pacific coast of Guatemala) are the two Central American populations with high frequencies of *Aco-1A*, an allele that is predominant in domesticated populations of Colombia, Ecuador, and Venezuela.

Based on this evidence, the South American populations were probably introduced from approximately the Rio Motagua area or south of Rio Motagua. Of the less common and unique alleles that occur in Central America, only two (*Ugp-A* in DBUE and *Tpi-2C* in DBUE and DVEN) are present in South America as well (Table 4.4). It may not be mere coincidence that these alleles are found in Buenaventura, Colombia, and Venezuela, because these two places represent the South American coasts nearest to where domesticated papaya might have been brought from the north in Panama, Costa Rica, Honduras, and Guatemala (Rio Motagua and Pacific Coast). This is supported by the presence of these alleles in some of these populations as well. It is probable that from the pattern of allelic frequency distribution that the domesticated papaya population spread from Central America to South America via Buenaventura, Colombia, and Venezuela.

Historical trade routes of Mesoamerica may offer the mechanisms by which *C. papaya* was transported from the Yucatan-Peten-San Ignacio-Rio Motagua area, the

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area of domestication and center of diversity as indicated by the PCA and genetic identity results, to other places in the region. Mesoamerica is defined as the area that includes the modern political entities of Mexico (from the mouth of the Panuco River on the Gulf Coast to the Rio Grande de Santiago on the Pacific side), Guatemala, El Salvador, Belize, and the western part of Honduras, Nicaragua, and Costa Rica to an approximate boundary that extends from the mouth of the Ulua River and Lake Yojoa in Honduras to the Gulf of Nicoya in Costa Rica (Kirchoff 1943). The rest of the area southeast of Mesoamerica was referred to simply as Central America by Kirchoff (1943).

According to Chapman's (1957) analyses of Aztec-Mayan trade prior to the arrival of Europeans in the 16th century, this same region was heavily trafficked by traders, whose routes to major metropolitan areas and ports of trade are depicted in Fig. 4.10. Chapman's work was based heavily on Bernardino de Sahagun's Florentine Codex Book 9 (1959) that described trading expeditions that went to coastal regions of southern Mesoamerica. The major metropolitan center of the Aztec civilization was in the basin of Mexico (Mexico City), while the Mayan's was on the northeast coast of the Yucatan peninsula. The ports of trade that supplied goods to these two metropolitan areas were located in Xicalango on the gulf coast (present states of Veracruz, Tabasco, and Campeche), the Pacific coast in the province of Xoconusco (present states of Oaxaca and Guerrero in Mexico and part of the Pacific coast of Guatemala), Acalan (in the upper course of the Candelaria river system in the present

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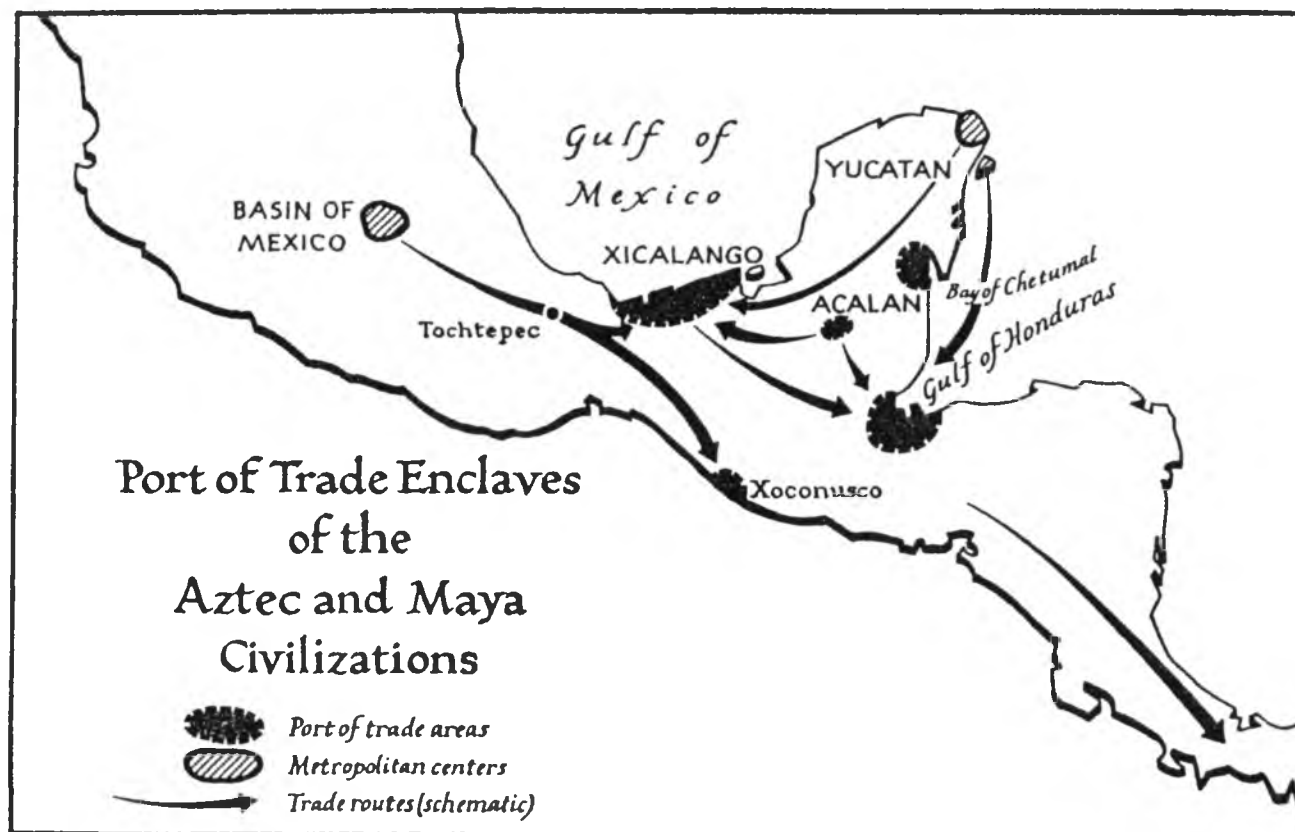
Fig. 4.10. Port of trade enclaves of the Aztec and Maya civilizations.

From Chapman (1957:118). In: K. Polanyi, C.M. Arensberg, and H.W. Pearson (eds.), *Trade and Market in the Early Empires*. Copyright © 1957 by The Free Press, an imprint of Simon & Schuster. Reprinted with permission of the publisher.

state of Campeche, near the Peten region of Guatemala), and the coastal area (Motagua

valley) on the Gulf of Honduras. These areas were also cacao-growing regions. Cacao

was the universal currency in the Mesoamerican and Central American regions at that

time. Traders from Acalan passed through the Peten region of Guatemala on their way

to the Gulf of Honduras. Obsidian trade analysis by Hammond (1981) confirmed the

trade routes that existed in these areas. Obsidian mined at El Chayal, 20 km northeast

of Guatemala City, was found in northeastern Peten and Belize (Hammond 1981).

Obsidian mined in Ixtepeque (Asuncion Mita) was apparently transported down the Rio

Motagua and up the Caribbean coast to Belize, to Guatemala (Peten), and to Mexico

(Yucatan) (Hammond 1981). With the existence of these trade routes, domesticated

papaya could have been traded within the Yucatan-Peten-San Ignacio-Rio Motagua

region. This might explain why the PCA results indicate that the domesticated

C. papaya from within the Yucatan-San Ignacio-Rio Motagua-northwestern Honduras

area appear closely related. Lothrop (1950) indicated that journeys by groups of people

within Mesoamerica were exemplified today by his personal encounter of Indians from

Mexico in Guatemala and vice versa. Lothrop (1950) believed that such journeys must

have taken place from time immemorial.

From the Yucatan-Peten-San Ignacio-Rio Motagua area, *C. papaya* could have

been brought southwards to Nicaragua, Costa Rica, and Panama. The long-distance

Aztec traders or "pochteca" were known to travel as far south as the present Costa

Rica-Panama border for gold (Lothrop 1950). The Rio Motagua area on the Gulf of

Honduras coast represented a trading bridge connecting Mesoamerica with Central America (Chapman 1957). This could explain why the wild Rio Motagua papayas appear to have influenced the domesticated papayas south of Rio Motagua in Costa Rica, Panama, and subsequently in South America as indicated by the genetic identity and PCA results.

Lothrop (1950) regarded Panama as the cross-roads of Central and South America in recent and aboriginal times. The archaeological sites on the isthmus revealed the occurrence of gold plaque from Peru and Olmec jade from Mexico. According to Lothrop (1950) such artifacts indicated long distance trading activities between the regions. Organized trade both by land and sea was indicated by the presence of the Aztec-speaking Sigua and the Churchures from Honduras in Panama. The navigational skill and boat building capability of the Mosquito Indians of Nicaragua is evidenced by their sea raids of Guatemala and Panama in the seventeenth and eighteenth centuries. Large traffic of small boats along the Central American coast from the Yucatan to Panama still cater to people who are unable to afford the steamer rates according to Lothrop (1950). Stone (1977) also found that both coastal and international trade between Central America, Mexico, and northwestern South America (especially Ecuador) existed at least at the time of the Spanish arrival.

The proximity of Panama to South America would have facilitated papaya's continued spread southwards (Patiño 1963), although it is unclear from the available

historical records whether *C. papaya* was brought to South America before or after the arrival of the Spaniards. Papaya was probably known to the tribes between San Miguel bay (Panama) and the Cabo Corrientes (Colombia) before the arrival of the Spaniards (Patiño 1963). However, papaya might not have been grown much in the western part of the Colombian coast because that region (Choco) is rather wet and papaya prefers a dry climate (Patiño 1963). As noted by Nordenskiold in 1928 (as cited by Wassen 1935), the Choco Indians of Munguido Island on the Rio San Juan (Colombia) had difficulty planting *C. papaya* due to floods.

In his chronicle, Oviedo (1959a), who first mentioned seeing domesticated papaya fruits on the west shore of Nicaragua near Leon in 1526, also stated that papayas were taken from Nicaragua to be planted in the province of Darien in Panama (Chapter 2). This seems to indicate that domesticated papaya was not present in Darien before Oviedo's arrival in 1525. *Carica papaya* was found by Pizarro on the dry coast of Ecuador in 1531 (Trujillo 1948 as cited by Prance 1984); known to occur in Valencia, Venezuela in 1532 (Aguado 1919 as cited by Patiño 1963); and seen on the eastern flanks of the Andes in 1582 (Jimenez de la Espada 1897 as cited by Prance 1984). Gonzalez Suarez (1890 as cited by Patiño 1963) and Prance (1984) interpreted this to mean that *C. papaya* was probably well-distributed in Central and South America before colonial times. However, it is very plausible that *C. papaya*, being a species that can fruit in nine months, could have spread to South America from Panama

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in six years. Based on her archaeological work, Towle (1961) asserted that *C. papaya* was not grown in Peru in prehispanic times.

Regardless of whether *C. papaya* was widespread in Central and South America before or after the arrival of the Europeans, it does not rule out that *C. papaya* was brought from Central America to South America as indicated by the genetic results obtained in this study. Furthermore, the historical trade routes could have facilitated the probable movement of *C. papaya* southwards from its center of domestication. The alternative scenario of *C. papaya* being domesticated in South America and spread northward to Central America seems less plausible in light of the above evidence.

Domestication of *Carica papaya*

Plant domestication is an evolutionary process by which humans modify plant populations over time by changing plants' biological factors such as gene frequencies and morphology (Davis and Bye 1982). Through continued selection during the domestication process, wild plants are altered in such a way that they become dependent upon humans in varying degrees for their survival and reproduction (Ladizinsky 1985).

In nature, *C. papaya* is a seral pioneer species and is a colonizer of disturbed habitats and light gaps in forests. Like other pioneer species, *C. papaya* is not a good

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competitor and does not persist once the forest canopy closes (Whitmore 1990). Having originated in physically disturbed habitats, wild *C. papaya* is preadapted to succeed in gardens and areas around dwellings that are actually "human-disturbed" habitats. This ability to thrive in such areas allows the wild *C. papaya* to be a "camp-follower" of humans, and thus increases opportunity for human manipulation. Alcorn (1984) in her study of the Huastec Mayan ethnobotany described wild papaya seedlings as among the spontaneous vegetation that were spared when regrowth was slashed back after the first harvest of maize from a milpa (or subsistence-level field) site. The ripe fruits of this spontaneous, small-fruited wild type were eaten and the leaves were used as forage for pigs.

Papaya fruits with desirable characteristics, such as slightly larger size, thicker flesh, and sweeter taste, were probably collected in the wild, and the fruits consumed and seeds discarded near dwellings. A study by Miksichek (1983) found remnants of wild papaya seeds associated with dwellings rather than the field habitats in the Pulltrouser Swamp archaeological site in Belize. The progenies of these selected papayas growing around human dwellings formed the next generation that might be further selected, consumed and dispersed to new habitats. Thus, the first step of the domestication process began the moment humans selected the plants whose attributes were desirable to them. Continued selections by humans narrowed the genetic variability of papaya populations. When humans began actively sowing the seeds of plant species that were harvested in the wild, the selection pressures operating in the

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cultivated fields were mostly human-induced and different from the selection pressures operating in the wild. Disruptive selection may occur if the population in the cultivated field is isolated long enough from the wild population. Eventually, this results in a divergence in morphological, genetic, and ecological characters (Doggett and Majisu 1968).

Further steps in the domestication process involved changing the various undesirable attributes that distinguished the wild papaya to desirable ones associated with the large, thick-fleshed domesticated papaya. While germinating and establishing seedlings for isozyme analysis in this dissertation, a reduction or lack of dormancy during the germination of the domesticated papayas was apparent. This was not observed in the wild papayas germinated. The domesticated papayas germinated uniformly at about two weeks after sowing, while the wild papayas germinated at various times from about three weeks to two months after sowing. The phenomenon of delayed germination in the wild populations, and the uniform, rapid germination in the cultivated populations has been noted in other plant species, such as sunflowers (Heiser 1985). Delayed germination in wild plants is an advantage in the natural environment because it protects the population from being destroyed when stochastic environmental conditions are not favorable. However, delayed germination is undesirable in cultivated plants because it results in uneven stands, greater weed competition, and requires more seed for sowing (Evans 1993). The delayed-germination characteristic was probably removed by selection in the domesticated papaya, i.e., late-emerging

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seedlings may have been weeded out to reduce competition with the early-germinating individuals already established in the garden. Ladizinsky (1987) indicated that this scenario happened in the domestication of lentils.

The most striking feature distinguishing domesticated papaya from the wild papaya is fruit size. The domesticated papaya fruits can be 100 to 450 times larger than those of the wild type. Gigantism in morphological structures, especially the organs harvested by humans, is common in many cultivated plants including tomatoes, celery, squash, and chili pepper (Schwanitz 1967). How is it possible to get the large-fruited, domesticated papayas from the small-fruited, wild papayas? What is the significance, if any, of the presence of the hermaphroditic type in the domesticated papaya?

Storey (1967) theorized that the ancestral species of *C. papaya* was a bisexual prototype that is now extinct. Humans probably played a role in the increase and perpetuation of the various hermaphroditic types in the domesticated *C. papaya* by crossing and selection. Without human intervention, *C. papaya* would probably be known strictly as a dioecious species today. In the genus *Carica*, dioecism is the rule rather than the exception. The other two species that deviate from dioecy, *C. pubescens* (which has a hermaphroditic sex type) and *C. monoica* (which is monoecious), have also been domesticated. The question becomes, was the initial

starting material for the domestication of *C. papaya* the hermaphroditic or the small-fruited dioecious type?

The starting material for the domestication of papaya could have been the dioecious, small-fruited wild *C. papaya* such as that found in the Yucatan-Peten-San Ignacio-Rio Motagua area. There is no evidence to prove absolutely that papaya was domesticated from the dioecious type. Although no hermaphrodites were observed in the wild *C. papaya* populations (Chapter 3), some wild papaya male trees that were planted at Poamoho were capable of producing fruits. However, dioecism in nature usually indicates an underlying need to cross-fertilize in order to maintain populations that are highly heterozygous with deleterious alleles at various loci (Crumpacker 1964). The absence of hermaphrodites in the wild might mean that they are not adaptive in the natural environment. Perhaps the self-fertility of hermaphrodites may be a disadvantage in locations where papaya population is high because inbreeding depression would produce less competitve progenies than cross-fertilization. On the other hand, dioecious individuals are at a disadvantage at the outer boundaries of the natural range of the species because of the lower probabilities of encountering potential mates. Hermaphroditic papayas could have arisen in the periphery of the species range. However, the lack of hermaphrodites in the wild, and thus the ability to self-fertilize, did not mean domestication was not possible. *Carica goudotiana* is a domesticated species that is dieocious.

If hermaphroditism was not available initially, how was isolation achieved? The initial isolating mechanism might be in the form of spatial isolation, where plants are established around human dwellings away from the original wild populations. Isolating mechanisms are important because for the domestication process to be effective, isolation between the newly "selected" population and the wild population is necessary to ensure the divergence of the cultivated population from the wild population (Rindos 1980; Zohary 1969). Otherwise, the continual introgression between the cultivated population and the wild population would undo the domestication process because the more common wild population would swamp the less common, newly "selected" plants (Rindos 1980; Zohary 1969). Effective isolation can be achieved through spatial isolation or isolation by mating system such as self-pollination (Ladizinsky 1985). The initial progress in the domestication of papaya might have been slow in achieving the desirable characteristics such as fruit size until the appearance and selection of hermaphroditism. Hermaphroditism made self-pollination possible that was not available to the dioecious papaya.

Although there are many examples of crops that are still predominantly outbreeding, such as maize, rye, pearl millet, sorghum, amaranths, brassicas, sugar beet, and sweet potato, generally domestication is accompanied by a change from out-breeding to self-fertilization (Evans 1993). Humans exerted such strong selection pressure for selfing in domesticated species that often the domesticated species would be the one with the selfing reproductive mode, while the wild relatives would remain

predominantly outcrossers. An example of this is *Anthirrhinum majus*, the cultivated snapdragon, in which the cultivated form can reproduce by selfing, while its related wild species are self-incompatible (Stebbins 1957). This scenario is the same in *C. papaya* and its related *Carica* species. In wild and cultivated barleys and wheats, self-pollination is the predominant mating system. Because self-pollination allowed these species to be preadapted to domestication in comparison to cross-pollinated plants, it may not be mere chance that the first successful domesticates were selfers (Zohary 1969).

The motivation that led humans to first select for the hermaphroditic type was probably because it was as productive as the female in producing harvestable fruit. In a dioecious line, only the female is dependable for producing harvestable fruits while the male are generally non-productive. It seems likely that this is the reason for selecting the hermaphroditic type in the domesticated papaya. This was also evident in tomato. Prior to its introduction to Europe, the floral morphology of the tomato was such that it required insect pollinators because the stigma was exserted well above the stamen. The lack of appropriate insect pollinators in foreign locations as well as the practice of greenhouse culture caused an intense selection for tomatoes with the ability to self-pollinate, i.e., for types whose stigmas are close to the anther because these are the ones that are fruitful (Rick 1976; Rick and Dempsey 1969).

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Alternatively, if the initial starting material in the domestication of *C. papaya* was the hermaphroditic types, then the issue of isolating mechanism is solved. The ability to self-pollinate in the hermaphroditic plants would have greatly expedited the process of domestication. The increase in the fruit size would have been easily attained, especially since fruit size is generally a highly heritable character (Owens et al. 1985). This is because the hermaphroditism provides the ability to self-fertilize and desirable characters can be selected and easily fixed in the domesticated papaya. The high propensity of the hermaphrodite papaya population to self-pollinate is supported by its high inbreeding coefficient compared to the female domesticated type (Table 4.8). In addition, the female, wild population exhibited the lowest inbreeding coefficient compared to both the hermaphrodite and the female domesticates. This indicates that the dioecious, wild female outcrossed more than either of the domesticates. Like other plants such as cowpea (Lush 1979), tomato (Rick and Dempsey 1969; Rick 1983), and chili pepper (Pickersgill 1968), an increase in inbreeding has accompanied domestication in papaya.

As mentioned earlier, the hermaphrodite's ability to self-fertilize provides an effective isolating mechanism allowing the domesticated population to diverge from its wild counterpart. This isolating mechanism is not by any means complete, as shown in several crops with the capacity for some outbreeding following domestication, such as sunflower, sorghum, pearl millet, maize, tomatoes, potatoes, and rice (Evans 1993). In papaya, this point is apparent, since there is an indication that alleles such as *Skd-A,*

and *Tpi-1A* from the wild may have influenced the domesticated populations, while others such as *Aco-2A, Aco-2B, Pgi-2C, Pgm-2A,* and *Tpi-2C* indicate that they might have transferred from the crop to the wild.

At the time of the discovery of the New World, papaya was already a domesticated species. Oviedo (1959b) described first seeing papaya fruits on the west shore of Nicaragua near Leon in 1526 that were "as large as the big watermelons of Spain." Oviedo not only recognized the great variability in fruit sizes but also in fruit shapes that existed at that time. This record indicated that some of the papaya fruits were long while others were rounded. Because hermaphroditic papaya trees tend to produce elongated fruits compared to the rounded fruits of female trees, the "long" fruits could have come from hermaphroditic papaya trees while the "rounded" fruits could have come from female papaya trees. The elongated papaya fruit shapes could mean that gynodioecious domesticated papayas were in existence at the time of Oviedo's observation. Although Oviedo made no mention of the presence of the small-fruited, wild papayas in Central America, this did not mean it was absent in the area at the time. The Mayans used the word "chichput" (meaning bird papaya) for the small-fruited, wild papaya (Roys 1931), and "chichioalxochitl" (meaning flower of the breast) for the domesticated papaya (Hernandez 1943), which indicates that they were aware of different types. It could be interpreted that the wild *C. papaya* was in existence throughout the Mayan history and were not of recent introduction. Roys

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(1972) reported that the Mayans of the Yucatan cultivated many domesticated fruits including papaya at the time of the Spanish discovery of the Yucatan.

In summary, domestication has influenced the genetic variability in *C. papaya* as a species by increased inbreeding. The domestication process is facilitated by the exclusive presence of the hermaphrodites in the domesticated papaya. Humans probably played a large role in the perpetuation of the hermaphroditic type. This study supports Central America as the center of diversity for *C. papaya* rather than South America. The Peten region in Guatemala is the area with greatest diversity, with the next highest diversity found collectively in Belize, Yucatan peninsula of Mexico, Honduras, and Costa Rica. The variability decreases the farther away the papaya population is from the Yucatan-Peten-San Ignacio-Rio Motagua center, with the least variability evident in South American papaya populations. Furthermore, this center of diversity coincides roughly with the ancient Mayan homeland. It seems likely that *C. papaya* was domesticated somewhere within this area of greatest diversity and that the ancient Mayans or their predecessors might have been responsible for the domestication of papaya.

Recommendations for future collections

Based on the results of this study, the following recommendations on future collecting expeditions and conservation of *C. papaya* genetic resources are suggested.

The material collected during the course of this study and in the NCGR collection in Hilo perhaps represents the largest repository of *C. papaya* germplasm in the world at this time. There are areas in the Central and South American region that were not covered by this study and warrant future collecting trips. The west coast of Central America— Guatemala, Honduras, El Salvador, Nicaragua, and particularly in the states of Guerrero, Oaxaca, and Chiapas, Mexico, should be explored for the small-fruited, wild *C. papaya* and its genetic variability investigated. Wild *C. papaya* is known to occur in Chiapas, Mexico (Richard Hamilton, personal communication) and the Pacific coast of Guatemala (Juan Jose, personal communication). El Salvador and Nicaragua merit priority in any future collecting expedition because they represent a knowledge gap in the pattern of the genetic variability in *C. papaya*. Because Oviedo (1952) mentioned Nicaragua to be the first place where he saw *C. papaya*, it might be worthwhile to search the province of Olocoton in Nicaragua, which was supposedly by the old city of Leon (Chapter 2). Wild *C. papaya* exists in Honduras, although none of the seeds collected during the expedition in 1992 would germinate, and thus were not available for genetic analysis (Chapter 3). It is possible that wild *C. papaya* also exists in Nicaragua. A genetic analysis of the Nicaraguan material would strengthen the current delineation of the center of diversity as being in the Yucatan-Peten-San Ignacio-Rio Motagua area if the genetic variability of the Nicaraguan material is lower than that found in the center of diversity. If the Nicaraguan material has genetic variability as high as that of the Yucatan-Peten-San Ignacio-Rio Motagua area, the center of diversity would need to be expanded to include Nicaragua.

Conservation of species and populations in their natural habitats, *in situ* conservation, would be the most ideal method for conserving genetic resources of crop species (Williams 1993). Priority should be given to the crop's center of diversity when designating areas for *in situ* conservation. In the case of *C. papaya*, this would include the area extending from the Yucatan peninsula, Mexico to Belize, Guatemala, and Honduras. However, depending on political, social, and biogeographic factors *in situ* conservation may not always be feasible. *Ex situ* conservation has been used as a major strategy to conserve the genetic resources of plant species with known economic value (Heywood 1993). In crop production areas outside the native range of the species (as in the case of papaya production in Hawaii), there is no alternative but to adopt the *ex situ* conservation in order to ensure continual access of the germplasm that is needed for the improvement of the crop. A combination of *in situ* conservation strategy in the area of origin of the crop and *ex situ* conservation in the form of seeds and living collections in areas outside the native range of the species is ideal.

CHAPTER 5

GENETIC RELATIONSHIP BETWEEN *CARICA PAPAYA* AND ITS RELATED

TAXA

Most of the members of the *Carica* genus occur in South America, especially

along the eastern flanks of the Andes from Ecuador to Venezuela (Badillo 1971).

Several authors have suggested that *Carica papaya* originated on the eastern slope of

the Andes, where numerous endemic *Carica* species exist (Brucher 1989; Prance

1984). Of the 23 species in the genus *Carica*, the only species found in Central

America thus far are *C. papaya*, *C. cauliflora*, *C. microcarpa*, *C. pubescens*, and the

recently discovered *C. cnidoscoloides* Lorence & Torres (Lorence and Torres 1988).

However, papaya does not hybridize easily with any other *Carica* species through

conventional breeding methods (Litz 1986). Papaya's reproductive isolation from other

Carica species has been demonstrated through interspecific hybridization attempts

(Sawant 1958; Horovitz and Jimenez 1967; Mekako and Nakasone 1975; Manshardt

and Wenslaff 1989a and b).

Isozymes have been successfully used to ascertain relationships among plant

species (Crawford 1990; Gottlieb 1977). An objective of the present study is to

compare the interspecific relationships within the genus *Carica* using isozyme

techniques. By examining the genetic similarity between *C. papaya* and the other

Carica species, it is possible to determine whether *C. papaya* is distantly related to

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other members of the genus as previous studies indicated, and whether or not any of the other present-day *Carica* species is a wild progenitor of *C. papaya*.

MATERIALS AND METHODS

Of the 23 *Carica* species, 13 species including three subspecies and two natural hybrids were investigated using isozyme analysis. Details regarding the germplasm investigated are given in Chapter 3 of this dissertation (Table 3.2). The species accessions were analyzed for variation in nine enzyme systems, including aconitase (ACO: EC 4.2.1.3), isocitrate dehydrogenase (IDH: EC 1.1.1.42), malate dehydrogenase (MDH: EC 1.1.1.37), glucosephosphate isomerase (PGI: EC 5.3.1.9), phosphoglucomutaase (PGM: EC 2.7.5.1.), shikimate dehydrogenase (SKD: EC 1.1.1.25), triosephosphate isomerase (TPI: EC 5.3.1.1), uridine diphosphoglucose pyrophosphorylase (UGP: EC 2.7.7.9), and 6-phosphogluconate dehydrogenase (6-PGD: EC 1.1.1.44), as described in Chapter 4 of this dissertation. Among the nine enzymes assayed, ACO, IDH, 6-PGD, and SKD were poorly resolved and inconsistent. Triosephosphate isomerase and PGI exhibited complex banding patterns. Hence, these six enzymes were excluded from the analyses. Bands at five loci, *Pgm-1*, *Pgm-2*, *Mdh-1*, *Mdh-2*, and *Ugp*, were scored as described in Chapter 4.

Not all of the populations of *C. papaya* from Chapter 4 were used in the analyses in this chapter. The allelic data for 464 out of 871 individuals of *C. papaya*

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featured in Chapter 4, were included in the analysis of genetic identity in this chapter. The allelic data for *Pgm-1*, *Pgm-2*, *Mdh-1*, *Mdh-2*, and *Ugp* for *C. papaya* was from all the wild and hybrid populations and from a selected group of domesticated populations (DVER, DSAN, DRIO, DPAC, and DHON) in Central America (Table 3.1). The basis for choosing all of the wild, the hybrid, and the above mentioned domesticated populations was their high intrapopulational variability measures (A and PLP) as indicated in Table 4.6 (Chapter 4). Although DVER and DYUC have similar values for A and PLP, DVER was chosen over DYUC because DVER consisted of four accessions while DYUC had only two (Appendix A and Table 3.1). *Carica papaya* was used as a marker while scoring the bands of the other *Carica* species. Because bands with slower mobilities than those observed in *C. papaya* were encountered in the other *Carica* species, the alleles in *C. papaya* were renamed. For example, *Pgm-1A* and *Pgm-1B* in Chapter 4 were redesignated as *Pgm-1E* and *Pgm-1F*, respectively (Appendix E).

Cluster analysis based on allelic frequencies

In order to examine relationships between species in a concise way, population allele frequencies at five genetically interpretable, polymorphic loci (*Pgm-1*, *Pgm-2*, *Mdh-1*, *Mdh-2*, and *Ugp*) were computed from genotypes of all individuals comprising each species sample. The genetic interpretations of banding patterns were putative in all the *Carica* species included in this study except for papaya. Based on the allele

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frequencies, Nei's unbiased genetic identity (Nei 1978) and Rogers' distance coefficients were computed using the software BIOSYS-1 (Swofford and Selander 1981). To portray the species relationships in a dendrogram, cluster analysis was performed on the identity matrix with the UPGMA algorithm included in BIOSYS-1. The cophenetic correlation coefficient (Rolf and Sokal 1981) between cophenetic matrix and Nei's genetic identity matrix was also computed using BIOSYS-1 to test the congruity of the genetic identity matrix and the dendrogram. The banding pattern of *C. pulchra* was not genetically interpretable in MDH and was not included in the genetic identity computations or the cluster analysis based on the genetic identity values.

Principal component and cluster analysis based on binary data

The allelic data for each individual plant of each species were converted into binary data by indicating the presence of an allele as (1) or absence of an allele as (0). Using this binary description of isozyme banding patterns, Jaccard's coefficient of similarity (Jaccard 1908) was computed for all possible pair-wise comparisons of individuals. Also by using the binary description of the isozyme bands, it was possible to include *C. pulchra* in the species relationship assessment. Only unique zymotypes were used in the computation of Jaccard's similarity coefficients. In *C. papaya*, the 464 individuals studied were made up of 13 unique zymotypes.

The resultant Jaccard's similarity matrix was subjected to a UPGMA cluster analysis (CA) (Sneath and Sokal 1973) and the results were illustrated in a dendrogram. To test the goodness of fit of the CA with the original Jaccard's similarity matrix, the cophenetic correlation coefficient (Rolf and Sokal 1981) between the cophenetic matrix and the Jaccard similarity matrix was computed. Principal components analysis (PCA) was used to examine the multivariate relationships among zymotypes. The numerical taxonomy and multivariate analyses program, NTSYS (version 1.6) (Exeter Publishing Ltd., Setauket, N.Y. 1987) was employed for all computations.

RESULTS

Genetic relationships among *Carica* species based on genetic identities

The schematic representation of banding patterns observed at five loci for three enzyme systems is presented in Fig. 5.1. Six different alleles were observed for *Pgm-1*, seven in *Pgm-2*, two for *Mdh-1*, three for *Mdh-2*, and five for *Ugp*.

Species-wise allele frequencies for the five putative loci indicated some species-specific alleles (Table 5.1). In *Pgm-1*, allele D is unique to *C. parviflora*, whereas allele F is unique to *C. papaya*. In *Pgm-2*, allele G is unique to *C. papaya*. Allele B in *Mdh-1* occurs only in *C. papaya*. While allele A in *Mdh-2* is found only in *C. crassipetala*, and allele B is unique to *C. quercifolia*.

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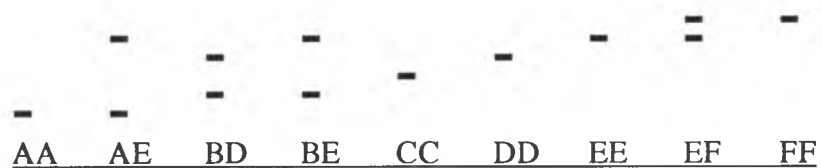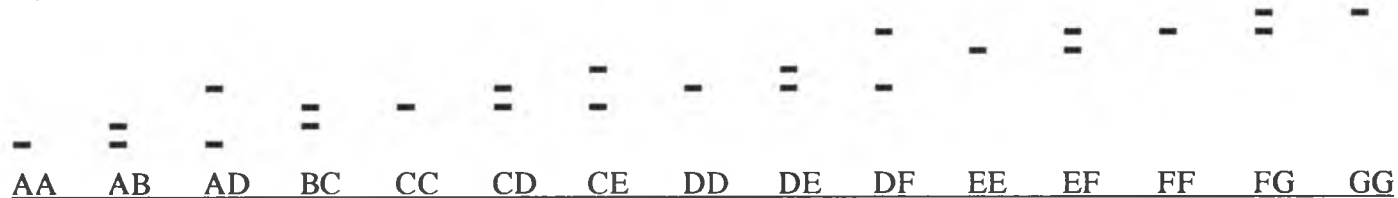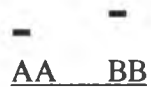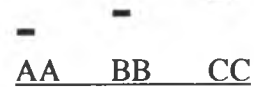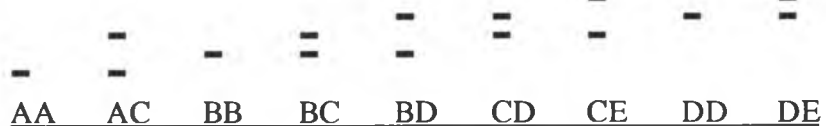
Fig. 5.1. Electrophoretic phenotypes observed in *Carica* species.

Table 5.1. Allele frequencies in *Carica* species.

		Species							
Locus	Allele	1	2	3	4	5	6	7	8
	(N)	464	297	13	44	51	30	22	30
Pgm-1	A		0.929	1.000				1.000	
	B								
	C						1.000		
	D								
	E	0.256	0.071		1.000	1.000			1.000
	F	0.744							
Pgm-2	A					0.902			
	B					0.098	0.100		
	C						0.900	0.955	
	D							0.045	0.617
	E		1.000	0.846	1.000				0.283
	F	0.031		0.154					0.100
	G	0.969							
Mdh-1	A		1.000	1.000	1.000	1.000	1.000	1.000	1.000
	B	1.000							
Mdh-2	A						1.000		
	B			1.000					
	C	1.000	1.000		1.000	1.000		1.000	1.000
Ugp	A						0.583		
	B	0.045				0.010			0.117
	C		1.000	1.000	0.534	0.765	0.417	1.000	0.850
	D	0.948			0.466				0.033
	E	0.006				0.225			

Note: Blanks indicate zero values.
1– *C. papaya*; 2– *C. goudotiana*; 3– *C. quercifolia*; 4– *C. pubescens*;
5– *C. sphaerocarpa*; 6– *C. crassipetala*; 7– *C. cauliflora*;
8– *C. microcarpa* ssp *microcarpa*; 9– *C. microcarpa* ssp *microcarpa*;
10– *C. microcarpa* ssp *baccata*; 11– *C. microcarpa* ssp *heterophylla*;
12– *C. microcarpa* ssp (?); 13– *C. glandulosa*; 14– *C. parviflora*;
15– *C. monoica*; 16– *C. stipulata*; 17– *C.* x *heilbornii* nm *pentagona*

Table 5.1. (Continued) Allele frequencies in *Carica* species.

Locus	Allele	Species 9	10	11	12	13	14	15	16	17
	(N)	19	8	1	1	4	2	5	1	2
Pgm-1	A									
	B						0.250			0.250
	C					1.000				
	D						0.750			
	E	1.000	1.000	1.000	1.000			1.000	1.000	0.750
	F									
Pgm-2	A									0.250
	B									
	C	1.000	0.563	0.500	1.000	1.000				
	D			0.500					1.000	0.750
	E		0.438				1.000			
	F							1.000		
	G									
Mdh-1	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	B									
Mdh-2	A									
	B									
	C	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Ugp	A		0.125							
	B									
	C	1.000	0.750	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	D		0.125							
	E									

Note: Blanks indicate zero values.
1- *C. papaya*; 2- *C. goudotiana*; 3- *C. quercifolia*; 4- *C. pubescens*;
5- *C. sphaerocarpa*; 6- *C. crassipetala*; 7- *C. cauliflora*;
8- *C. microcarpa* ssp *microcarpa*; 9- *C. microcarpa* ssp *microcarpa*;
10- *C. microcarpa* ssp *baccata*; 11- *C. microcarpa* ssp *heterophylla*;
12- *C. microcarpa* ssp (?); 13- *C. glandulosa*; 14- *C. parviflora*;
15- *C. monoica*; 16- *C. stipulata*; 17- *C.* x *heilbornii* nm *pentagona*

The species *C. pulchra* was excluded from the analysis due to genetically uninterpretable banding pattern in MDH.

Species pair-wise unbiased genetic identity (Nei 1978) values are presented in Table 5.2. The result of the cluster analysis based on the genetic identity data is depicted in a dendrogram (Fig. 5.2). The cophenetic correlation coefficient for the cluster analysis based on genetic identities was 0.919. Two major groups are revealed: Group A— *Carica papaya*; Group B— other *Carica* species. Group B is further subdivided into two clusters: Cluster (1) containing all remaining *Carica* species except *C. crassipetala*, and Cluster (2) consisting of *C. crassipetala* alone. *Carica papaya* has an average genetic identity of less than 0.30 with the other *Carica* species. *Carica crassipetala* has an average genetic identity of less than 0.40 with the other *Carica* species. Cluster (1) has an average genetic identity of greater than 0.60. *Carica goudotiana* and *C. parviflora* shared a genetic identity of 0.86 (Table 5.2 and Fig. 5.2), and were related to *C. quercifolia* in the Subcluster (a). In Subcluster (b), the natural hybrids were identical to *C. stipulata* with the genetic identity of 1. *Carica microcarpa* subspecies *microcarpa* (UH Accession no. 1009) shared a genetic identity of 1 with *C. microcarpa* subspecies (unknown—UH Accession no. 1118). In addition, *C. microcarpa* (all three subspecies) was next most closely related to *C. stipulata* and the natural hybrids at a genetic identity of greater than 0.87. As a group, these members of Subgroup (b) were equally related to *C. sphaerocarpa* and *C. monoica*. *Carica pubescens* joined the rest of Subcluster (b) at a genetic identity of greater than

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Table 5.2. Genetic identity and distance estimates for *Carica* spp.
from different geographical areas.

Species	1	2	3	4	5	6	7	8	9
1 PAPA	*****	.219	.001	.379	.282	.000	.214	.300	.266
2 GOUD	.854	*****	.787	.770	.609	.309	.804	.709	.622
3 QUER	.959	.454	*****	.516	.385	.313	.622	.473	.411
4 PUBS	.746	.465	.669	*****	.762	.277	.539	.864	.745
5 SPHA	.800	.605	.753	.463	*****	.303	.591	.845	.798
6 CRAS	.938	.798	.790	.799	.783	*****	.494	.318	.498
7 CAUL	.859	.439	.604	.659	.620	.685	*****	.634	.798
8 MC1M	.779	.517	.688	.347	.369	.764	.580	*****	.841
9 MC2M	.833	.611	.758	.493	.439	.686	.448	.388	*****
10 MC-B	.762	.495	.678	.285	.376	.682	.494	.279	.218
11 MC-H	.803	.568	.724	.440	.378	.714	.491	.198	.224
12 MIC2	.833	.611	.758	.493	.439	.686	.448	.338	.000
13 GLAN	.864	.622	.758	.666	.627	.520	.448	.592	.447
14 PARV	.842	.386	.606	.454	.596	.783	.595	.507	.602
15 MONO	.830	.611	.737	.493	.439	.806	.626	.362	.447
16 STIP	.833	.611	.758	.493	.439	.806	.618	.166	.447
17 HEI	.795	.549	.706	.467	.350	.758	.556	.182	.418

Notes: Above diagonal-- Nei's (1978) coefficients of unbiased genetic identity;
Below diagonal-- modified Rogers' distances (Wright, 1978).

1- *C. papaya*; 2- *C. goudotiana*; 3- *C. quercifolia*; 4- *C. pubescens*;
5- *C. sphaerocarpa*; 6- *C. crassipetala*; 7- *C. cauliflora*;
8- *C. microcarpa* ssp *microcarpa*; 9- *C. microcarpa* ssp *microcarpa*;
10- *C. microcarpa* ssp *baccata*; 11- *C. microcarpa* ssp *heterophylla*;
12- *C. microcarpa* ssp (?); 13- *C. glandulosa*; 14- *C. parviflora*;
15- *C. monoica*; 16- *C. stipulata*; 17- *C.* x *heilbornii* nm *pentagona*

Table 5.2. (Continued) Genetic identity and distance estimates for
Carica spp. from different geographical areas.

Species	10	11	12	13	14	15	16	17
1 PAPA	.324	.281	.266	.212	.223	.273	.266	.282
2 GOUD	.735	.656	.622	.608	.855	.622	.622	.692
3 QUER	.485	.434	.411	.411	.617	.443	.411	.460
4 PUBS	.914	.786	.745	.534	.786	.745	.745	.774
5 SPHA	.842	.841	.798	.586	.618	.798	.798	.886
6 CRAS	.453	.423	.498	.713	.321	.305	.305	.341
7 CAUL	.738	.745	.798	.798	.638	.605	.615	.685
8 MC1M	.915	.957	.841	.622	.721	.863	.975	.992
9 MC2M	.959	.949	1.00	.800	.632	.800	.800	.839
10 MC-B	*****	.945	.959	.737	.747	.834	.834	.870
11 MC-H	.232	*****	.949	.738	.667	.843	.949	.972
12 MIC2	.218	.224	*****	.800	.632	.800	.800	.839
13 GLAN	.498	.500	.447	*****	.632	.600	.600	.671
14 PARV	.485	.559	.602	.602	*****	.632	.632	.722
15 MONO	.400	.387	.447	.632	.602	*****	.800	.839
16 STIP	.400	.224	.447	.632	.602	.447	*****	1.00
17 HEI	.368	.224	.418	.570	.524	.418	.158	*****

Notes: Above diagonal-- Nei's (1978) coefficients of unbiased genetic identity;
Below diagonal-- modified Rogers' distances (Wright, 1978).

1- *C. papaya*; 2- *C. goudotiana*; 3- *C. quercifolia*; 4- *C. pubescens*;
5- *C. sphaerocarpa*; 6- *C. crassipetala*; 7- *C. cauliflora*;
8- *C. microcarpa* ssp *microcarpa*; 9- *C. microcarpa* ssp *microcarpa*;
10- *C. microcarpa* ssp *baccata*; 11- *C. microcarpa* ssp *heterophylla*;
12- *C. microcarpa* ssp (?); 13- *C. glandulosa*; 14- *C. parviflora*;
15- *C. monoica*; 16- *C. stipulata*; 17- *C. x heilbornii* nm *pentagona*

Genetic Similarity

0.20	0.33	0.47	0.60	0.73	0.87	1.00

(A)   1 papaya

(a)   2 goudotiana
            14 parviflora
            3 quercifolia

            4 pubescens
            5 sphaerocarpa
(1)   8 microcarpa M1
(b)   16 stipulata
            17 heilbornii
            11 microcarpa H
            9 microcarpa M2
            10 microcarpa B
            12 microcarpa (ssp?)
            15 monoica

(B)   7 cauliflora
(c)   13 glandulosa
(2)   6 crassipetala

Cophenetic correlation coefficient = 0.919
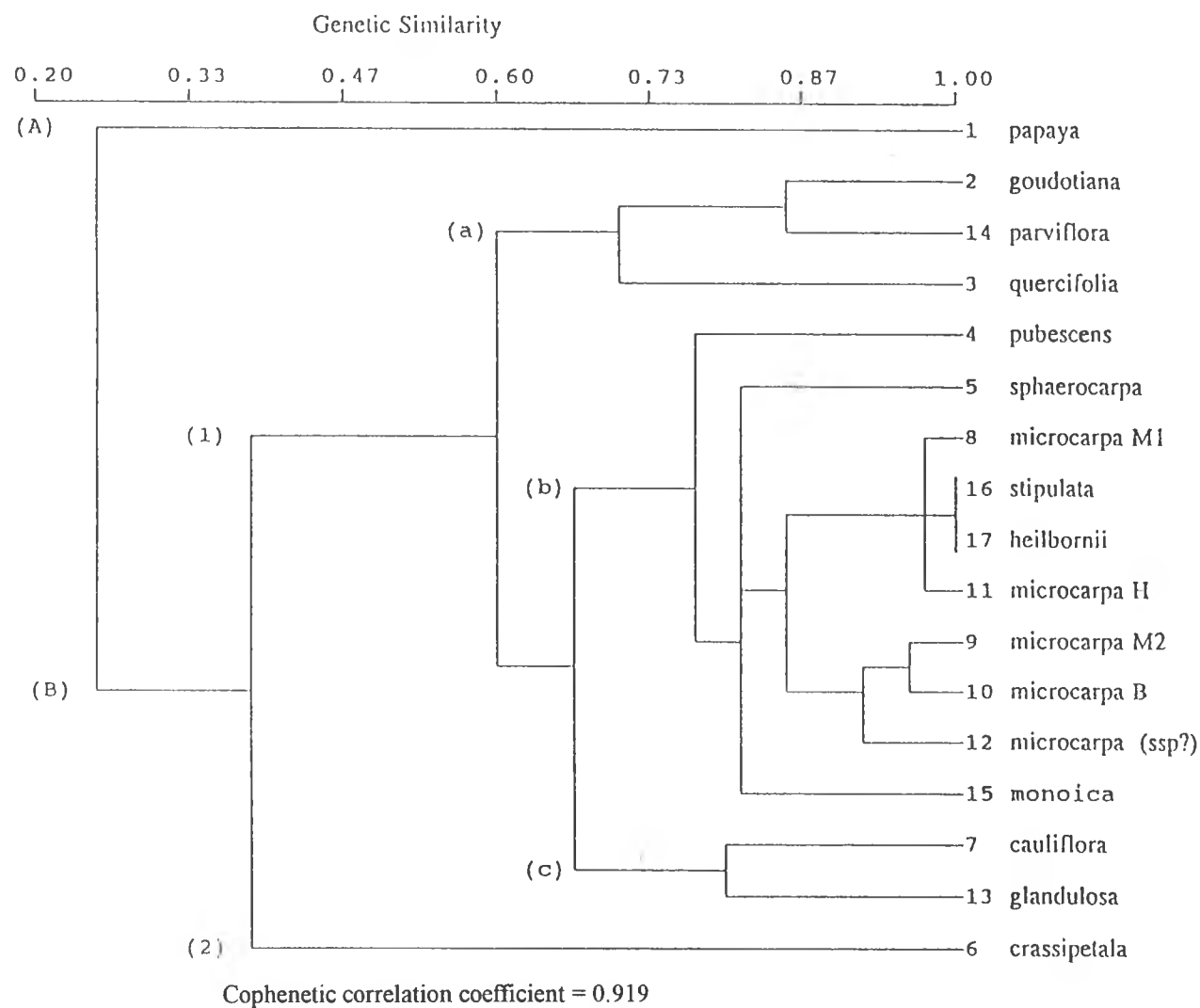
Fig. 5.2. Dendrogram of *Carica* species based on genetic identities.

0.73. Subcluster (c) consisted of *C. cauliflora* and *C. glandulosa*. Subcluster (b) and (c) joined Subcluster (a) at a genetic identity level of 0.6.

Carica species relationships based on binary data

Principal component analysis (PCA) was used to visualize the relationships between species in a 3-dimensional graph. The first three principal components accounted for 17.0 percent, 13.0 percent, and 10.3 percent of the variance, respectively. These three orthogonal vectors for the *Carica* species are plotted in Fig. 5.3. The PCA revealed two major groupings in the *Carica* species investigated: (1) *C. papaya*; and (2) other *Carica* species consisting of *C. cauliflora*, *C. crassipetala, C. goudotiana, C. pubescens, C. stipulata, C. microcarpa, C. quercifolia, C. monoica, C. parviflora, C. pulchra,* and *C. glandulosa*. *Carica crassipetala* can be distinguished from the *Carica* species group by the third principal component.

The UPGMA cluster analysis based on Jaccard's similarity matrix using individuals as taxonomic units, revealed two major clusters joined at less than 25 percent similarity (Fig. 5.4). Zymotypes of *C. papaya* formed one major cluster A, while the rest of the *Carica* species formed the other major cluster B. The cophenetic correlation coefficient of 0.909 indicates that the dendrogram is a good representation

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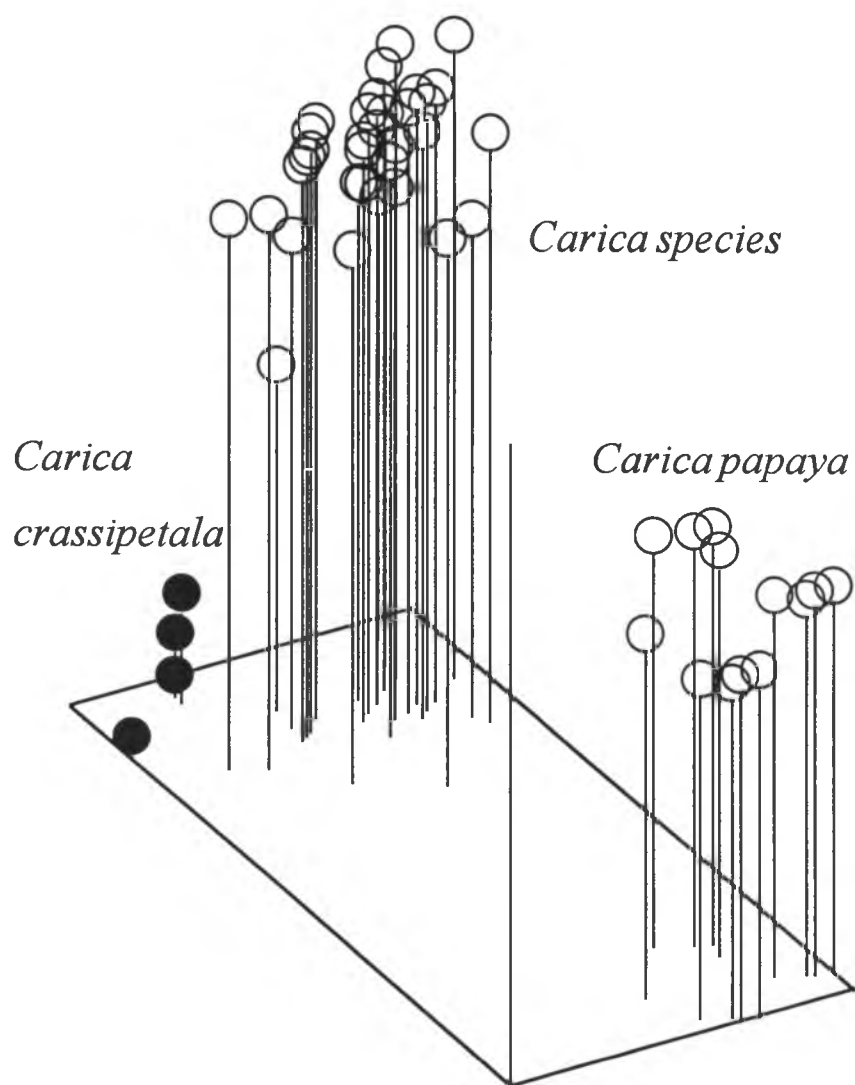
Fig. 5.3. Principal component analysis of *Carica* species.
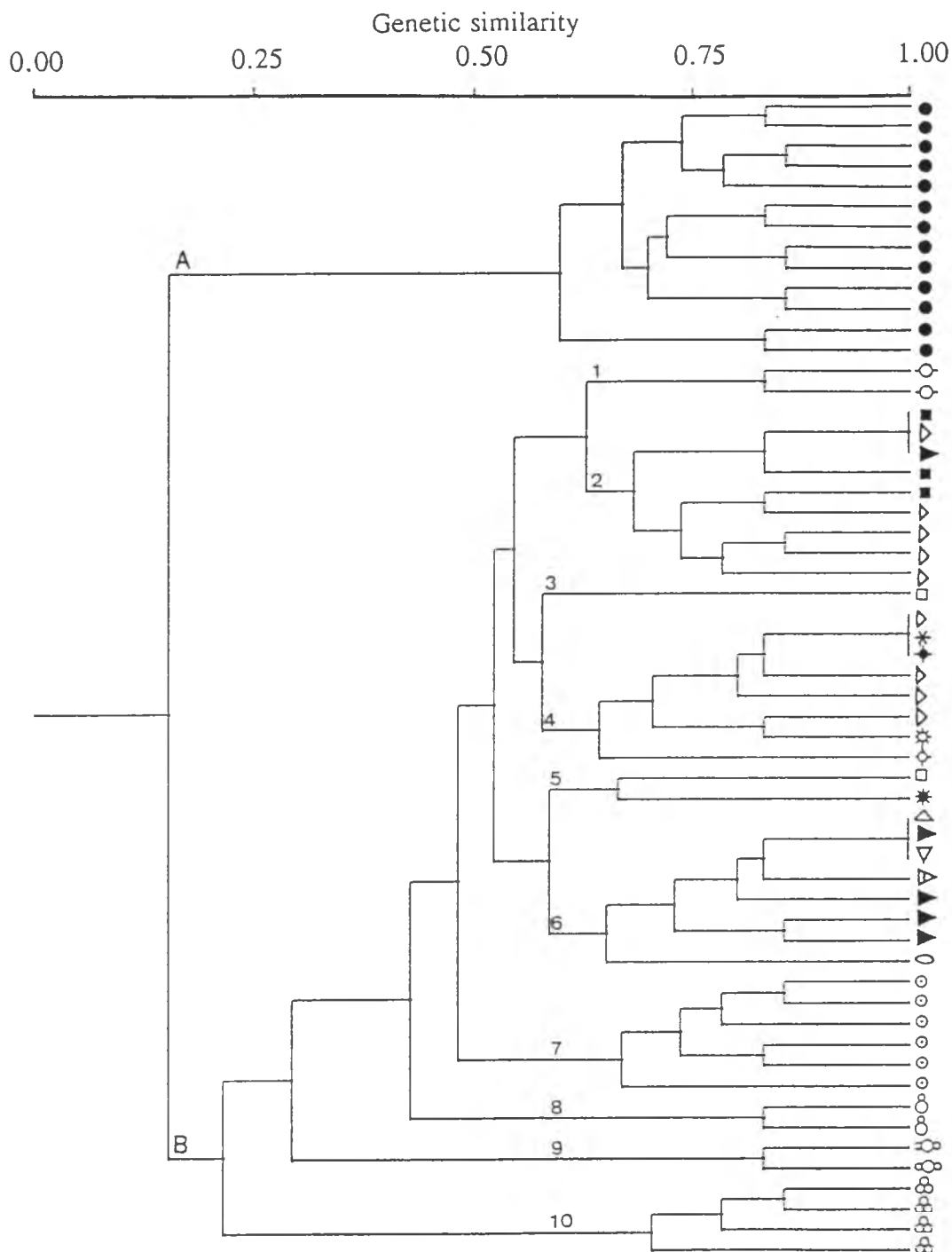
Fig. 5.4. Dendrogram based on Jaccard's coefficients of
similarity among *Carica* species.

Carica species epithet key:

□ *cauliflora*; ⚭ *crassipetala*; ✳ *glandulosa*, ⊙ *goudotiana*; ▷ *microcarpa* ssp *heterophylla*;
▶ *microcarpa* ssp *baccata*; △ *microcarpa* ssp *microcarpa* (UH 1009);
◁ *microcarpa* ssp *microcarpa* (UH 1069); ▽ *microcarpa* ssp (?); ✿ *monoica*; ● *papaya*;
⚇ *parviflora*; ■ *pubescens*; ⬭ *pulchra*; ⬮ *quercifolia*; ⊙ *sphaerocarpa*; ✳ *stipulata*;
◇ *carica* x *heilbornii* (UH 1103); ◆ *carica* x *heilbornii* (UH 1117).

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of the relationships among the different zymotypes as shown in Jaccard's similarity matrix.

In major cluster B, the two zymotypes of *C. goudotiana* formed a distinct cluster 1. Most of the zymotypes of the Colombian *C. microcarpa* ssp. *microcarpa* (UH accession no. 1069), all three zymotypes of *C. pubescens*, and one zymotype of *C. microcarpa* ssp. *baccata* occurred in cluster 2. Also in cluster 2, one *C. pubescens* zymotype was identical to one zymotype observed in each of *C. microcarpa* ssp. *microcarpa* and *C. microcarpa* ssp *baccata*. *Carica cauliflora* occurred in two different clusters (clusters 3 and 5). *Carica cauliflora* shared cluster 5 with *C. glandulosa*. Cluster 4 consisted of *C. monoica*, *C. stipulata*, the natural hybrids (UH accession no. 1117 and 1103), and mostly *C. microcarpa* ssp *microcarpa* (UH accession no. 1069) zymotypes. In cluster 4, one zymotype of *C. microcarpa* ssp. *microcarpa* (UH accession no. 1069) was identical to *C. stipulata* and the natural hybrid (UH accession no. 1117). Cluster 6 was made up of *C. pulchra* and other subspecies of *C. microcarpa*. The Venezuelan *C. microcarpa* ssp *microcarpa* (UH accession no. 1009) had only one zymotype, which was identical to one of the *C. microcarpa* ssp. *baccata* zymotypes in cluster 6 and the *C. microcarpa* with the unknown subspecies (UH accession no. 1118). *Carica sphaerocarpa* had six zymotypes and formed its own cluster 7. *Carica parviflora* and *C. quercifolia* each had its own cluster (clusters 8 and 9, respectively). *Carica crassipetala*, which had four zymotypes, formed its own distinct cluster 10.

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DISCUSSION

Carica papaya's distant relationship with other *Carica* species

All measures of genetic relationship employed in this study indicate the relative

genetic isolation of *C. papaya* from the other members of the genus, including

C. cauliflora, *C. microcarpa*, and *C. pubescens* that also occur in Central America.

The groupings depicted by the PCA, the dendrogram based on the genetic identities,

and the dendrogram based on the binary data all demonstrate this major distinction

between *C. papaya* and the other *Carica* species. In each analysis, *C. papaya* forms

one major group while the other *Carica* species together form the other major group.

Even though *C. cauliflora* and *C. microcarpa* do occur in Central America,

neither occupy the same ecological niche as *C. papaya*. *Carica papaya* prefers open,

disturbed, and lower-elevation habitats, while *C. cauliflora*, and *C. microcarpa* are

found in the shady understory of forest trees and can grow at slightly higher elevations

than papaya. *Carica pubescens* is a cool-climate, higher-elevation (1,500-3,000 m)

species compared to *C. papaya* (0-1,500 m) (Badillo 1971). The results of the isozyme

analysis agree with Badillo's (1971) classification of *C. papaya* as constituting a

separate section (*Carica*) of the genus on the basis of morphology. The remaining

members of the genus *Carica* belong to the section *Vasconcellea*. *Carica papaya* is the

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only species in this study whose fruit cavity consists of a single locule; the other *Carica* species all have five locules (Badillo 1971; Lorence and Torres 1988).

The allozyme evidence suggests that none of the other *Carica* species in this study has sufficiently close genetic affinity to have been a direct ancestor of *C. papaya* in the recent past (the last 10,000 years). Neither wild nor domesticated *Carica papaya* is derived from any of the other *Carica* species. Instead the progenitor of *C. papaya* might have dispersed from South America and evolved to the present-day *C. papaya* in Central America.

Relationships among other *Carica* species

The results suggest that *C. crassipetala* is differentiated from the rest of the *Carica* species included in this study. While no previous study has reported on the genetic compatibility between *C. crassipetala* and the other members of the genus, the genetic identity data indicate that like *C. papaya*, *C. crassipetala* has diverged from the other *Carica* species.

Except for *C. papaya* and *C. crassipetala*, the PCA could not distinguish between the *Carica* species investigated (Fig 5.3). This could be attributed to the limitations of the data, such as low sample sizes in half of the species investigated and few enzyme systems that were resolved across all species studied. However, a more

likely explanation as to why the PCA could not distinguish between members of the *Carica* group B is probably due to their recent evolution as species from a common ancestor during the period of uplift that created the Andes mountains. The members of this group are generally reproductively compatible which is another evidence of their common origin in the recent geological past. In particular, *C. cauliflora, C. goudotiana, C. microcarpa, C. monoica, C. pubescens*, and *C. stipulata* are intercompatible with each other and interspecific hybrids are fertile (Horowitz and Jimenez 1967; Zerpa 1967). Natural interspecific hybrids do occur in nature where these species overlap. Badillo (1971) listed at least four natural hybrids between *C. pubescens* and *C. stipulata*, such as *C.* x *heilbornii* nm. *heilbornii*, *C.* x *heilbornii* nm. *pentagona*, *C.* x *heilbornii* nm. *chrysopetala*, and *C.* x *heilbornii* nm. *fructifragrans*.

The groupings indicated by the dendrogram based on genetic identities are in agreement with those established by the dendrogram based on binary coding of the isozyme phenotypes (Fig. 5.2 and Fig. 5.4). This fact validates the putative genetic interpretation of the allelic variation in these species presented in this study. While no genetic identity value was available for *C. pulchra*, the dendrogram based on the binary coding (Fig. 5.4) indicates that it has the greatest affinity with *C. microcarpa*. Similarly, *C. monoica* is also allied with *C. microcarpa*. Interestingly, these three species are recognized in their native regions with the same vernacular name of "col de monte" (mountain cabbage) because their leaves are utilized as vegetables. Both

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dendrograms also indicate the close alliance of *C. glandulosa* with *C. cauliflora*, which contradicts Badillo (1971) who indicated that *C. glandulosa* is closer to *C. quercifolia* on the basis of morphology. Minor discrepancies exist between the two dendrograms: *C. sphaerocarpa*, *C. parviflora*, and *C. quercifolia* are closely allied to the cluster of *C. crassipetala* in the dendrogram based on the binary data, while in the dendrogram based on the genetic identities, they are closer to *C. goudotiana* than to *C. crassipetala*.

Carica stipulata shares a genetic identity of 1 with the natural hybrids of *Carica* x *heilbornii*. Both dendrograms based on the genetic identities and the binary data also indicate the close identity of *C. stipulata* with the hybrids. These results support *C. stipulata* as one of the presumed parents of the natural hybrid *C.* x *heilbornii* (Badillo 1971). The other presumed parent of the natural hybrids is *C. pubescens*. *Carica pubescens* does not share as high a genetic identity with the natural hybrids as *C. stipulata* or even *C. microcarpa*. Doebley et al. (1984) found that the genetic identities of the domesticate and wild progenitor of *Zea mays* to range from 0.755 to 0.975. The genetic identity of 0.77 between *C. pubescens* and *C.* x *heilbornii* is still within the range for it to have been a potential parent.

Those observations suggest that specific adaptations as a result of ecological isolation might have played a major role in the evolution of the members of this group as compared to reproductive barriers. This is consistent with the rapid geological

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change in the Andes. With its deeply-cut valleys and steep slopes, the Andean mountain chain provides numerous unique microhabitats for the various species.

Biogeography of *Carica papaya*

Caricaceae has a Central American-South American-African distribution (Badillo 1971). The most primitive genus in Caricaceae is *Cylicomorpha,* which is found exclusively in equatorial Africa (Badillo 1971). The genera *Jacaratia* and *Carica* have differentiated and dispersed in Central and South America (Badillo 1971). The distribution of Caricaceae over both the continents of Africa and South America, which are now distantly separated by the Atlantic Ocean, could be explained by plate tectonic events. South America and Africa formed West Gondwana after the separation of India, Australia, and Antarctica from Gondwanaland during the Jurassic (more than 145 million years ago) (Goldblatt 1993). About 135 million years ago (Ma), South America and Africa began to fragment and complete separation was achieved between 106 and 84 Ma (Pitman et al. 1993; Rabinowitz and LaBrecque 1979). The first fossils of angiosperms appeared at about this time and probably had their origins in West Gondwanaland (Raven and Axelrod 1974). By the beginning of the fragmentation of West Gondwana, the angiosperms were thought to have differentiated (Crane 1987). Also at the time that angiosperms first appeared (at 138 Ma), the North American continent was not connected to South America (Pitman et al. 1993). About 84 Ma, the Maya Mountains of Belize and the Cordillera Central of Colombia were "connected"

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by scattered volcanic islands. There might also have been chains of volcanic islands along the Greater Antilles and Lesser Antilles that "connected" North and South America at this time (Pindell and Dewey 1982). These scattered islands enabled long-distance dispersal via island hopping (Raven and Axelrod 1974). Later direct connection through the present isthmus of Panama at about 3-5.7 Ma (Kaneps 1970; Haffer 1970; Emiliani et al. 1972; Simpson 1980; Marshall et al. 1982) further facilitated migrations between the two continents.

Caricaceae is closely related to Passifloraceae and Cucurbitaceae (Badillo 1971), which belong to the same order, Cistales, that appeared to have differentiated in West Gondwanaland in the Upper Cretaceous (110 Ma) (Raven and Axelrod 1974). Passifloraceae is mainly African with some genera in tropical Asia and America, while Cucurbitaceae is found mainly in South America, Africa, and tropical Asia. The ancestral Caricaceae probably arose in western Gondwanaland during the Upper Cretaceous. When the African and South American continents finally separated at about 100 Ma, one genus that gave rise to *Cylicomorpha* remained as the only representative in Africa. Speciation in the genus *Carica* was more prolific in South America, particularly as the Andean uplift occurred during the close of the Cretaceous (about 65 Ma). This geological event created diverse environments in which adaptive radiation of *Carica* occurred. The prototype species that gave rise to *C. papaya* probably originated in South America and dispersed northward to the Yucatan-Peten-Belize region where it evolved to its present form.

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In angiosperm evolution, the earliest reproductive organs known had free carpels. Fused carpels with ovaries divided into a number of locules appeared later and ovaries with one locule represent yet more advanced taxa (Friis and Crepet 1987). Morphologically, *C. papaya* has one locule, which is considered more advanced phylogenetically than the other members of the *Carica* genus (all of which have five locules). This distinction is supported by the allozyme evidence reported here, where *C. papaya* is more distantly related to the other members of the genus. One plausible hypothesis is that the prototype species (having five locules) dispersed from northwestern South America northward into the Yucatan and evolved one locule to give rise to the present-day *C. papaya*. What remains of the prototype species in northwestern South America gave rise to the numerous *Carica* species during the Andean uplift. An alternative hypothesis is that the prototype species evolved from having five locules to one locule in South America, then spread to Central America and gave rise to *C. papaya*, then disappearing into extinction in South America.

A more remote possibility is *C. cnidoscoloides* as a potential progenitor of *C. papaya*. *Carica cnidoscoloides* was not included in the study because no specimen was encountered during the collecting expeditions (Chapter 3). Besides *C. papaya*, *C. cnidoscoloides* is the other *Carica* species with one locule and is a Central American species exclusively (Lorrence and Torres 1988). *Carica cnidoscoloides* does not, however, resemble *C. papaya* morphologically and the urticating trichomes in

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C. cnidoscoloides are unique in Caricaceae, which may warrant the classification of this species as a separate genus (Victor M. Badillo, personal communication). This possibility cannot be ruled out based on morphology alone because as shown in maize, the wild progenitor teosinte does not resemble maize morphologically. Similarly, the genus *Jarilla* is different from *C. papaya* morphologically, except for the unilocular ovary and being exclusively Central American. The genus *Jarilla* is endemic to Mexico, but its ancestor must have arrived from South America (Raven and Axelrod 1974). Isozyme analysis of *C. cnidoscoloides* and *Jarilla* in the future would determine with certainty their genetic relationships with *C. papaya*.

Although the domesticated *C. papaya* is now presently found in both tropical regions of Central and South America due to human dissemination, the small-fruited, wild *C. papaya* ("chichput") is found on the Caribbean shores of Central America (Chapter 3). The issue of domestication of *C. papaya* is a much more recent story than speciation, and centered around the Mayan culture from 20,000 to 5,000 years BP. In Chapter 4, the center of domestication of *C. papaya* was determined to be in the Yucatan-Peten-San Ignacio-Rio Motagua area, where the Mayans probably practiced breeding improvement to produce the large-fruited domesticates that were distributed by traders to other parts of Central America and to South America.

Recommendations for future collection of *Carica* species other than *Carica papaya*.

Because the recommendations for future collection and conservation of *Carica papaya* have already been discussed in Chapter 4, this section will focus on the future collection and conservation of other *Carica* species included in this study. Smith et al. (1992) believed that genetic erosion of *Carica* species is not a significant issue because members of this taxon exploit disturbed sites. Even if urgent "rescue" missions are not needed to safeguard *Carica* germplasm in the wild at the moment, it would be prudent to monitor the status of the species existing in their native regions. In fact, several of the domesticated species may be dependent primarily on human propagation and protection. For example, *Carica pubescens* and *C. goudotiana*, both of which had been domesticated, exist mostly in backyard gardens (Chapter 3). Another domesticated species, *Carica monoica*, which supposedly occurs in Ecuador but was not encountered during the collecting expedition in 1993 (Chapter 3), should be investigated further. The indigenous knowledge of these *Carica* species tends to be among older folks. Because the younger generations are either unaware or uninterested in acquiring this knowledge, it may be lost.

One of the limitations of this study is that for approximately half of the *Carica* species investigated only a few individuals of each species were found and collected. This is a function of limited time and financial resources. In the future, ideally each species should be studied with a population genetic approach as was accomplished for

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C. papaya (Chapter 4). *Carica* species such as *C. microcarpa* present such a great variability in morphology that perhaps a population genetic approach might resolve various subspecies relationships.

According to Badillo (1971), Colombia and Ecuador have the greatest diversity of *Carica* species. Similarly, of the countries visited during the collecting expeditions in 1992 and 1993, the largest number of *Carica* species encountered were in these same two countries (Appendix B). Based on the results of this study, Colombia and Ecuador deserve the highest priority in terms of *in situ* conservation of *Carica* species; followed closely by Venezuela. Throughout South America, especially in countries such as Argentina, Bolivia, Chile, and Peru where *Carica* species exist, *in situ* conservation and future collecting expeditions should occur. Although these countries may not have as large a number of different *Carica* species as do Colombia and Ecuador, each may have its own endemic species that merit attention. For example, *C. candicans* is known to occur only in Peru and the endangered *C. chilensis* occurs only in Chile (Badillo 1971). Furthermore, the Andean region deserves further exploration because of the striking geographic contrasts that provide diverse microhabitats conducive to species differentiation. There might be new *Carica* species yet to be discovered in some of the Andean valleys (Victor Manuel Patiño, personal communication).

Like *C. papaya*, *ex situ* conservation in the form of seed and living collections would be recommended in areas outside the native range of the *Carica* species. The

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USDA National Clonal Germplasm Repository in Hilo and the Department of Horticulture at the University of Hawaii have accomplished major efforts in this context. Working relationships with other institutions in Latin America must continue to be nurtured so that the *Carica* germplasm can be protected and exchanged readily between the different institutions. This will help ensure the perpetuation of the *Carica* species for the benefit of humans.

APPENDIX A
CENTRAL AND SOUTH AMERICAN *CARICA PAPAYA* ACCESSIONS

Acc.# (UH)	Country	Province	Locality	Type*	Weight (g)	Sex**	TSS (%)	Flesh***
800	Mexico	Mexico	Texcoco	d	2300	h	8.0	y
801	Mexico	Mexico	Texcoco	d	2250	h	8.4	r
802	Mexico	Veracruz	Veracruz	d	1800	h	14.2	r
803	Mexico	Veracruz	Veracruz	d	-	-	-	-
804	Mexico	Veracruz	Veracruz	d	3400	h	9.2	r
805	Mexico	Veracruz	Veracruz	d	3900	f	9.4	y
806	Mexico	Veracruz	Veracruz	h	150	f	-	-
807	Mexico	Veracruz	Veracruz	d	-	f	-	-
808	Mexico	Yucatan	Merida	w	35	f	-	y
809	Mexico	Yucatan	Merida	w	-	f	-	-
810	Mexico	Yucatan	Muna	h	115	f	-	-
811	Mexico	Yucatan	Uxmal	w	40	f	-	-
812	Mexico	Yucatan	Uxmal	w	25	f	-	y
813	Mexico	Yucatan	Uxmal	w	40	f	-	y
814	Mexico	Yucatan	Oxkutzcab	d	2550	h	-	r
815	Mexico	Yucatan	Oxkutzcab	h	125	f	6.7	y
816	Mexico	Yucatan	Loltun	w	55	f	-	-
817	Mexico	Yucatan	Loltun	w	-	f	-	-
818	Mexico	Yucatan	Cooperativa	w	-	f	-	-
819	Mexico	Yucatan	Cooperativa	w	-	f	-	y
820	Mexico	Yucatan	Cooperativa	d	625	f	-	y
821	Mexico	Yucatan	Oxkutzcab	d	2750	f	6.3	r
822	Mexico	Yucatan	Uxmal	w	-	f	-	y
823	Mexico	Quintana Roo	Quintana Roo	h	80	f	-	o
824	Belize	Cayo	Central Farm	h	150	f	-	y

Acc.# (UH)	Country	Province	Locality	Type*	Weight (g)	Sex**	TSS (%)	Flesh***
825	Belize	Cayo	S. Ignacio	d	-	h	-	r
826	Belize	Cayo	S. Ignacio	h	100	f	-	y
827	Belize	Cayo	S. Ignacio	w	30	f	12.0	y
828	Belize	Cayo	S. Ignacio	w	50	f	-	y
829	Belize	Cayo	S. Ignacio	w	25	f	-	y
830	Belize	Cayo	S. Ignacio	w	50	f	-	y
831	Belize	Cayo	S. Ignacio	w	75	f	-	y
832	Belize	Cayo	S. Ignacio	h	300	f	-	y
833	Belize	Cayo	S. Ignacio	w	35	f	-	y
834	Belize	Cayo	S. Ignacio	w	-	-	-	-
835	Belize	Cayo	S. Ignacio	w	35	f	-	y
836	Belize	Cayo	S. Ignacio	w	25	f	13.2	y
837	Belize	Cayo	S. Ignacio	w	-	f	-	-
839	Guatemala	Guatemala	Guatemala	d	1850	h	6.7	r
840	Guatemala	Guatemala	Guatemala	d	2200	f	11.0	r
841	Guatemala	Guatemala	Guatemala	d	1025	f	15.4	r
842	Guatemala	Peten	Flores	w	40	f	12.0	y
843	Guatemala	Peten	Juntecholol	w	30	f	-	-
844	Guatemala	Peten	Tikal	w	100	f	-	y
845	Guatemala	Peten	Tikal	w	40	f	-	-
846	Guatemala	Peten	Santa Elena	d	50	f	-	r
847	Guatemala	Peten	La Libertad	w	15	f	-	-
848	Guatemala	Peten	La Libertad	w	25	f	-	y
849	Guatemala	Peten	La Libertad	h	270	f	-	y
850	Guatemala	Peten	La Libertad	d	1200	f	-	r
851	Guatemala	Peten	La Libertad	h	350	f	13.2	y
852	Guatemala	Peten	La Libertad	w	25	f	11.0	y
853	Guatemala	Peten	La Libertad	w	25	f	14.7	-

Acc.# (UH)	Country	Province	Locality	Type*	Weight (g)	Sex**	TSS (%)	Flesh***
854	Guatemala	Peten	La Libertad	w	50	f	-	y
855	Guatemala	Peten	San Benito	w	40	f	-	y
856	Guatemala	Peten	San Benito	w	35	f	-	y
857	Guatemala	Peten	San Benito	w	40	f	-	y
858	Guatemala	Peten	San Benito	w	25	f	-	y
859	Guatemala	Peten	San Benito	w	50	f	-	y
860	Guatemala	Peten	San Andres	w	50	f	12.5	y
861	Guatemala	Peten	San Andres	w	25	f	14.5	y
862	Guatemala	Peten	San Andres	w	66	f	15.6	y
863	Guatemala	Izabal	Los Amates	h	100	f	-	-
864	Guatemala	Izabal	Los Amates	h	167	f	17.5	y
865	Guatemala	Izabal	Los Amates	h	125	f	-	y
866	Guatemala	Izabal	Los Amates	w	90	f	16.2	y
867	Guatemala	Izabal	Quirigua	w	15	f	-	y
868	Guatemala	Izabal	Morales	h	325	-	-	-
869	Guatemala	Izabal	Morales	h	450	-	16.1	o
870	Guatemala	Izabal	Morales	h	200	f	14.1	y
871	Guatemala	Izabal	Rio Dulce	w	40	f	12.4	y
872	Guatemala	Izabal	Rio Dulce	h	200	f	9.2	y
873	Guatemala	Izabal	Rio Dulce	h	325	f	17.2	y
874	Guatemala	Izabal	Puerto Barrios	h	125	f	-	y
875	Guatemala	Izabal	Puerto Barrios	h	190	f	-	y
876	Guatemala	Izabal	Morales	h	375	f	12.2	y
877	Guatemala	Izabal	Puerto Barrios	h	550	f	-	y
878	Guatemala	Izabal	Puerto Barrios	d	1950	h	-	y
879	Guatemala	Zacapa	Dona Maria	d	1350	h	12.1	y
880	Guatemala	Zacapa	Dona Maria	d	1375	f	10.5	r
881	Guatemala	Zacapa	Dona Maria	d	1750	f	12.4	r

Acc.# (UH)	Country	Province	Locality	Type*	Weight (g)	Sex**	TSS (%)	Flesh***
882	Guatemala	Zacapa	Dona Maria	d	2700	h	-	r
883	Guatemala	Suchitepequez	Monte Ilana	d	2500	f	12.0	r
884	Guatemala	Suchitepequez	Monte Ilana	d	2800	h	11.4	r
885	Guatemala	Suchitepequez	Alden Cutzan	d	1900	f	9.9	r
886	Guatemala	Suchitepequez	Alden Cutzan	d	1300	f	10.5	r
887	Guatemala	Suchitepequez	Alden Cutzan	d	1800	f	-	r
888	Guatemala	Suchitepequez	Sn Miguel Moca	d	2000	f	12.6	r
889	Guatemala	Suchitepequez	Sn. Antonio Such	d	1500	h	12.2	r
890	Guatemala	Retalhuleu	Sn.AndresVillaSeca	d	1500	f	10.0	r
891	Guatemala	Retalhuleu	San Sebastian	d	2100	h	10.0	r
892	Guatemala	Retalhuleu	San Sebastian	d	2400	h	8.5	r
893	Guatemala	Retalhuleu	San Sebastian	d	2200	h	9.8	r
894	Guatemala	Retalhuleu	Sibana	d	2300	h	12.4	r
895	Guatemala	Retalhuleu	San Sebastian	d	500	h	14.2	r
896	Guatemala	Retalhuleu	San Sebastian	d	600	h	14.1	r
897	Guatemala	Retalhuleu	San Sebastian	d	1100	h	16.0	r
898	Honduras	Cortes	La Lima	h	200	f	14.3	y
899	Honduras	Cortes	La Lima	d	1600	-	9.2	y
900	Honduras	Cortes	Chamelecon	w	25	f	-	-
901	Honduras	Cortes	Chamelecon	w	75	f	-	-
902	Honduras	Cortes	San Pedro Sula	d	4320	h	6.8	s
903	Honduras	Cortes	San Pedro Sula	d	5000	h	7.2	s
904	Honduras	Cortes	Motrique	d	-	-	-	-
905	Honduras	Cortes	Motrique	d	1500	f	-	r
906	Honduras	Cortes	Baracoa	h	100	f	-	-
907	Honduras	Cortes	La Entrada	h	500	f	11.6	y
908	Honduras	Cortes	La Entrada	h	325	f	15.4	y
909	Honduras	Cortes	La Lima	h	150	f	14.5	y

Acc.# (UH)	Country	Province	Locality	Type*	Weight (g)	Sex**	TSS (%)	Flesh***
910	Honduras	Cortes	La Lima	d	250	f	14.5	r
911	Honduras	Atlantida	Metalia	h	125	f	13.0	y
912	Honduras	Atlantida	Metalia	h	150	f	9.0	y
913	Honduras	Atlantida	Tela	-	-	-	-	r
914	Honduras	Atlantida	Tela	h	150	f	-	y
915	Honduras	Atlantida	Las Mangas	h	65	f	-	-
916	Costa Rica	Alajuela	Orotina	d	1150	h	13.0	r
917	Costa Rica	Alajuela	Orotina	d	1400	f	12.4	r
918	Costa Rica	Alajuela	Coopebarro RL	d	1700	h	11.5	r
919	Costa Rica	Alajuela	Coopebarro RL	d	1650	f	15.0	r
920	Costa Rica	Limon	Rio Frio	h	-	f	-	y
921	Costa Rica	Puntarenas	Buenos Aires	d	-	h	12.8	r
922	Costa Rica	Puntarenas	Buenos Aires	d	625	h	15.4	r
923	Costa Rica	San Jose	San Isidro General	d	1900	h	13.2	r
924	Costa Rica	San Jose	San Isidro General	h	100	f	-	r
925	Costa Rica	Valle de Genera	Paso Real	h	150	f	-	-
926	Costa Rica	Puntarenas	Potrero Grande	h	2400	f	10.3	y
927	Costa Rica	Puntarenas	Potrero Grande	h	500	f	10.8	y
928	Costa Rica	Puntarenas	Potrero Grande	h	850	f	-	y
929	Costa Rica	Cartago	E.A.R.T.H. Campus	h	700	h	12.5	y
930	Costa Rica	Puntarenas	El Brujo	h	500	f	11.5	y
931	Costa Rica	San Jose	San Isidro General	d	2250	f	14.7	y
932	Costa Rica	San Jose	San Isidro General	d	1750	h	12.0	r
1001	Venezuela	Federal	Caracas	d	3600	h	7.3	r
1002	Venezuela	Federal	Caracas	d	3250	f	8.9	r
1003	Venezuela	Aragua	Maracay	d	2100	h	11.2	y
1004	Venezuela	Falcon	Boca De Tocuyo	d	1100	h	12.5	y
1005	Venezuela	Falcon	Mirimito	h	125	f	10.3	y

Acc.# (UH)	Country	Province	Locality	Type*	Weight (g)	Sex**	TSS (%)	Flesh***
1006	Venezuela	Falcon	Mirimito	h	500	h	19.2	y
1008	Venezuela	Aragua	Rancho Grande	h	100	f	14.4	y
1010	Venezuela	Aragua	LaTrilla	d	900	-	-	-
1011	Venezuela	Aragua	PaloNegro	d	1200	f	-	y
1012	Venezuela	Aragua	Guacamaya	d	2300	h	-	r
1038	Colombia	ValleDeCauca	Buenaventura	d	1150	h	10.5	o
1039	Colombia	ValleDeCauca	Buenaventura	d	1050	h	10.4	o
1040	Colombia	ValleDeCauca	Buenaventura	d	1700	f	-	y
1041	Colombia	ValleDeCauca	Buenaventura	d	1500	f	-	y
1042	Colombia	ValleDeCauca	Buenaventura	d	1100	f	-	o
1043	Colombia	ValleDeCauca	Buenaventura	d	1600	h	-	r
1044	Colombia	ValleDeCauca	Bajo Calima	d	1250	h	-	y
1045	Colombia	ValleDeCauca	Bajo Calima	d	950	f	-	y
1046	Colombia	ValleDeCauca	Bajo Calima	d	2150	h	11.4	y
1047	Colombia	ValleDeCauca	Bajo Calima	d	1300	h	11.8	y
1048	Colombia	ValleDeCauca	Buenaventura	d	1350	f	10.6	y
1049	Colombia	ValleDeCauca	San Marco	d	1800	h	12.6	y
1050	Colombia	ValleDeCauca	El Chaucel	d	2250	h	10.9	y
1051	Colombia	ValleDeCauca	El Placer	d	2700	f	10.6	y
1052	Colombia	ValleDeCauca	El Placer	d	1100	h	12.2	y
1067	Colombia	Boyaca	Yopal	d	1300	f	-	y
1068	Colombia	Boyaca	Yopal	d	425	f	12.8	y
1075	Ecuador	Pichincha	Patricia Pilar	d	500	-	-	y
1076	Ecuador	Pichincha	La Independencia	d	1000	f	-	y
1077	Ecuador	Pichincha	La Independencia	d	700	f	11.5	y
1078	Ecuador	Pichincha	La Independencia	d	900	f	-	y
1079	Ecuador	Esmeraldas	La Marujita	d	800	h	11.5	y
1080	Ecuador	Pichincha	Limon	d	1250	h	-	y

Acc.# (UH)	Country	Province	Locality	Type*	Weight (g)	Sex**	TSS (%)	Flesh***
1081	Ecuador	Pichincha	Santo Domingo	d	1500	h	10.5	-
1082	Ecuador	Pichincha	Santo Domingo	d	2200	f	11.0	-
1083	Ecuador	Pichincha	Aylluriquin	d	1250	f	-	y
1084	Ecuador	Pichincha	Santo Domingo	d	-	-	-	r
1094	Ecuador	Napo	Momdayacu	d	1000	f	12.4	y
1095	Ecuador	Napo	Tena	d	300	h	8.5	r
1096	Ecuador	Napo	Tena	d	1300	f	9.4	y
1097	Ecuador	Napo	Tena	d	750	f	13.0	y
1098	Ecuador	Napo	Tena	d	1000	f	8.5	y
1109	Ecuador	Azuay	Sarayunga	d	1500	f	9.0	y
1110	Ecuador	Azuay	Sarayunga	d	500	f	10.2	y
1111	Ecuador	Azuay	Sarayunga	d	150	-	8.5	y
1123	Panama	Panama	Panama City	h	50	f	-	y
1124	Panama	Panama	Panama City	h	50	f	-	y
1126	Panama	Panama	Panama City	d	1750	f	9.6	r
1127	Panama	Panama	Panama City	d	1750	f	10.8	r
1128	Panama	Panama	Panama City	d	1550	h	7.7	r

*d = domesticated; h = hybrid; w = wild

**f = female; h = hermaphrodite

***o = orange; r = red; s=salmon; y = yellow

APPENDIX B
CENTRAL AND SOUTH AMERICAN *CARICA* SPECIES ACCESSIONS

Acc.# Species (UH)	Country	Province	Locality	Seed Germ
1007 *cauliflora*	Venezuela	Aragua	Rancho Grande	Yes
1015 *cauliflora*	Colombia	V. de Cauca	Tulua	Yes
1119 *cauliflora*	Panama	Panama	Panama City	No
1120 *cauliflora*	Panama	Panama	Panama City	No
1121 *cauliflora*	Panama	Panama	Panama City	Yes
1122 *cauliflora*	Panama	Panama	Panama City	No
1124 *cauliflora*	Panama	Panama	Panama City	Yes
1125 *cauliflora*	Panama	Panama	Panama City	No
1018 *crassipetala*	Colombia	Risaralda	Termales	Yes
1019 *crassipetala*	Colombia	Risaralda	Termales	Yes
1130 *glandulosa*	Brazil	Brasilia	Brasilia	Yes
1016 *goudotiana*	Colombia	Risaralda	Santa Rosa de Cabal	Yes
1017 *goudotiana*	Colombia	Risaralda	Santa Rosa de Cabal	Yes
1021 *goudotiana*	Colombia	Quindio	Boquia	Yes
1022 *goudotiana*	Colombia	Quindio	Boquia	Yes
1023 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1024 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1025 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1026 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1027 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1028 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1029 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1030 *goudotiana*	Colombia	V. de Cauca	Pavitas	Yes
1031 *goudotiana*	Colombia	V. de Cauca	Pavitas	Yes
1032 *goudotiana*	Colombia	V. de Cauca	Pavitas	Yes
1033 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes

Acc.# (UH) Species	Country	Province	Locality	Seed Germ
1034 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1035 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1036 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1037 *goudotiana*	Colombia	V. de Cauca	La Cumbre	Yes
1057 *goudotiana*	Colombia	Risaralda	Santa Rosa de Cabal	Yes
1102 *heilbornii*	Ecuador	Chimbarazo	Compud	Stem
1103 *heilbornii*	Ecuador	Chimbarazo	Compud	Stem
1104 *heilbornii*	Ecuador	Azuay	Giron	Stem
1117 *heilbornii*	Ecuador	Tungurahua	San Javier	Stem
1116 *heilbornii nm pentagona*	Ecuador	Tungurahua	San Javier	Stem
1114 *heilbornii nm pentagona*	Ecuador	Tungurahua	Patate	Stem
1115 *heilbornii nm pentagona*	Ecuador	Tungurahua	San Javier	Stem
1014 *hybrid (unknown)*	Venezuela	Aragua	Colonia Tovar	Stem
1099 *microcarpa ssp. (?)*	Ecuador	Pasteza	Mera	No
1118 *microcarpa ssp. (?)*	Ecuador	Pasteza	Mera	Stem
1070 *microcarpa ssp. baccata*	Ecuador	Pichincha	Patricia Pilar	No
1071 *microcarpa ssp. baccata*	Ecuador	Pichincha	Patricia Pilar	No
1072 *microcarpa ssp. baccata*	Ecuador	Pichincha	Patricia Pilar	Yes
1073 *microcarpa ssp. baccata*	Ecuador	Pichincha	Patricia Pilar	No
1074 *microcarpa ssp. baccata*	Ecuador	Pichincha	Patricia Pilar	No
1009 *microcarpa ssp. microcarpa*	Venezuela	Aragua	Rancho Grande Park	Yes
1069 *microcarpa ssp. microcarpa*	Colombia	Boyaca	Huerte Vieja	Yes
1100 *microcarpa ssp. heterophylla*	Ecuador	Pasteza	Mera	Stem
1129 *monoica*	Brazil	Brasilia	Brasilia	Yes
1020 *pubescens*	Colombia	Quindio	Boquia	Yes
1058 *pubescens*	Colombia	Cundinamarca	Tocancipa	Yes
1059 *pubescens*	Colombia	Cundinamarca	Tocancipa	Yes
1060 *pubescens*	Colombia	Cundinamarca	Sesquile	Yes
1061 *pubescens*	Colombia	Cundinamarca	Sesquile	Yes

Acc.# Species (UH)	Country	Province	Locality	Seed Germ
1062 *pubescens*	Colombia	Cundinamarca	Sesquile	Yes
1063 *pubescens*	Colombia	Cundinamarca	Villapinzon	Yes
1064 *pubescens*	Colombia	Boyaca	Parroquia Vieja	Yes
1065 *pubescens*	Colombia	Boyaca	Parroquia Vieja	Yes
1066 *pubescens*	Colombia	Boyaca	Rancherios district	Yes
1086 *pubescens*	Ecuador	Napo	Cuyuja	No
1087 *pubescens*	Ecuador	Napo	Cuyuja	No
1088 *pubescens*	Ecuador	Napo	Cuyuja	No
1089 *pubescens*	Ecuador	Napo	Cuyuja	No
1090 *pubescens*	Ecuador	Napo	Cuyuja	No
1091 *pubescens*	Ecuador	Napo	Baeza	No
1092 *pubescens*	Ecuador	Napo	S.Elena de Los Huacamayo	No
1093 *pubescens*	Ecuador	Napo	S.Elena de Los Huacamayo	No
1101 *pubescens*	Ecuador	Tungurahua	Ulvilla	No
1112 *pubescens*	Ecuador	Tungurahua	Salasaca	No
1113 *pubescens*	Ecuador	Tungurahua	Panatu	No
1085 *pulchra*	Ecuador	Pichincha	Chiriboga,stem	Stem
1013 *quercifolia*	Venezuela	Aragua	Colonia Tovar	No
1054 *sphaerocarpa*	Colombia	V. de Cauca	La Elsa	Yes
1055 *sphaerocarpa*	Colombia	V. de Cauca	La Elsa	Yes
1056 *sphaerocarpa*	Colombia	V. de Cauca	La Elsa	No
1105 *stipulata*	Ecuador	Azuay	Rio de Rircay	No
1106 *stipulata*	Ecuador	Azuay	Rio de Rircay	No
1107 *stipulata*	Ecuador	Azuay	Rio de Rircay	No
1108 *stipulata*	Ecuador	Azuay	Rio de Rircay	No

*Seed Germ.-- Yes =seeds germinated; No =seeds did not germinate; Stem=stem cuttings
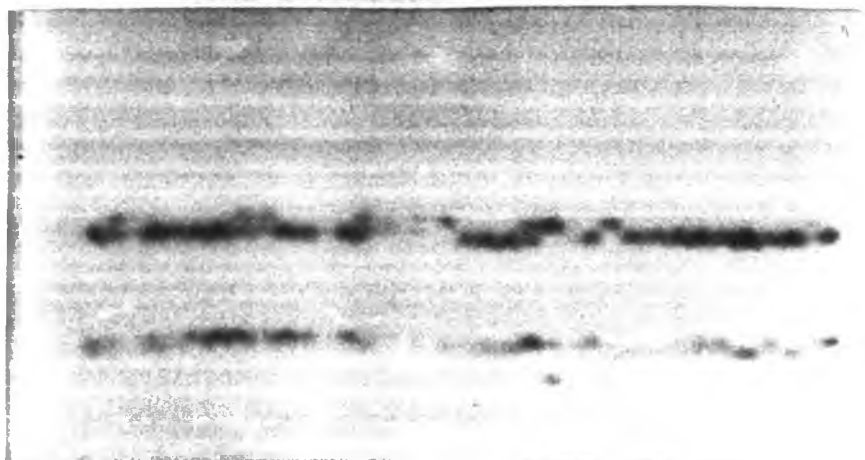
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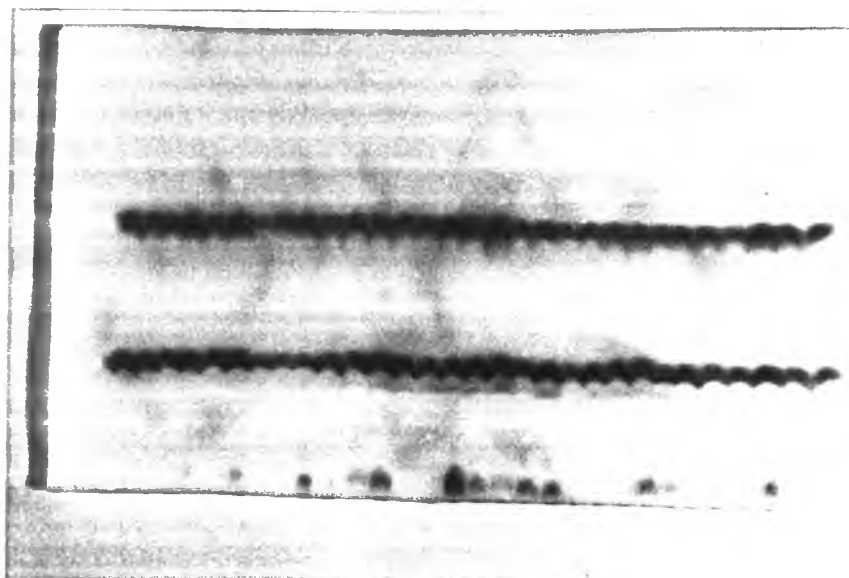
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MDH (EC 1.1.1.37)

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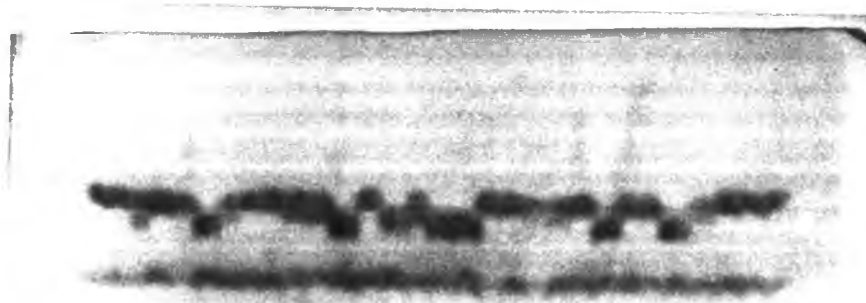
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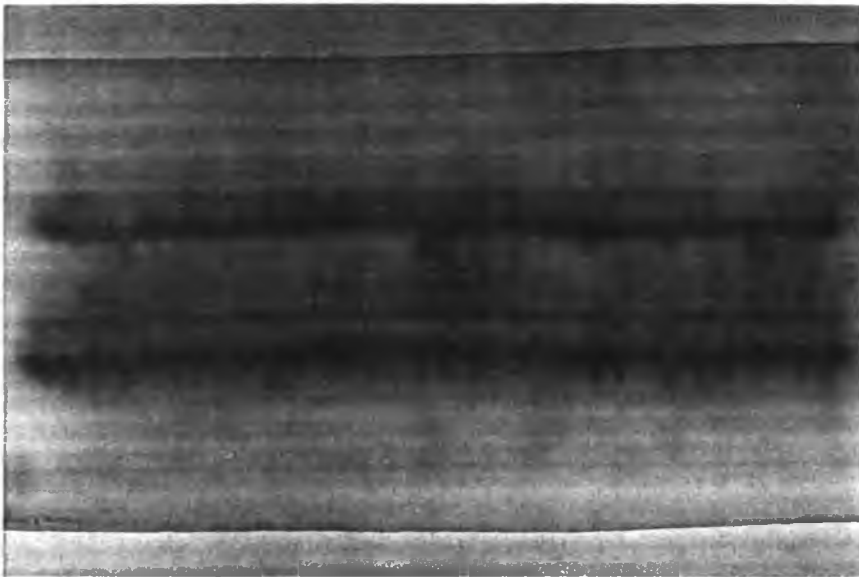
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UGP (EC 2.7.7.9)
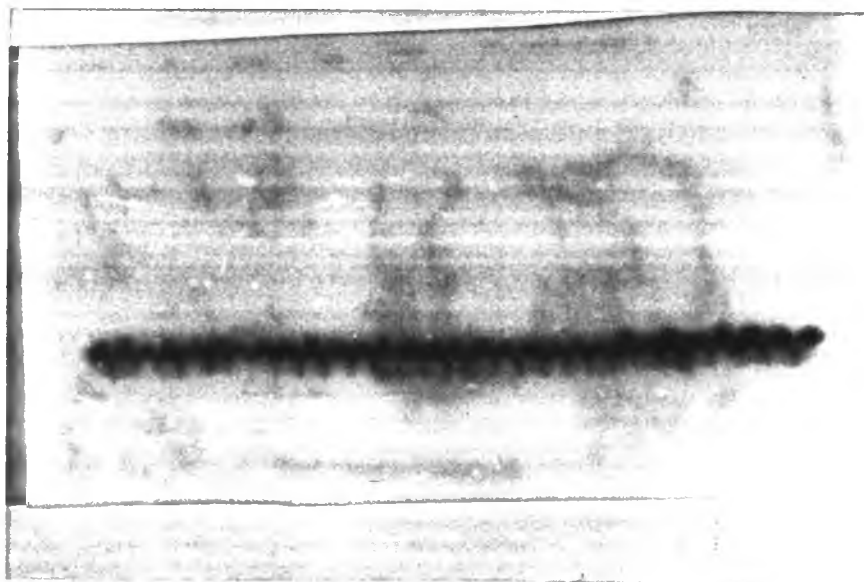
6-PGD (EC 1.1.1.44)

LOCUSWISE GENOTYPE DATA FOR DIFFERENT POPULATIONS OF
CARICA PAPAYA

DVER

		PGM1	PGM2	PGI	IDH	MDH1	MDH2	6PGD	ACO1	ACO2	UGP	SKD	TPI1	TPI2
0800	FJ1	AA	BB	BC	AA	AA	AA	AA	AA	CC	BB	BB	BB	BB
0800	S01	BB	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0801	FJ1	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0801	FJ2	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0801	FJ5	BB	BB	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0804	FJ3	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	FJ4	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S01	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S02	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S03	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S04	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S05	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S06	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S07	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S08	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S09	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S10	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S11	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S12	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S13	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S14	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S15	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S16	AA	BB	BC	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S17	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S18	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S19	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S20	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0804	S21	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0805	FJ1	BB	AB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	FJ2	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	FJ3	AB	BB	BC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	FJ4	BB	AB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	S01	AB	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	S02	AB	AB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	S03	BB	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	S04	BB	AB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	S05	AB	BB	BC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	S06	BB	AB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0805	S07	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB

DYUC

		PGM1	PGM2	PGI	IDH	MDH1	MDH2	6PGD	ACO1	ACO2	UGP	SKD	TPI1	TPI2
0814	S01	AA	BB	CC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0814	S02	AA	BB	CC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0814	S03	AA	BB	CC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0814	S04	AA	BB	CC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB

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0814   S05    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S06    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S07    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S08    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S09    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S10    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S11    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S12    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S13    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S14    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S15    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S16    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S17    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S18    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S19    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S20    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S21    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S22    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S23    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S24    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S25    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S26    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S27    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S28    AA BB CC AA AA AA AA BB BB BB BB BB BB
0814   S29    AA BB CC AA AA AA AA BB BB BB BB BB BB
0820   FJ1    BB BB BB AA AA AA AA AA AA BB BB AB BB
0820   FJ2    AB BB BB AA AA AA AA BB AA BB BB AB BB
0820   FJ4    AB BB BB AA AA AA AA AB AA BB BB AB BB
0820   FJ5    BB BB BB AA AA AA AA BB BC BB BB AB BB
0820   S01    BB BB BB AA AA AA AA AB AB BB BB AB BB
0820   S02    BB BB BB AA AA AA AA AB BB BB BB AB BB
0820   S03    AB BB BB AA AA AA AA AA BB BB BB AB BB
0820   S04    BB BB BB AA AA AA AA AB AB BB BB AB BB
0820   S05    AB BB BB AA AA AA AA AB BB BB BB AB BB
0820   S06    BB BB BB AA AA AA AA AB AB BB BB AB BB
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0820   S08    BB BB BB AA AA AA AA AB AB BB BB AB BB
0820   S09    BB BB BB AA AA AA AA AB AB BB BB AB BB
0820   S10    BB BB BB AA AA AA AA BB BB BB BB AB BB
0820   S11    AB BB BB AA AA AA AA AB BB BB BB AB BB
0820   S12    AB BB BB AA AA AA AA BB AB BB BB AB BB
0820   S13    BB BB BB AA AA AA AA AA AB BB BB AB BB
0820   S14    AB BB BB AA AA AA AA BB BB BB BB AB BB
0820   S15    BB BB BB AA AA AA AA BB BB BB BB AB BB
0820   S16    AB BB BB AA AA AA AA BB BB BB BB AB BB
0820   S17    BB BB BB AA AA AA AA BB AB BB BB AB BB
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0820   S21    BB  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  AB  BB
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DSAN
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0825   S01    AB  BB  BC  AA  AA  AA  AA  AB  BC  BB  BB  BB  BB
0825   S02    AB  BB  BC  AA  AA  AA  AA  AB  AB  BB  BB  BB  BB
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0825   S04    BB  BB  BC  AA  AA  AA  AA  BB  AB  BB  BB  BB  BB
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0825   S06    AB  BB  BC  AA  AA  AA  AA  BB  BC  BB  BB  BB  BB
0825   S07    BB  BB  BC  AA  AA  AA  AA  BB  BC  BB  BB  BB  BB
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0825   S09    AB  BB  BC  AA  AA  AA  AA  AB  AB  BB  BB  BB  BB
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0825   S11    AB  BB  BC  AA  AA  AA  AA  BB  AB  BB  BB  BB  BB
0825   S12    AB  BB  BC  AA  AA  AA  AA  BB  BB  BB  AB  BB  BB
0825   S13    AB  BB  BC  AA  AA  AA  AA  AB  BC  BB  BB  BB  BB
0825   S14    AB  BB  BC  AA  AA  AA  AA  AB  AB  BB  BB  BB  BB
0825   S15    BB  BB  BC  AA  AA  AA  AA  BB  AB  BB  BB  BB  BB
DRIO
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0878   FK3    BB  BB  CC  AA  AA  AA  AA  BB  CC  AA  BB  BB  BB
0878   FK4    BB  BB  CC  AA  AA  AA  AA  BB  CC  AA  BB  BB  BB
0879   S01    BB  BB  CC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BC
0879   S02    BB  BB  CC  AA  AA  AA  AA  BB  BB  BB  BB  BB  BB
0879   S03    BB  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
0879   S04    BB  BB  CC  AA  AA  AA  AA  BB  BB  BB  BB  BB  BC
0879   S05    BB  BB  CC  AA  AA  AA  AA  BB  BB  BB  BB  BB  BB
0879   S06    BB  BB  CC  AA  AA  AA  AA  BB  BB  BB  BB  BB  BC
0879   S07    BB  BB  CC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BC
0879   S08    BB  BB  CC  AA  AA  AA  AA  BB  BB  BB  BB  BB  BB
0879   S09    BB  BB  CC  AA  AA  AA  AA  BB  BB  BB  BB  BB  CC
0879   S10    BB  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
0879   S11    BB  BB  CC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BB
0879   S12    BB  BB  CC  AA  AA  AA  AA  BB  BB  BB  BB  BB  BC
0879   S13    BB  BB  CC  AA  AA  AA  AA  BB  BB  BB  BB  BB  CC
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0879	S14	BB	BB	CC	AA	AA	AA	AA	AB	BB	BB	BB	BB	CC
0879	S15	BB	BB	CC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0879	S16	BB	BB	CC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0879	S17	BB	BB	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BC
0879	S18	BB	BB	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BC
0879	S19	BB	BB	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0880	FJ1	BB	BB	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	CC
0880	FJ3	BB	BB	CC	AA	AA	AA	AA	AA	BB	BB	BC	BB	BC
0880	FK4	AB	BB	BC	AA	AA	AA	AA	AA	BC	BB	BB	BB	BC
0880	FK5	BB	BB	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	CC
0880	FK2	AB	BB	BC	AA	AA	AA	AA	AA	BC	BB	BB	BB	BC
0882	S01	BB	BB	CC	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
0882	S02	BB	BB	CC	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
0882	S03	BB	BB	CC	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
0882	S04	BB	BB	CC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0882	S05	BB	AB	CC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0882	S06	BB	BB	CC	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
0882	S07	BB	BB	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0882	S08	BB	BB	CC	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
0882	S09	BB	BB	CC	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
DPAC														
0883	FJ1	AA	AA	BC	AA	AA	AA	AA	AB	AC	BB	BB	BB	BB
0883	FJ2	AB	AB	CC	AA	AA	AA	AA	AB	AA	BB	BB	BB	BB
0883	FJ3	AB	AA	BC	AA	AA	AA	AA	AA	AD	BB	BB	BB	BB
0883	FJ4	AA	AA	CC	AA	AA	AA	AA	AA	AA	BB	BB	BB	BB
0883	FJ5	AB	AB	CC	AA	AA	AA	AA	AA	AC	BB	BB	BB	BB
0884	FK1	AA	AA	BB	AA	AA	AA	AA	AA	AA	BB	BB	BB	BB
0884	FK5	AA	AA	BC	AA	AA	AA	AA	AA	AA	BB	BB	BB	BB
0885	FL1	AA	AA	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0886	FJ4	AB	AB	CC	AA	AA	AA	AA	AA	CD	BB	BB	BB	BB
0886	FJ3	AB	AB	BC	AA	AA	AA	AA	AA	CD	BB	BB	BB	BB
0891	FK2	AA	BB	CC	AA	AA	AA	AA	AA	AA	BB	BB	BB	BB
0891	FK4	AA	BB	CC	AA	AA	AA	AA	AB	AA	BB	BB	BB	BB
0892	FK2	BB	BB	CC	AA	AA	AA	AA	AA	BC	BB	BB	BB	BB
0892	FK5	BB	BB	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0894	FK3	BB	BB	BC	AA	AA	AA	AA	AA	AA	BB	BB	BB	BB
0894	FK4	BB	BB	CC	AA	AA	AA	AA	AA	AA	BB	BB	BB	BB
0894	FK5	BB	BB	BC	AA	AA	AA	AA	AA	AA	BB	BB	BB	BB
0895	FK1	AA	BB	BC	AA	AA	AA	AA	AA	AA	BB	BB	BB	BB
0895	FK2	AA	BB	BC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0895	FK3	AA	BB	CC	AA	AA	AA	AA	AA	BB	BB	BB	BB	BB
0896	FK1	AB	BB	CC	AA	AA	AA	AA	AA	AA	BB	BB	BB	BB
0896	FK3	AB	AA	BC	AA	AA	AA	AA	AB	AA	BB	BB	BB	BB
0896	FK4	AB	AB	BC	AA	AA	AA	AA	AB	AA	BB	BB	BB	BB
0896	FK5	BB	AA	BC	AA	AA	AA	AA	BB	AA	BB	BB	BB	BB
0897	FK1	AA	AB	BC	AA	AA	AA	AA	AA	AB	BB	BB	BB	BC

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0897   FK2   AA BB BC AA AA AA AA AB BB BB BB BB BC
0897   FK3   AB BB BC AA AA AA AA AB AC BB BB BB BC
0897   FK4   AA AB BC AA AA AA AA AB AA BB BB BB BC
0897   FK5   AA BB BC AA AA AA AA AB AA BB BB BB BC
DHON
0899   FK1   AB BB BC AA AA AA AA AA BC BB BB BB BB
0899   FK2   AB BB BC AA AA AA AA AB BC BB BB BB BB
0899   FK4   BB BB BC AA AA AA AA AA BC BB BB BB BB
0899   FK5   AB BB CC AA AA AA AA AA BC BB BB BB BB
0902   FK1   BB AA CC AA AA AA AA BB BB BB BB BB BB
0902   FK2   BB AA CC AA AA AA AA BB BB BB BB BB BB
0902   FK3   BB AA CC AA AA AA AA BB BB BB BB BB BB
0902   FK4   BB AA CC AA AA AA AA BB BB BB BB BB BB
0902   FK5   BB AA CC AA AA AA AA BB BB BB BB BB BB
0903   FK1   BB BB CC AA AA AA AA AA BB BB BB BB BB
0903   FK2   BB BB CC AA AA AA AA AA BB BB BB BB BB
0903   FK3   BB BB CC AA AA AA AA AA BB BB BB BB BB
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0903   S02   BB BB CC AA AA AA AA AA BB BB BB BB BB
0903   S03   BB BB CC AA AA AA AA AA BB BB BB BB BB
0904   FK2   AB BB CC AA AA AA AA BB BB BB BB BB BC
0904   FK3   AB BB CC AA AA AA AA BB BB BB BB BB BC
0904   FK5   AB BB CC AA AA AA AA BB BB BB BB BB BC
0910   FK1   BB BB BB AA AA AA AA AB BB BB BB BB BB
0910   FK2   BB BB BB AA AA AA AA BB BB BB BB BB BB
0910   FK3   BB BB BB AA AA AA AA AB BB BB BB BB BB
0910   FK4   BB BB BB AA AA AA AA AB BB BB BB BB BB
0910   FK5   BB BB BB AA AA AA AA AB BB BB BB BB BB
DCOS
0916   FJ3   AA BB BC AA AA AA AA AA BC BB BB BB BB
0916   FJ4   AA BB BC AA AA AA AA AA BC BB BB BB BB
0916   S01   BB BB BB AA AA AA AA AA CC BB BB BB CC
0916   S02   AB BB BC AA AA AA AA AA CC BB BB BB BC
0916   S03   AB BB BC AA AA AA AA AA CC BB BB BB BC
0916   S04   AA BB BC AA AA AA AA AA CC BB BB BB BB
0916   S05   AB BB BB AA AA AA AA AA CC BB BB BB BC
0916   S06   AB BB BB AA AA AA AA AA BB BB BB BB CC
0916   S07   AB BB BC AA AA AA AA AA BB BB BB BB BB
0916   S08   AA BB CC AA AA AA AA AA CC BB BB BB BB
0917   FJ1   AB BB BC AA AA AA AA BB BB BB BB BB BB
0917   FJ3   BB BB BB AA AA AA AA AA BC BB BB BB BC
0917   FJ5   AB BB BB AA AA AA AA AB BC BB BB BB BC
0917   S01   BB BB BB AA AA AA AA AA BC BB BB BB BC
0917   S02   BB BB BB AA AA AA AA AA BB BB BC BB BC
0917   S03   BB BB BB AA AA AA AA AB BC BB BB BB BC
0917   S04   AB BB BB AA AA AA AA BB BC BB BB BB BB
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0917	S05	BB	BB	BB	AA	AA	AA	AA	AA	BC	BB	BB	BB	BC
0917	S06	BB	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	BC
0917	S07	BB	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	BC
0917	S08	BB	BB	BB	AA	AA	AA	AA	AA	BC	BB	BB	BB	BC
0918	FK1	AA	BB	BB	AA	AA	AA	AA	AA	CC	BB	BB	BB	BB
0918	FK2	AA	BB	BB	AA	AA	AA	AA	BB	CC	BB	BB	BB	BB
0918	FK3	AA	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0918	FK4	AA	BB	BB	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
0918	FK5	AA	BB	BB	AA	AA	AA	AA	AA	CC	BB	BB	BB	BB
0918	S01	AA	BB	BB	AA	AA	AA	AA	BB	CC	BB	BB	BB	CC
0918	S02	AA	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	BC
0918	S03	AA	BB	BB	AA	AA	AA	AA	BB	BB	BB	BB	BB	BC
0918	S04	AA	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	BC
0918	S05	AA	BB	BB	AA	AA	AA	AA	BB	BC	BB	BB	BB	CC
0918	S06	AA	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	BC
0918	S07	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BC
0918	S08	AA	BB	BB	AA	AA	AA	AA	BB	BC	BB	BB	BB	BC
0918	S09	AA	BB	BB	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0918	S10	AA	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	CC
0919	FJ1	AA	BB	BB	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
0919	FJ2	AA	BB	BB	AA	AA	AA	AA	BB	BB	BB	BB	BB	BC
0919	FJ3	AA	BB	BB	AA	AA	AA	AA	AB	BB	BB	BB	BB	BC
0919	FJ4	AA	BB	BB	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
0919	FJ5	AA	BB	BB	AA	AA	AA	AA	AA	BD	BB	BB	BB	BC
0919	S01	AA	BB	BB	AA	AA	AA	AA	AB	BB	BB	BB	BB	BB
0919	S02	AA	BB	BB	AA	AA	AA	AA	BB	BD	BB	BB	BB	BC
0919	S03	AA	BB	BC	AA	AA	AA	AA	AB	BB	BB	BB	BB	BC
0919	S04	AA	BB	BB	AA	AA	AA	AA	AB	BD	BB	BB	BB	BC
0919	S05	AA	BB	BB	AA	AA	AA	AA	AB	BD	BB	BB	BB	BC
0919	S06	AA	BB	BB	AA	AA	AA	AA	BB	BD	BB	BB	BB	BB
0919	S07	AA	BB	BB	AA	AA	AA	AA	AB	BD	BB	BB	BB	BB
0919	S08	AA	BB	BB	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0919	S09	AA	BB	BB	AA	AA	AA	AA	AA	BD	BB	BB	BB	BC
0919	S10	AA	BB	BB	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0923	FK1	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	BC
0923	FK2	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	CC
0923	FK3	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	CC
0923	FK4	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	CC
0923	FK5	AA	BB	BB	AA	AA	AA	AA	AA	BB	BB	BB	BB	CC
0931	FJ1	AB	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	BC
0931	FJ2	AA	BB	CC	AA	AA	AA	AA	BB	CC	BB	BB	BB	BB
0931	FJ3	AA	BB	BC	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0931	FJ4	AB	BB	CC	AA	AA	AA	AA	AB	CC	BB	BB	BB	BC
0931	S01	AA	BB	BC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
0931	S02	AA	BB	BB	AA	AA	AA	AA	AB	BB	BB	BB	BB	BC
0931	S03	AB	BB	CC	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB

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0931   S04   AA  BB  BC  AA  AA  AA  AA  AB  BC  BB  BB  BB  BB
0931   S05   AB  BB  BC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BC
0931   S06   AA  BB  BB  AA  AA  AA  AA  AB  BC  BB  BB  BB  BB
0931   S07   AA  BB  BC  AA  AA  AA  AA  BB  BB  BB  BB  BB  BB
0931   S08   AA  BB  BB  AA  AA  AA  AA  BB  BC  BB  BB  BB  BC
0931   S09   AA  BB  BC  AA  AA  AA  AA  BB  BB  BB  BB  BB  BB
0931   S10   AB  BB  BC  AA  AA  AA  AA  AB  BC  BB  BB  BB  BC
0932   S01   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
0932   S02   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
0932   S03   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  CC
0932   S04   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
0932   S05   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
0932   S06   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
0932   S07   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
0932   S08   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
DVEN
1001   S01   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1001   S02   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1001   S03   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1001   S04   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1001   S05   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1001   S06   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1001   S07   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1001   S08   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1001   S09   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1001   S10   AA  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1002   S01   AB  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
1002   S02   AA  BB  CC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BC
1002   S03   AB  BB  CC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BB
1002   S04   AA  BB  BC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BB
1002   S05   AB  BB  CC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BB
1002   S06   AB  BB  CC  AA  AA  AA  AA  AB  BC  BB  BB  BB  BC
1002   S07   AA  BB  CC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BB
1003   S01   BB  BB  BB  AA  AA  AA  AA  AA  BC  BB  BB  BB  BC
1003   S02   AB  BB  BC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
1003   S03   AA  BB  BC  AA  AA  AA  AA  AA  BB  BB  BB  BB  CC
1003   S04   AB  BB  BC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
1003   S05   AB  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BC
1004   S01   AA  BB  CC  AA  AA  AA  AA  BB  BC  BB  BB  BB  BC
1004   S02   AB  BB  CC  AA  AA  AA  AA  BB  BC  BB  BB  BB  BB
1004   S03   AB  BB  CC  AA  AA  AA  AA  BB  BC  BB  BB  BB  BB
1011   S01   AB  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1011   S02   BB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1011   S03   BB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1011   S04   AB  BB  CC  AA  AA  AA  AA  AB  BB  BB  BB  BB  BB
1011   S05   BB  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
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1012    S01    AB  BB  BB  AA  AA  AA  AA  BB  BB  BB  BB  BB  BC
1012    S02    AB  BB  CC  AA  AA  AA  AA  BB  CC  BB  BB  BB  BC
1012    S03    AB  BB  BC  AA  AA  AA  AA  BB  BC  BB  BB  BB  BC
1012    S04    BB  BB  BC  AA  AA  AA  AA  BB  BB  BB  BB  BB  BB
1012    S05    AB  BB  BC  AA  AA  AA  AA  AB  CC  BB  BB  BB  BB
DBUE
1038    S01    AA  BB  CC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1038    S02    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1039    S01    AA  BB  CC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1039    S02    AA  BB  CC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1040    S01    AB  BB  BB  AA  AA  AA  AA  AA  BB  AB  BB  BB  BB
1040    S02    AA  BB  BB  AA  AA  AA  AA  AA  BC  AB  BB  BB  BB
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1044    S01    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1044    S02    AA  BB  BB  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1044    S03    AA  BB  BB  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1045    S01    AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1046    S01    AA  BB  BB  AA  AA  AA  AA  AB  CC  BB  BB  BB  BB
1046    S02    AA  BB  BB  AA  AA  AA  AA  AB  CC  BB  BB  BB  BB
1047    S01    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1047    S02    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1048    S01    AA  BB  BB  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1048    S02    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1049    S01    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  CC
1049    S02    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  CC
1050    S01    AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
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1052    S02    AB  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1052    S03    AB  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
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DYOP
1067    S01    AB  BB  CC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1067    S02    BB  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1067    S03    BB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067    S04    BB  BB  CC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1067    S05    AB  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1067    S06    AB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067    S07    AB  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1067    S08    AA  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067    S09    AB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
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1067   S10    AB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S11    AB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S12    AA  BB  BC  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
1067   S13    AB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S14    AB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S15    AB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S16    BB  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1067   S17    AB  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1067   S18    AB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S19    BB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S20    AA  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S21    AB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S22    AA  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1067   S23    AB  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1067   S24    AB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S25    AA  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1067   S26    BB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S27    AB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
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1067   S29    AB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1067   S30    AB  BB  CC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1068   S01    AB  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1068   S02    AA  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
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1068   S06    BB  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1068   S07    AB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
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1068   S09    AA  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1068   S10    AB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1068   S11    AA  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
1068   S12    BB  BB  CC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
DDOM
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1075   S02    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1075   S03    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1075   S04    AA  BB  BB  AA  AA  AA  AA  AB  CC  BB  BB  BB  BB
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1075   S08    AA  BB  BB  AA  AA  AA  AA  AB  CC  BB  BB  BB  BB
1075   S09    AA  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1075   S10    AA  BB  BB  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
1075   S11    AB  BB  BB  AA  AA  AA  AA  AB  CC  BB  BB  BB  BB
1075   S12    AA  BB  BC  AA  AA  AA  AA  AA  BC  BB  BB  BB  BB
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1075  S14  AA BB BC AA AA AA AA AA CC BB BB BB BB
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1075  S16  AA BB BC AA AA AA AA AA CC BB BB BB BB
1075  S17  AA BB BC AA AA AA AA AB CC BB BB BB BB
1075  S18  AB BB BB AA AA AA AA AB CC BB BB BB BB
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1075  S20  AB BB BB AA AA AA AA AB CC BB BB BB BB
1075  S21  AB BB BB AA AA AA AA AB CC BB BB BB BB
1075  S22  AA BB BC AA AA AA AA AB CC BB BB BB BB
1075  S23  AB BB BC AA AA AA AA AB CC BB BB BB BB
1075  S24  AA BB BB AA AA AA AA AA BC BB BB BB BB
1075  S25  AB BB BC AA AA AA AA AB CC BB BB BB BB
1075  S26  AA BB BC AA AA AA AA AB CC BB BB BB BB
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1080  S02  AA BB BB AA AA AA AA AA BB BB BB BB BB
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1080  S04  AA BB BB AA AA AA AA AA BB BB BB BB BB
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1082  S02  AA BB BB AA AA AA AA AB CC BB BB BB BB
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1111   S08   BB BB BB AA AA AA AA AA CC BB BB BB BB
1111   S09   BB BB BB AA AA AA AA AA CC BB BB BB BB
1111   S10   AA BB BB AA AA AA AA AB CC BB BB BB BB
DNAP
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1094   S02   AA BB BC AA AA AA AA AA BC BB BB BB BB
1094   S03   AA BB BC AA AA AA AA AA BC BB BB BB BB
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1096   S02   AA  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
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1096   S04   AA  BB  BC  AA  AA  AA  AA  AA  CC  BB  BB  BB  BB
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DPAN
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1127   S02   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
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1127   S06   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
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1127   S08   AA  BB  BB  AA  AA  AA  AA  AA  BB  BB  BB  BB  BB
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1127   S10    AA BB BB AA AA AA AA AA BB BB BB BB BB
1128   S01    AA BB BB AA AA AA AA AA BB BB BB BB BB
1128   S02    AA BB BB AA AA AA AA AA BB BB BB BB BB
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1128   S06    AA BB BB AA AA AA AA AA BB BB BB BB BB
1128   S07    AA BB BB AA AA AA AA AA BB BB BB BB BB
1128   S08    AA BB BB AA AA AA AA AA BB BB BB BB BB
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1128   S10    AA BB BB AA AA AA AA AA BB BB BB BB BB
HVER
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0806   FJ2    BB BB BB AA AA AA AA AB BC BB BB BB BB
0806   FJ4    BB BB CC AA AA AA AA AB BB BB BB BB BB
0806   S01    BB BB BC AA AA AA AA AB BC BB BB BB BB
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HSAN
0826   FJ4    BB BB BB AA AA AA AA BB CC BB AB BB BB
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0832   FK3    AB BB BB AA AA AA AA BB BC BB BC BB BB
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0832   S07    AB BB BC AA AA AA AA BB AC BB BC AA BB
0832   S08    BB BB BC AA AA AA AA AB BC BB BC AA BB
0832   S09    AB BB BB AA AA AA AA BB AC BB CC AB BB
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0832   S12    BB BB BC AA AA AA AA BB AC BB CC BB BB
0832   S13    AB BB BC AA AA AA AA AB AC BB BB AA BB
0832   S14    BB BB BB AA AA AA AA BB BC BB CC AB BB
0832   S15    BB BB BC AA AA AA AA BB AC BB BC BB BB
HPET
0849   FK1    BB BB BC AA AA AA AA AB BC BB BB BB BB
0849   FK2    BB BB BC AA AA AA AA AB AC BB BB BB BB
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225

0849	FK4	BB	BB	BC	AA	AA	AA	AA	AB	BC	BB	AB	BB	BB
0849	FK5	BB	BB	BC	AA	AA	AA	AA	AB	AB	BB	AB	BB	BB
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0849	S02	BB	BB	BC	AA	AA	AA	AA	BB	AB	BB	BB	BB	BB
0849	S03	BB	BB	CC	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
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0849	S06	BB	BB	BB	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
0849	S07	BB	BB	CC	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
0849	S08	BB	BB	BC	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
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0849	S10	BB	BB	BB	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
0849	S11	BB	BB	BB	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
0849	S12	BB	BB	CC	AA	AA	AA	AA	BB	CC	BB	BB	BB	BB
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0849	S17	BB	BB	CC	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
0849	S18	BB	BB	CC	AA	AA	AA	AA	BB	CC	BB	BB	BB	BB
0849	S19	BB	BB	BC	AA	AA	AA	AA	BB	BC	BB	AB	BB	BB
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0849	S21	BB	BB	BC	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB
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0851	FK2	BB	BB	CC	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
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0851	S01	BB	BB	CC	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
0851	S02	BB	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0851	S03	BB	BB	BB	AA	AA	AA	AA	BB	CC	BB	BB	BB	BB
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0851	S19	BB	BB	BC	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
0851	S20	BB	BB	BC	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB

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0851  S21    BB BB BB AA AA AA AA BB BC BB BB BB BB
0851  S22    BB BB CC AA AA AA AA BB CC BB BB BB BB
HRIO
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0864  FK2    BB BB BC AA AA AA AA AA CC BB CC BB BB
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0898  FJ4    AB BB CC AA AA AA AA BB BC BB BB BB BB
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0907   FK2   BB BB BC AA AA AA AA AB CC BB BB BB BB
0907   FK3   AB BB BB AA AA AA AA AA AA BB BB BB BC
0907   FK4   BB BB BB AA AA AA AA AA AC BB BB BB BB
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0909   FK3   BB AB BB AA AA AA AA AB BB BB BB BB BB
0909   FK4   AB BB BB AA AA AA AA AA BB BB BB BB BB
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0911   S02   BB BB BC AA AA AA AA AA CC BB BB BB BB
0912   FL1   BB BB BB AA AA AA AA BB CC BB BB BB BB
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HCOS
0926   FK1   BB BB BC AA AA AA AA BB BC AB BB BB BB
0926   FK4   BB BB BC AA AA AA AA BB BC BB BB BB BB
0926   FK5   BB BB BC AA AA AA AA AB CC AB BB BB BB
0926   FL1   BB BB BC AA AA AA AA AB CC BB BB BB BB
0926   FL2   BB BB BD AA AA AA AA BB BB AB BB BB BB
0928   FJ1   AB BB DD AA AA AA AA BB BC BB BB BB BB
0928   FJ3   BB BB DD AA AA AA AA AB CC AB BB BB BB
0928   FJ4   BB BB BB AA AA AA AA AB BB AB BB BB BB
0928   FJ5   AA BB BB AA AA AA AA AA BB BB BB BB BC
0928   FK2   BB BB BB AA AA AA AA AB BC BB BB BB BB
0928   FK3   BB BB BD AA AA AA AA AB BC AA BB BB BB
0928   FK5   AB BB BB AA AA AA AA BB BB AB BB BB BB
0928   S01   BB BB BD AA AA AA AA BB BC AB BB BB BB
0928   S02   AB BB BD AA AA AA AA AB BB AB BB BB BC
0928   S03   BB BB BB AA AA AA AA BB BC AB BB BB BB
0928   S04   BB BB BD AA AA AA AA BB BC BB BB BB BB
0928   S05   AA BB BD AA AA AA AA BB CC AB BB BB BB
0928   S06   BB BB DD AA AA AA AA AB BB AB BB BB BB
0928   S07   AA BB BB AA AA AA AA BB CC AB BB BB BB
0928   S08   BB BB DD AA AA AA AA AB BC AB BB BB BB
0928   S09   AB BB BD AA AA AA AA AB BC AB BB BB BB
0928   S10   AA BB BD AA AA AA AA BB BC AB BB BB BC
0927   FK2   BB BB CC AA AA AA AA BB BB AA BB BB BB
0927   FK4   BB BB BB AA AA AA AA AB BC BB BB BB BB
```

0927	S01	AB	BB	BB	AA	AA	AA	AA	BB	BC	AA	CC	BB	BB
0927	S02	AB	BB	CC	AA	AA	AA	AA	AB	BC	AB	BB	BB	BB
0927	S03	AB	BB	BB	AA	AA	AA	AA	BB	BC	AB	BB	BB	BB
0927	S04	BB	BB	BC	AA	AA	AA	AA	BB	CC	BB	BC	BB	BB
0920	FJ1	BB	BB	BD	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0920	FJ3	BB	BB	CD	AA	AA	AA	AA	AA	CC	BB	BB	BB	BC
0920	FK4	BB	BB	BD	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
0920	FK5	BB	BB	DD	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
0925	FK2	AB	BB	CD	AA	AA	AA	AA	BB	CC	AA	BB	BB	BB
0925	FK3	AB	BB	DD	AA	AA	AA	AA	AB	CC	AB	BB	BB	BB
0929	FK2	BB	BB	CC	AA	AA	AA	AA	AB	BC	AB	BB	BB	BB
0929	FK3	BB	BB	BB	AA	AA	AA	AA	AB	CC	AB	BB	BB	BB
0929	FK4	BB	BB	BC	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0929	FK5	BB	BB	BB	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
0930	FK1	BB	BB	DD	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
0930	FK2	BB	BB	DD	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0930	FK3	BB	BB	DD	AA	AA	AA	AA	AA	CC	AB	BB	BB	BB
0930	FK4	BB	BB	BD	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
0930	FK5	BB	BB	DD	AA	AA	AA	AA	AB	BC	AB	BB	BB	BB
0930	S01	BB	BB	DD	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
0930	S02	BB	BB	BD	AA	AA	AA	AA	AB	CC	AB	BB	BB	BB
0930	S03	BB	BB	DD	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
0930	S04	BB	BB	DD	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0930	S05	BB	BB	DD	AA	AA	AA	AA	AA	BC	BB	BB	BB	BB
0930	S06	BB	BB	BD	AA	AA	AA	AA	AA	BC	AB	BB	BB	BB
0930	S07	BB	BB	DD	AA	AA	AA	AA	AB	CC	AB	BB	BB	BB
0930	S08	BB	BB	DD	AA	AA	AA	AA	AA	BC	AB	BB	BB	BB
0930	S09	BB	BB	BD	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0930	S10	BB	BB	DD	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0930	S11	BB	BB	DD	AA	AA	AA	AA	AA	CC	BB	BB	BB	BB
0930	S12	BB	BB	BD	AA	AA	AA	AA	BB	CC	AB	BB	BB	BB
0930	S13	BB	BB	DD	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
0930	S14	BB	BB	BD	AA	AA	AA	AA	BB	CC	BB	BB	BB	BB
0930	S15	BB	BB	DD	AA	AA	AA	AA	AB	BC	AB	BB	BB	BB
HVEN														
1006	S01	AB	BB	BC	AA	AA	AA	AA	AA	BC	BB	BB	BB	BB
1006	S02	AA	BB	BB	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
1006	S03	AB	BB	BC	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
1006	S04	AA	BB	BB	AA	AA	AA	AA	AA	BC	BB	BB	BB	BB
1006	S05	AB	BB	BB	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
1006	S06	AA	BB	BB	AA	AA	AA	AA	AB	BC	BB	BB	BB	BB
1006	S07	AA	BB	BB	AA	AA	AA	AA	AA	BC	BB	BB	BB	BB
1006	S08	AA	BB	BB	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB
1006	S09	AA	BB	BC	AA	AA	AA	AA	AA	CC	BB	BB	BB	BB
1006	S10	AB	BB	BC	AA	AA	AA	AA	AB	CC	BB	BB	BB	BB
1006	S11	AB	BB	BB	AA	AA	AA	AA	BB	BC	BB	BB	BB	BB

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1006   S12   AB BB BC AA AA AA AA AB BC BB BB BB BB
1006   S13   AA BB BB AA AA AA AA BB CC BB BB BB BB
1006   S14   AB BB BC AA AA AA AA AB BC BB BB BB BB
1006   S15   AB BB BB AA AA AA AA AA CC BB BB BB BB
1006   S16   AB BB BB AA AA AA AA AB CC BB BB BB BB
1006   S17   AA BB BC AA AA AA AA AB CC BB BB BB BB
1006   S18   AB BB BB AA AA AA AA AB CC BB BB BB BB
1006   S19   AA BB BC AA AA AA AA BB CC BB BB BB BB
1006   S20   AB BB BC AA AA AA AA AB BC BB BB BB BB
1008   S01   AB BB BC AA AA AA AA AB CC BB BB BB BB
1008   S02   AB BB BC AA AA AA AA AB CC BB BB BB BB
1008   S03   AA BB CC AA AA AA AA AB CC BB BB BB BB
1008   S04   AA BB BC AA AA AA AA AB CC BB BB BB BB
1008   S05   AA BB CC AA AA AA AA AB CC BB BB BB BB
1008   S06   AA BB BC AA AA AA AA AB CC BB BB BB BB
1008   S07   AB BB BC AA AA AA AA AB CC BB BB BB BB
1008   S08   AB BB CC AA AA AA AA AB CC BB BB BB BB
1008   S09   AB BB BC AA AA AA AA AB CC BB BB BB BB
1008   S10   AB BB BC AA AA AA AA AA CC BB BB BB BB
1008   S11   BB BB BC AA AA AA AA AA CC BB BB BB BB
1008   S12   AB BB CC AA AA AA AA AA CC BB BB BB BB
1008   S13   BB BB BC AA AA AA AA AA CC BB BB BB BB
WYUC
0808   S01   BB BB BB AA AA AA AA AB BB BB BB BB BB
0808   S02   BB BB BC AA AA AA AA AB BB BB BB BB BB
0812   S01   BB BB BB AA AA AA AA BB CC BB BB AB BB
0812   S02   AB BB BB AA AA AA AA BB CC BB BB AB BB
0812   S03   AB BB BB AA AA AA AA BB CC BB BB AB BB
0813   FK2   BB BB BB AA AA AA AA AB AC BB BB AB BB
0813   FK4   BB BB BB AA AA AA AA AA CC BB AB AB BB
0813   FK5   BB BB BB AA AA AA AA AA BC BB AB AB BB
WSAN
0827   FK4   BB BB BB AA AA AA AA AB CC BB AC BB BB
0827   FK1   BB BB BB AA AA AA AA AB CC BB AC BB BB
0828   FJ2   BB BB BB AA AA AA AA AA BB BB AB BB BB
0828   FJ4   BB BB BB AA AA AA AA AA BC BB AC BB BB
0828   FJ5   BB BB BB AA AA AA AA AB BB BB AB BB BB
0829   FK1   BB BB BB AA AA AA AA AA AB BB AB BB BB
0829   FK3   BB BB BB AA AA AA AA AB AB BB BC BB BB
0829   FK4   BB BB BB AA AA AA AA AB AB BB BB BB BB
0829   FK5   BB BB BB AA AA AA AA AB AB BB AA BB BB
0830   FK2   BB BB BB AA AA AA AA AB CC BB BB AB BB
0830   FK3   BB BB BB AA AA AA AA AA CC BB AB BB BB
0830   FK4   BB BB BB AA AA AA AA AB BC BB BB BB BB
0830   FK5   BB BB BB AA AA AA AA AB BC BB BB BB BB
0830   FK1   BB BB BB AA AA AA AA BB CC BB BB BB BB
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0835   FK1   AB BB BB AA AA AA AA BB CC BB BC BB BB
0835   FK2   BB BB BB AA AA AA AA BB CC BB AC BB BB
0835   FK3   BB BB BB AA AA AA AA BB AC BB BC BB BB
0835   FK5   BB BB BB AA AA AA AA AB CC BB BB BB BB
0836   FK1   BB BB BC AA AA AA AA BB CC BB AC BB BB
0836   FK2   BB BB BB AA AA AA AA AB CC BB BB BB BB
0836   FK3   BB BB BC AA AA AA AA AB AC BB BB BB BB
0836   FK4   BB BB BB AA AA AA AA AA CC BB BC BB BB
0836   FK5   BB BB BB AA AA AA AA AB AC BB BC AB BB
0836   FL6   BB BB BB AA AA AA AA BB CC BB AB BB BB
0837   FK2   BB BB BB AA AA AA AA AA CC BB BC AB BB
0837   FK3   BB BB BB AA AA AA AA AA CC BB BC AB BB
0837   FK4   BB BB BB AA AA AA AA AA CC BB CC AB BB
0837   FK5   BB BB BB AA AA AA AA AA CC BB BC BB BB
NEXT
GUA    WPET
0842   FK1   BB BB BB AA AA AA AA BB AA BB AC BB BB
0842   FK2   BB BB BB AA AA AA AA AA CC BB BC BB BB
0842   FK3   BB BB BB AA AA AA AA AB CC BB AB BB BB
0842   FK4   BB BB BB AA AA AA AA BB AA BB AC AB BB
0842   FK5   BB BB BB AA AA AA AA AB AC BB AA BB BB
0843   FL2   BB BB BB AA AA AA AA AB AC BB AB BB BB
0843   FL3   BB BB BB AA AA AA AA BB AA BB BB BB BB
0843   FL4   BB BB BB AA AA AA AA AA AC BB AB BB BB
0843   FL5   BB BB BB AA AA AA AA AB AC BB AB BB BB
0843   FL8   BB BB BB AA AA AA AA BB BC BB AB BB BB
0848   FJ1   BB BB BC AA AA AA AA AB AA BB BB BB BB
0848   FJ2   BB BB BB AA AA AA AA AB AC BB BB BB BB
0848   FJ3   BB BB BB AA AA AA AA BB CC BB BB AB BB
0852   FK1   BB BB BB AA AA AA AA AB AC BB BC BB BB
0852   FK2   BB BB BB AA AA AA AA AB AC BB AA BB BB
0852   FK3   BB BB BB AA AA AA AA AB CC BB AC BB BB
0852   FK5   BB BB BB AA AA AA AA AB AC BB CC BB BB
0853   FL1   BB BB BB AA AA AA AA BB CC BB AB BB BB
0854   FK1   BB BB BB AA AA AA AA AB BB BB BB BB BB
0854   FK2   BB BB BB AA AA AA AA AB BB BB BB BB BB
0854   FK4   BB BB BB AA AA AA AA AB AC BB BB BB BB
0854   FK5   BB BB BB AA AA AA AA AB BB BB BB BB BB
0855   FK1   BB BB BB AA AA AA AA AB AA BB BB BB BB
0855   FK2   BB BB BB AA AA AA AA AB CC BB BB BB BB
0855   FK3   BB BB BB AA AA AA AA AB CC BB BB BB BB
0857   FL6   BB BB BB AA AA AA AA AB CC BB BC BB BB
0858   FL2   BB BB BB AA AA AA AA BB BB BB BB AB BB
0859   FK1   BB BB BB AA AA AA AA BB AC BB BB BB BB
0859   FK2   BB BB BB AA AA AA AA BB CC BB BB BB BB
0859   FK3   BB BB BB AA AA AA AA BB CC BB BB BB BB
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0859   FK4     BB BB BB AA AA AA AA BB CC BB AB BB BB
0859   FK5     BB BB BB AA AA AA AA AA CC BB BB BB BB
0860   FJ1     AB BB BB AA AA AA AA BB CC BB BC BB BB
0860   FJ3     AB BB BB AA AA AA AA BB CC BB BC BB BB
0860   FJ4     AB BB BB AA AA AA AA AB CC BC AB BB BB
0860   FJ5     BB BB BB AA AA AA AA AB CC BC AB BB BC
0861   FL2     AB BB BB AA AA AA AA AB CC BB BB BB BB
0861   FL3     AB BB BB AA AA AA AA AB BC BB BC BB BB
0861   FL4     BB BB BB AA AA AA AA BB CC BB BC BB BB
0861   FL5     AB BB BB AA AA AA AA AB BC BB BB AB BB
0861   FL6     BB BB BB AA AA AA AA BB CC BB BC AB BB
0862   FJ2     BB BB BB AA AA AA AA AA BC BB BB BB BB
0862   FJ3     BB BB BB AA AA AA AA AA BC BC BB BB BB
0862   FJ4     AB BB BB AA AA AA AA AA CC BB BB BB BC
0862   FJ5     AB BB BB AA AA AA AA AA CC BC AB BB BC
WRIO
0866   FJ1     BB BB BB AA AA AA AA AA CC BB BB BB BB
0866   FJ3     BB BB BB AA AA AA AA AA CC BB BB BB BB
0866   FJ4     BB BB BB AA AA AA AA AA CC BB BC BB BB
0866   FJ5     BB BB BB AA AA AA AA AB DD BB BB BB BB
0867   FJ1     AA BB BB AA AA AA AA AA CC BB BB BB BB
0867   FJ2     AB BB BB AA AA AA AA AA CC BB BB BB AB
0871   FL3     BB BB BB AA AA AA AA AA CC BB BB BB BB
```

APPENDIX E

LOCUSWISE GENOTYPE DATA FOR DIFFERENT *CARICA* SPECIES

```
PAPAYA 1       PGM1 PGM2 MDH1 MDH2 UGP1
0800   FJ1     EE  GG   BB   CC   DD
0800   S01     FF  GG   BB   CC   DD
0801   FJ1     EE  GG   BB   CC   DD
0801   FJ2     EE  GG   BB   CC   DD
0801   FJ5     FF  GG   BB   CC   DD
0804   FJ3     EE  GG   BB   CC   DD
0804   FJ4     EE  GG   BB   CC   DD
0804   S01     EE  GG   BB   CC   DD
0804   S02     EE  GG   BB   CC   DD
0804   S03     EE  GG   BB   CC   DD
0804   S04     EE  GG   BB   CC   DD
0804   S05     EE  GG   BB   CC   DD
0804   S06     EE  GG   BB   CC   DD
0804   S07     EE  GG   BB   CC   DD
0804   S08     EE  GG   BB   CC   DD
0804   S09     EE  GG   BB   CC   DD
0804   S10     EE  GG   BB   CC   DD
0804   S11     EE  GG   BB   CC   DD
0804   S12     EE  GG   BB   CC   DD
0804   S13     EE  GG   BB   CC   DD
0804   S14     EE  GG   BB   CC   DD
0804   S15     EE  GG   BB   CC   DD
0804   S16     EE  GG   BB   CC   DD
0804   S17     EE  GG   BB   CC   DD
0804   S18     EE  GG   BB   CC   DD
0804   S19     EE  GG   BB   CC   DD
0804   S20     EE  GG   BB   CC   DD
0804   S21     EE  GG   BB   CC   DD
0805   FJ1     FF  FG   BB   CC   DD
0805   FJ2     EE  GG   BB   CC   DD
0805   FJ3     EF  GG   BB   CC   DD
0805   FJ4     FF  FG   BB   CC   DD
0805   S01     EF  GG   BB   CC   DD
0805   S02     EF  FG   BB   CC   DD
0805   S03     FF  GG   BB   CC   DD
0805   S04     FF  FG   BB   CC   DD
0805   S05     EF  GG   BB   CC   DD
0805   S06     FF  FG   BB   CC   DD
0805   S07     EE  GG   BB   CC   DD
0825   FJ4     EF  GG   BB   CC   DD
0825   S01     EF  GG   BB   CC   DD
0825   S02     EF  GG   BB   CC   DD
0825   S03     EF  GG   BB   CC   DD
0825   S04     EF  GG   BB   CC   DD
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0825   S05   EF  GG  BB  CC  DD
0825   S06   EF  GG  BB  CC  DD
0825   S07   FF  GG  BB  CC  DD
0825   S08   EF  GG  BB  CC  DD
0825   S09   EF  GG  BB  CC  DD
0825   S10   FF  GG  BB  CC  DD
0825   S11   EF  GG  BB  CC  DD
0825   S12   EF  GG  BB  CC  DD
0825   S13   EF  GG  BB  CC  DD
0825   S14   EF  GG  BB  CC  DD
0825   S15   FF  GG  BB  CC  DD
0878   FK1   FF  GG  BB  CC  BB
0878   FK3   FF  GG  BB  CC  BB
0878   FK4   FF  GG  BB  CC  BB
0879   S01   FF  GG  BB  CC  DD
0879   S02   FF  GG  BB  CC  DD
0879   S03   FF  GG  BB  CC  DD
0879   S04   FF  GG  BB  CC  DD
0879   S05   FF  GG  BB  CC  DD
0879   S06   FF  GG  BB  CC  DD
0879   S07   FF  GG  BB  CC  DD
0879   S08   FF  GG  BB  CC  DD
0879   S09   FF  GG  BB  CC  DD
0879   S10   FF  GG  BB  CC  DD
0879   S11   FF  GG  BB  CC  DD
0879   S12   FF  GG  BB  CC  DD
0879   S13   FF  GG  BB  CC  DD
0879   S14   FF  GG  BB  CC  DD
0879   S15   FF  GG  BB  CC  DD
0879   S16   FF  GG  BB  CC  DD
0879   S17   FF  GG  BB  CC  DD
0879   S18   FF  GG  BB  CC  DD
0879   S19   FF  GG  BB  CC  DD
0880   FJ1   FF  GG  BB  CC  DD
0880   FJ3   FF  GG  BB  CC  DD
0880   FK4   EF  GG  BB  CC  DD
0880   FK5   FF  GG  BB  CC  DD
0880   FK2   EF  GG  BB  CC  DD
0882   S01   FF  GG  BB  CC  DD
0882   S02   FF  GG  BB  CC  DD
0882   S03   FF  GG  BB  CC  DD
0882   S04   FF  GG  BB  CC  DD
0882   S05   FF  FG  BB  CC  DD
0882   S06   FF  GG  BB  CC  DD
0882   S07   FF  GG  BB  CC  DD
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0882    S08     FF  GG  BB  CC  DD
0882    S09     FF  GG  BB  CC  DD
0883    FJ1     EE  GG  BB  CC  DD
0883    FJ2     EF  FG  BB  CC  DD
0883    FJ3     EF  GG  BB  CC  DD
0883    FJ4     EE  GG  BB  CC  DD
0883    FJ5     EF  FG  **BB**  CC  DD
0884    FK1     EE  GG  BB  CC  DD
0884    FK5     EE  GG  BB  CC  DD
0885    FL1     EE  GG  BB  CC  DD
0886    FJ4     EF  FG  BB  CC  DD
0886    FJ3     EF  FG  BB  CC  DD
0891    FK2     EE  GG  BB  CC  DD
0891    FK4     EE  GG  BB  CC  DD
0892    FK2     FF  GG  BB  CC  DD
0892    FK5     FF  GG  BB  CC  DD
0894    FK3     FF  GG  BB  CC  DD
0894    FK4     FF  GG  BB  CC  DD
0894    FK5     FF  GG  BB  CC  DD
0895    FK1     EE  GG  BB  CC  DD
0895    FK2     EE  GG  BB  CC  DD
0895    FK3     EE  GG  BB  CC  DD
0896    FK1     EF  GG  BB  CC  DD
0896    FK3     EF  FF  BB  CC  DD
0896    FK4     EF  FG  BB  CC  DD
0896    FK5     FF  FF  BB  CC  DD
0897    FK1     EE  FG  BB  CC  DD
0897    FK2     EE  GG  BB  CC  DD
0897    FK3     EF  GG  BB  CC  DD
0897    FK4     EE  FG  BB  CC  DD
0897    FK5     EE  GG  BB  CC  DD
0899    FK1     EF  GG  BB  CC  DD
0899    FK2     EF  GG  BB  CC  DD
0899    FK4     FF  GG  BB  CC  DD
0899    FK5     EF  GG  BB  CC  DD
0902    FK1     FF  FF  BB  CC  DD
0902    FK2     FF  FF  BB  CC  DD
0902    FK3     FF  FF  BB  CC  DD
0902    FK4     FF  FF  BB  CC  DD
0902    FK5     FF  FF  BB  CC  DD
0903    FK1     FF  GG  BB  CC  DD
0903    FK2     FF  GG  BB  CC  DD
0903    FK3     FF  GG  BB  CC  DD
0903    S01     FF  GG  BB  CC  DD
0903    S02     FF  GG  BB  CC  DD
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0903   S03    FF  GG  BB  CC  DD
0904   FK2    EF  GG  BB  CC  DD
0904   FK3    EF  GG  BB  CC  DD
0904   FK5    EF  GG  BB  CC  DD
0910   FK1    FF  GG  BB  CC  DD
0910   FK2    FF  GG  BB  CC  DD
0910   FK3    FF  GG  BB  CC  DD
0910   FK4    FF  GG  BB  CC  DD
0910   FK5    FF  GG  BB  CC  DD
0806   FJ1    FF  GG  BB  CC  DD
0806   FJ2    FF  GG  BB  CC  DD
0806   FJ4    FF  GG  BB  CC  DD
0806   S01    FF  GG  BB  CC  DD
0806   S02    FF  GG  BB  CC  DD
0806   S03    FF  GG  BB  CC  DD
0806   S04    FF  GG  BB  CC  DD
0826   FJ4    FF  GG  BB  CC  DD
0826   FJ5    EE  GG  BB  CC  DD
0832   FK5    EF  GG  BB  CC  DD
0832   FK1    EF  GG  BB  CC  DD
0832   FK2    EF  GG  BB  CC  DD
0832   FK3    EF  GG  BB  CC  DD
0832   FK4    FF  GG  BB  CC  DD
0832   S01    FF  GG  BB  CC  DD
0832   S02    EF  GG  BB  CC  DD
0832   S03    EF  GG  BB  CC  DD
0832   S04    EF  GG  BB  CC  DD
0832   S05    EF  GG  BB  CC  DD
0832   S06    EF  GG  BB  CC  DD
0832   S07    EF  GG  BB  CC  DD
0832   S08    FF  GG  BB  CC  DD
0832   S09    EF  GG  BB  CC  DD
0832   S10    EF  GG  BB  CC  DD
0832   S11    FF  GG  BB  CC  DD
0832   S12    FF  GG  BB  CC  DD
0832   S13    EF  GG  BB  CC  DD
0832   S14    FF  GG  BB  CC  DD
0832   S15    FF  GG  BB  CC  DD
0849   FK1    FF  GG  BB  CC  DD
0849   FK2    FF  GG  BB  CC  DD
0849   FK4    FF  GG  BB  CC  DD
0849   FK5    FF  GG  BB  CC  DD
0849   S01    FF  GG  BB  CC  DD
0849   S02    FF  GG  BB  CC  DD
0849   S03    FF  GG  BB  CC  DD
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0849    S04    FF GG BB CC DD
0849    S05    FF GG BB CC DD
0849    S06    FF GG BB CC DD
0849    S07    FF GG BB CC DD
0849    S08    FF GG BB CC DD
0849    S09    FF GG BB CC DD
0849    S10    FF GG BB CC DD
0849    S11    FF GG BB CC DD
0849    S12    FF GG BB CC DD
0849    S13    FF GG BB CC DD
0849    S14    FF GG BB CC DD
0849    S15    FF GG BB CC DD
0849    S16    EF GG BB CC DD
0849    S17    FF GG BB CC DD
0849    S18    FF GG BB CC DD
0849    S19    FF GG BB CC DD
0849    S20    FF GG BB CC DD
0849    S21    FF GG BB CC DD
0851    FK1    FF GG BB CC DD
0851    FK2    FF GG BB CC DD
0851    FK5    FF GG BB CC DD
0851    S01    FF GG BB CC DD
0851    S02    FF GG BB CC DD
0851    S03    FF GG BB CC DD
0851    S04    FF GG BB CC DD
0851    S05    FF GG BB CC DD
0851    S06    FF GG BB CC DD
0851    S07    FF GG BB CC DD
0851    S08    FF GG BB CC DD
0851    S09    FF GG BB CC DD
0851    S10    FF GG BB CC DD
0851    S11    FF GG BB CC DD
0851    S12    FF GG BB CC DD
0851    S13    FF GG BB CC DD
0851    S14    FF GG BB CC DD
0851    S15    FF GG BB CC DD
0851    S16    FF GG BB CC DD
0851    S17    FF GG BB CC DD
0851    S18    FF GG BB CC DD
0851    S19    FF GG BB CC DD
0851    S20    FF GG BB CC DD
0851    S21    FF GG BB CC DD
0851    S22    FF GG BB CC DD
0863    FK1    FF GG BB CC DE
0863    FK2    FF GG BB CC DD
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0863    FK3    FF  GG  BB  CC  DE
0863    FK5    FF  GG  BB  CC  DD
0864    FK1    FF  GG  BB  CC  DD
0864    FK2    FF  GG  BB  CC  DD
0864    FK3    FF  GG  BB  CC  DD
0864    FK4    FF  GG  BB  CC  DD
0864    FK5    FF  GG  BB  CC  DD
0865    FL1    FF  GG  BB  CC  DD
0869    FK1    FF  GG  BB  CC  DD
0869    FK3    FF  GG  BB  CC  DD
0869    FK4    FF  GG  BB  CC  DD
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0928   FJ5   EE GG BB CC DD
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0928   FK5   EF GG BB CC BD
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0928   S02   EF GG BB CC BD
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0927   FK4   FF GG BB CC DD
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0927   S04   FF GG BB CC DD
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0858   FL2    FF  GG  BB  CC  DD
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0859   FK3    FF  GG  BB  CC  DD
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0860   FJ3    EF  GG  BB  CC  DD
0860   FJ4    EF  GG  BB  CC  DE
0860   FJ5    FF  GG  BB  CC  DE
0861   FL2    EF  GG  BB  CC  DD
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0861   FL4    FF GG BB CC DD
0861   FL5    EF GG BB CC DD
0861   FL6    FF GG BB CC DD
0862   FJ2    FF GG BB CC DD
0862   FJ3    FF GG BB CC DE
0862   FJ4    EF GG BB CC DD
0862   FJ5    EF GG BB CC DE
0866   FJ1    FF GG BB CC DD
0866   FJ3    FF GG BB CC DD
0866   FJ4    FF GG BB CC DD
0866   FJ5    FF GG BB CC DD
0867   FJ1    EE GG BB CC DD
0867   FJ2    EF GG BB CC DD
0871   FL3    FF GG BB CC DD
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1016   S02    AA EE AA CC CC
1016   S03    AE EE AA CC CC
1016   S04    AA EE AA CC CC
1016   S05    AE EE AA CC CC
1016   S06    AE EE AA CC CC
1016   S07    AE EE AA CC CC
1016   S08    AE EE AA CC CC
1016   S09    AE EE AA CC CC
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1021   S01    AA EE AA CC CC
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1022   S02    AA EE AA CC CC
1022   S03    AA EE AA CC CC
```

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1025   S23     AE EE AA CC CC
1025   S24     AA EE AA CC CC
1025   S25     AA EE AA CC CC
```

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1025   S30    AE  EE  AA  CC  CC
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1026   S02    AA  EE  AA  CC  CC
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1026   S11    AA  EE  AA  CC  CC
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1034   S13     AA  EE  AA  CC  CC
1034   S14     AA  EE  AA  CC  CC
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1036    S13    AA  EE  AA  CC  CC
1036    S14    AA  EE  AA  CC  CC
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1037   S19    AA EE AA CC CC
1037   S20    AA EE AA CC CC
1037   S21    AA EE AA CC CC
1037   S22    AA EE AA CC CC
1037   S23    AA EE AA CC CC
1037   S24    AA EE AA CC CC
1057   S01    AA EE AA CC CC
1057   S02    AA EE AA CC CC
1057   S03    AA EE AA CC CC
1057   S04    AA EE AA CC CC
1057   S05    AA EE AA CC CC
1057   S06    AA EE AA CC CC
1057   S07    AA EE AA CC CC
1057   S08    AA EE AA CC CC
NEXT
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QUERCIFOLIA 3
H226   Q01    AA EE AA BB CC
H226   Q02    AA EE AA BB CC
H226   Q03    AA EE AA BB CC
H226   Q04    AA EE AA BB CC
H226   Q05    AA EE AA BB CC
H226   Q21    AA EE AA BB CC
H226   Q22    AA EE AA BB CC
H226   Q23    AA EE AA BB CC
H226   Q24    AA EE AA BB CC
H226   Q31    AA EF AA BB CC
H226   Q32    AA EF AA BB CC
H226   Q41    AA EF AA BB CC
H226   Q42    AA EF AA BB CC
NEXT
PUBESCENS 4
1063   S01    EE EE AA CC CD
1063   S02    EE EE AA CC CD
1063   S03    EE EE AA CC CD
1063   S04    EE EE AA CC CD
1063   S05    EE EE AA CC CD
1063   S06    EE EE AA CC CD
1063   S07    EE EE AA CC CD
1063   S08    EE EE AA CC CD
1063   S09    EE EE AA CC CD
1063   S10    EE EE AA CC CD
1063   S11    EE EE AA CC CD
1063   S12    EE EE AA CC CD
1063   S13    EE EE AA CC CD
1063   S14    EE EE AA CC CD
1066   S15    EE EE AA CC CD
1066   S16    EE EE AA CC CD
1066   S17    EE EE AA CC CD
1066   S18    EE EE AA CC CD
1066   S19    EE EE AA CC CD
1066   S20    EE EE AA CC CD
1066   S21    EE EE AA CC CD
1066   S22    EE EE AA CC CD
1066   S23    EE EE AA CC CD
1066   S24    EE EE AA CC CD
1066   S25    EE EE AA CC CD
1020   S01    EE EE AA CC CC
1020   S02    EE EE AA CC CC
1020   S03    EE EE AA CC CC
1020   S04    EE EE AA CC CC
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1020    S05     EE  EE  AA  CC  CC
1020    S06     EE  EE  AA  CC  CC
1062    S07     EE  EE  AA  CC  CD
1062    S08     EE  EE  AA  CC  DD
1062    S09     EE  EE  AA  CC  CD
1062    S10     EE  EE  AA  CC  CD
1062    S11     EE  EE  AA  CC  CD
1062    S12     EE  EE  AA  CC  DD
1062    S13     EE  EE  AA  CC  DD
1062    S14     EE  EE  AA  CC  CD
1065    S15     EE  EE  AA  CC  CD
1065    S16     EE  EE  AA  CC  CD
1065    S17     EE  EE  AA  CC  CD
1065    S18     EE  EE  AA  CC  DD
1065    S19     EE  EE  AA  CC  CC
NEXT
SPHAEROCARPA 5
1054    S01     EE  AA  AA  CC  CE
1054    S02     EE  AA  AA  CC  BC
1054    S03     EE  AA  AA  CC  CE
1054    S04     EE  AA  AA  CC  CE
1054    S05     EE  AA  AA  CC  CE
1054    S06     EE  AA  AA  CC  CC
1054    S07     EE  AA  AA  CC  CE
1054    S08     EE  AA  AA  CC  CC
1054    S09     EE  AA  AA  CC  CE
1054    S10     EE  AA  AA  CC  CE
1054    S13     EE  AA  AA  CC  CC
1054    S14     EE  AA  AA  CC  CE
1054    S15     EE  AA  AA  CC  CE
1054    S16     EE  AA  AA  CC  CE
1054    S17     EE  AA  AA  CC  EE
1054    S18     EE  AA  AA  CC  CE
1054    S19     EE  AA  AA  CC  CE
1054    S20     EE  AA  AA  CC  CE
1054    S21     EE  AA  AA  CC  CE
1054    S22     EE  AA  AA  CC  CC
1054    S25     EE  AA  AA  CC  CC
1054    S26     EE  AA  AA  CC  CC
1054    S27     EE  AA  AA  CC  CC
1054    S28     EE  AA  AA  CC  CC
1054    S29     EE  AA  AA  CC  CE
1054    S30     EE  AA  AA  CC  CE
1054    S31     EE  AA  AA  CC  CC
1054    S32     EE  AA  AA  CC  CC
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1054    S33     EE AA AA CC CE
1054    S34     EE AA AA CC CE
1055    S01     EE AB AA CC CC
1055    S02     EE AA AA CC CC
1055    S03     EE AB AA CC CE
1055    S04     EE AB AA CC CE
1055    S05     EE AA AA CC CC
1055    S06     EE AA AA CC CC
1055    S07     EE AB AA CC CC
1055    S08     EE AB AA CC CC
1055    S09     EE AA AA CC CC
1055    S10     EE AB AA CC CC
1055    S11     EE AA AA CC CC
1055    S12     EE AA AA CC CC
1055    S13     EE AB AA CC CC
1055    S14     EE AA AA CC CC
1055    S15     EE AB AA CC CC
1055    S16     EE AB AA CC CC
1055    S17     EE AA AA CC CC
1055    S18     EE AA AA CC CC
1055    S19     EE AA AA CC CE
1055    S20     EE AA AA CC CC
1055    S21     EE AB AA CC CC
NEXT
CRASSIPETALA 6
1018    S01     CC CC AA AA AC
1018    S02     CC CC AA AA AC
1018    S03     CC CC AA AA AC
1018    S04     CC CC AA AA AC
1018    S05     CC CC AA AA AA
1018    S06     CC CC AA AA AC
1018    S07     CC CC AA AA AC
1018    S08     CC BC AA AA CC
1018    S09     CC CC AA AA AC
1018    S10     CC BC AA AA AC
1018    S13     CC CC AA AA AC
1018    S14     CC CC AA AA AC
1018    S15     CC CC AA AA AC
1018    S16     CC CC AA AA AC
1018    S17     CC CC AA AA AC
1018    S18     CC BC AA AA AC
1018    S19     CC CC AA AA AC
1018    S20     CC CC AA AA AC
1018    S21     CC CC AA AA AA
1018    S22     CC CC AA AA AA
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1018    S25     CC CC AA AA AC
1018    S26     CC CC AA AA AA
1018    S27     CC CC AA AA AA
1018    S28     CC BC AA AA AC
1018    S29     CC CC AA AA AC
1018    S30     CC CC AA AA AA
1018    S31     CC BC AA AA CC
1018    S32     CC BC AA AA AC
1018    S33     CC CC AA AA AA
1018    S34     CC CC AA AA AC
NEXT
CAULIFLORA 7
1124    S01     AA CC AA CC CC
1124    S02     AA CC AA CC CC
1007    S03     AA CC AA CC CC
1007    S04     AA CC AA CC CC
1007    S05     AA CC AA CC CC
1007    S06     AA CC AA CC CC
1007    S07     AA CC AA CC CC
1007    S08     AA CC AA CC CC
1007    S09     AA CC AA CC CC
1007    S10     AA CC AA CC CC
1007    S11     AA CC AA CC CC
1007    S12     AA CC AA CC CC
1007    S13     AA CC AA CC CC
1007    S14     AA CC AA CC CC
1007    S15     AA CC AA CC CC
1015    S27     AA DD AA CC CC
1015    S28     AA CC AA CC CC
1015    S29     AA CC AA CC CC
1015    S30     AA CC AA CC CC
1015    S31     AA CC AA CC CC
1015    S32     AA CC AA CC CC
1121    S26     AA CC AA CC CC
NEXT
MICROCARPA M1 8
1069    S01     EE DD AA CC CC
1069    S02     EE EE AA CC CD
1069    S03     EE DD AA CC CD
1069    S04     EE DD AA CC CC
1069    S05     EE DE AA CC CC
1069    S06     EE DE AA CC BC
1069    S07     EE DE AA CC CC
1069    S08     EE DF AA CC CC
1069    S09     EE DD AA CC CC
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1069   S10     EE EE AA CC BC
1069   S13     EE DD AA CC CC
1069   S14     EE DF AA CC CC
1069   S15     EE DD AA CC CC
1069   S16     EE DE AA CC CC
1069   S17     EE DE AA CC CC
1069   S18     EE DE AA CC CC
1069   S19     EE DD AA CC CC
1069   S20     EE DD AA CC BC
1069   S21     EE DE AA CC BC
1069   S22     EE DE AA CC BC
1069   S25     EE DD AA CC CC
1069   S26     EE DD AA CC CC
1069   S27     EE DF AA CC CC
1069   S28     EE DF AA CC CC
1069   S29     EE EF AA CC CC
1069   S30     EE DF AA CC CC
1069   S31     EE DE AA CC CC
1069   S32     EE DE AA CC BC
1069   S33     EE DE AA CC BC
1069   S34     EE DE AA CC CC
NEXT
MICROCARPA M2 9
1009   S09     EE CC AA CC CC
1009   S10     EE CC AA CC CC
1009   S11     EE CC AA CC CC
1009   S12     EE CC AA CC CC
1009   S13     EE CC AA CC CC
1009   S14     EE CC AA CC CC
1009   S15     EE CC AA CC CC
1009   S19     EE CC AA CC CC
1009   S20     EE CC AA CC CC
1009   S21     EE CC AA CC CC
1009   S22     EE CC AA CC CC
1009   S23     EE CC AA CC CC
1009   S24     EE CC AA CC CC
1009   S25     EE CC AA CC CC
1009   S26     EE CC AA CC CC
1009   S27     EE CC AA CC CC
1009   S28     EE CC AA CC CC
1009   S29     EE CC AA CC CC
1009   S30     EE CC AA CC CC
NEXT
MICROCARPA B 10
1072   S01     EE CE AA CC AC
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1072    S02     EE CE AA CC CC
1072    S03     EE CC AA CC CC
1072    S04     EE CE AA CC AC
1072    S05     EE CE AA CC CC
1072    S06     EE CE AA CC CC
1072    S07     EE CC AA CC CD
1072    S08     EE EE AA CC CD
NEXT
MICROCARPA H 11
1100    S01     EE CD AA CC CC
NEXT
MICROCARPA SSP(?) 12
1118    S00     EE CC AA CC CC
NEXT
GLANDULOSA 13
9424    G01     CC CC AA CC CC
9424    G02     CC CC AA CC CC
9424    G03     CC CC AA CC CC
9424    G04     CC CC AA CC CC
NEXT
PARVIFLORA 14
H179    P01     DD EE AA CC CC
H179    P02     BD EE AA CC CC
NEXT
MONOICA 15
1129    S01     EE FF AA CC CC
1129    S03     EE FF AA CC CC
1129    S04     EE FF AA CC CC
1129    S05     EE FF AA CC CC
1129    S06     EE FF AA CC CC
NEXT
STIPULATA 16
STIP    S01     EE DD AA CC CC
NEXT
HEILBORNII 17
1117    S0B     EE DD AA CC CC
1103    S0D     BE AD AA CC CC
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BIBLIOGRAPHY

Acquaah, G. 1992. *Practical protein electrophoresis for genetic research.* Dioscorides Press. Portland, Oregon.

Aguado, P. de. 1919. *Historia de Venezuela.* Prologo, notas y apendices de Jeronimo Becker. Tomo II. Real Academia de la Historia. Madrid.

Alcedo, A. de. 1967(a). *Diccionario geografico de las Indias Occidentales O America.* I Bibiloteca de Autores Españoles. Madrid.

Alcedo, A. de. 1967(b). *Diccionario geografico de las Indias Occidentales O America.* III Bibiloteca de Autores Espanoles. Madrid.

Alcorn, J.B. 1984. *Huastec Mayan ethnobotany.* University of Texas Press. Austin, Texas.

Allard, R.W. 1988. Genetic changes associated with the evolution of adaptedness in cultivated plants and their wild progenitors. *Journal of Heredity*, 79:225-238.

Allard, R.W. 1992. Predictive methods for germplasm identification. In: H.T. Stalker and J.P. Murphy (eds.), *Plant breeding in the 1990s*, pp: 119-146. CAB International. Wallingford, United Kingdom.

Allard, R.W., G.R. Babbel, M.T. Clegg and A.L. Kahler. 1972. Evidence for coadaptation in *Avena barbata*. *Proceedings of the National Academy of Sciences*, USA, 69:3043-3048.

Anderson, E. 1954. *Plants, man and life*. A. Melrose. London.

Arulsekar, S. and Parfitt, D.E. 1986. Isozyme analysis procedures for stone fruits, almonds, grape, walnut, pistachio, and fig. *Hortscience*, 21:928-933.

Badillo, V. 1971. *Monografia de la familia Caricaceae*. Maracay, Venezuela.

Becker, S. 1958. The production of papain-- an agricultural industry for tropical America. *Economic Botany*, 12:62-79.

Bliss, F.A. 1990. Utilization of genetic resources for crop improvement: the common bean. In: Brown, A.H.D., M.T. Clegg, A.L. Kahler and B.S.Weir (eds.), *Plant Population Genetics, Breeding, and Genetic Resources*, pp: 317-333. Sinauer Associates. Sunderland, Massachusetts.

Bousquet, J., Cheliak, W.M., and Lalonde, M. 1987. Allozyme variability in natural populations of green alder (*Alnus crispa*) in Quebec. *Genome*, 29:345-352.

Broschat, T.K. 1974. Principal component analysis in horticultural research. *Hortscience*, 14(2):114-117.

Brown, A.H.D. and B.S. Weir. 1983. Measuring genetic variability in plant populations. In: S.D. Tanksley and T.J. Orton (eds.), *Isozymes in plant genetics and breeding*, Part A, pp: 219-239. Elsevier, Amsterdam.

Brown, A.H.D., M.T. Clegg, A.L. Kahler, B.S. Weir (eds.). 1990. *Plant Population Genetics, Breeding, and Genetic Resources*. Sinauer Associates. Sunderland, Massachusetts.

Brucher, H. 1989. *Useful plants of Neotropical origin and their wild relatives*. Springer-Verlag, Berlin.

Campbell, C.W. 1986. Tropical fruit crops in Florida– a rapidly changing situation. *Proceedings of the Florida Horticultural Society*, 99:217-219.

Candolle, A. de 1908. *Origin of cultivated plants*. D. Appleton & Company. New York.

Cardy, B.J., Stuber, C.W., Wendel, J.F. and Goodman, M.M. 1983. *Techniques for starch gel electrophoresis from Maize (Zea mays L.).* Mimeograph Series No. 1317, Institute of Statistics, North Carolina State University-Raleigh. Raleigh.

Chapman, A.C. 1957. Port of trade enclaves in Aztec and Maya civilizations. In: Karl Polanyi, Conrad M. Arensberg, and Harry W. Pearson (eds.), *Trade and market in the early empires,* pp: 114-153. Free Press and Falcon's Wing Press. Glencoe, Illinois.

Chia, C.L., D.O. Evans, K.G. Rohrbach, N.P. Kefford. 1990. *Papaya Industry Analysis No.5.* CTAHR, University of Hawaii at Manoa. Honolulu.

Cobley, L.S. 1956. *An introduction to the botany of tropical crops.* Longmans, Green and Company. London.

Conover, R.A., R.E. Litz, and S.E. Malo. 1986. 'Cariflora'– a papaya ringspot virus-tolerant papaya for South Florida and the Caribbean. *Hortscience*, 21:1072.

Corney, B.G. 1913. *The quest and occupation of Tahiti by emissaries of Spain during the years 1772-1776.* Series 2, No. 32. Hakluyt Society. London.

Crane, P.R. 1987. Vegetational consequences of the angiosperm diversification. In: Else Marie Friis, William G. Chaloner, and Peter R. Crane (eds.), *The origin of angiosperms and their biological consequences*, pp: 107-144. Cambridge University Press. Cambridge.

Crawford, D.J. 1990. *Plant molecular systematics*. John Wiley and Sons. New York.

Crumpacker, D.W. 1964. Genetic loads in *Zea mays* L. and other cross-fertilized plants and animals. *Evolutionary Biology*, 1:306-324.

Cummins, J.S. 1962. *The travels and controversies of Friar Domingo Navarrete 1618-1686*. Volume 1. Series 2. Hakluyt Society. London.

Darlington, C.D. and E.K.J. Ammal. 1945. *Chromosome atlas of cultivated plants*. George Allen and Unwin. London.

Davis, T. and R.A. Bye, Jr. 1982. Ethnobotany and progressive domestication of *Jaltomata* (Solanaceae) in Mexico and Central America. *Economic botany*, 36(2):225-241.

Decker, D.S. and H.D. Wilson. 1987. Allozyme variation in the *Cucurbita pepo* complex: *C. pepo* var. *ovifera* vs. *C. texana*. *Systematic Botany*, 12:263-273.

Dewald, M.G., G.A. Moore and W.B. Sherman. 1988. Identification of pineapple cultivars by isozyme genotypes. *Journal of the American Society for Horticultural Sciences*, 113:935-938.

Doebley, J. 1989. Isozymic evidence and evolution of crop plants. In: D. Soltis and P. Soltis (eds.), *Isozymes in Plant Biology*, pp: 165-191. Dioscorides Press. Portland, Oregon.

Doebley, J., M.M. Goodman, and C.W. Stuber. 1984. Isoenzymatic variation in *Zea* (Gramineae). *Systematic Botany*, 9(2):203-218.

Doebley, J., M.M. Goodman, and C.W. Stuber. 1987. Patterns of isozyme variation between maize and Mexican annual teosinte. *Economic Botany*, 41(2):234-246.

Doggett, H. and B.N. Majisu. 1968. Disruptive selection in crop development. *Heredity*, 23(1):1-23.

Ellstrand, N.C. and J.M. Lee. 1987. Cultivar identification of cherimoya (*Annona cherimoya* Mill.) using isozyme markers. *Scientia Horticulturae*, 32:25-31.

Emiliani, C., S. Gaertner, and B. Lidz. 1972. Neogene sedimentation on the Blake Plateau and the emergence of the Central American isthmus. *Palaeogeography Palaeoclimatology Palaeoecology*, 11:1-10.

Evans, L.T. 1993. *Crop evolution, adaptation and yield.* Cambridge University Press. Cambridge.

Ferreira, S.A., R.F.L. Mau, R.M. Manshardt, K.Y. Pitz and D.Gonsalves. 1992. Field evaluation of papaya ringspot virus cross protection. *Proceedings: 28th. Annual Hawaii Papaya Industry Association Conference*, pp: 14-19. HITAHR, College of Tropical Agriculture and Human Resources, University of Hawaii. Honolulu.

Fitch, M.M.M., R.M. Manshardt, D. Gonsalves, J.L. Slightom and J.C. Stanford. 1992. Virus resistant papaya plants derived from tissues bombarded with the coat protein gene of papaya ringspot virus. *Bio/Technology*, 10:1466-1472.

Food and Agriculture Organization. 1994. *Food and Agriculture Organization Yearbook Production 1993*, Volume 47. FAO Statistics series No. 117. FAO. Rome.

Fowler, C. and P. Mooney. 1990. *Shattering– Food, Politics, and the Loss of Genetic Diversity.* University of Arizona Press. Tucson.

Frankel, O.H. 1974. Genetic conservation: our evolutionary responsibility. *Genetics*, 78:53-65.

Frankel, O.H. 1988. Genetic resources: Evolutionary and social responsibilities. In: J.R. Kloppenburg, Jr. (ed.), *Seeds and Sovereignty: The Use and Control of Plant Genetic Resources*, pp: 19-46. Duke University Press. Durham, North Carolina.

Frankel, O.H. and E. Bennett. 1970. Genetic resources-- Introduction. In: O.H. Frankel and E. Bennett (eds.), *Genetic Resources in Plants: Their Exploration and Conservation*, pp: 7-17. Blackwell Scientific Publications. Oxford and Edinburgh.

Friss, E.M. and W.L. Crepet. 1987. Time of appearance of floral features. In: Else Marie Friis, William G. Chaloner, and Peter R. Crane (eds.), *The origins of angiosperms and their biological consequences*, pp: 145-180. Cambridge University Press. Cambridge.

Gepts, P. 1990. Genetic diversity of seed storage proteins in plants. In: Brown, A.H.D., M.T. Clegg, A.L. Kahler and B.S.Weir (eds.), *Plant Population Genetics, Breeding, and Genetic Resources*, pp: 64-82. Sinauer Associates. Sunderland, Massachusetts.

Gepts, P., T.C. Osborn, K. Rashka and F.A. Bliss. 1986. Phaseolin-protein variability in wild form and landraces of the common bean (*Phaseolus vulgaris*): evidence for multiple centers of domestication. *Economic Botany*, 40:451-468.

Giacometti, D.C. 1987. Papaya breeding. *Acta Horticultura*, 196:53-60.

Goldblatt, P. 1993. Biological relationships between Africa and South America: an overview. In: Peter Goldblatt (ed.), *Biological relationships between Africa and South America*, pp: 3-14. Yale University Press. New Haven.

Gonzalez Suarez, F. 1890. *Historia general de la Republica del Ecuador*. I, XV. Quito. Imprenta del Clero.

Gottlieb, L.D. 1977. Electrophoretic data and plant systematics. *Annals of the Missouri Botanical Garden*, 64:161-180.

Gottlieb, L.D. 1981. Electrophoretic evidence and plant populations. *Progress in Phytochemistry*, 7:1-46.

Guillen Chaparro, F. 1889. Memoria de los pueblos de la Governacion de Popayan y cosas y constelaciones que hay en ellos, son las siguientes: *Anales de la Intruccion Publica*, tomo XV, No. 85:146-156. Agosto. Bogota.

Haffer, J. 1970. Geologic-climatic history and zoogeographic significance of the Uraba region in northwestern Colombia. *Caldasia*, 10:603-636.

Hamilton, R. and P. Ito. 1968. 'Sunrise solo': a different colored 'Solo' papaya. *Hawaii Agricultural Experiment Station, Circular* No. 69. Honolulu.

Hammond, N. 1981. Obsidian trade routes in the Mayan area. In: John A. Graham (ed.), *Ancient Mesoamerica*, pp: 193-196. Peek Publications. Palo Alto, California.

Hamrick, J L. and M. J. Godt. 1990. Allozyme diversity in plant species. In: Brown, A.H.D., M.T. Clegg, A.L. Kahler, B.S. Weir (eds.), *Plant Population Genetics, Breeding, and Genetic Resources*, pp: 43-63. Sinauer Associates. Sunderland, Massachusetts.

Hamrick, J.L. and L.R. Holden. 1979. Influence of microhabitat heterogeneity on gene frequency distribution and gametic phase disequilibrium in *Avena barbata*. *Evolution*, 33:521-533.

Hancock, J.F. 1992. *Plant evolution and the origin of crop species*. Prentice Hall. New Jersey.

Harlan, J.R. 1975. Our vanishing genetic resources. *Science*, 188: 618-621.

Harlan, J.R. 1992. *Crops and Man*. Second edition. American Society of Agronomy. Crop Science Society of America. Madison, Wisconsin.

Hawaii Agricultural Statistics Service. 1995. *Statistics of Hawaiian agriculture 1994*. Honolulu, Hawaii.

Heiser, C.B. Jr. 1985. Some botanical considerations of early domesticated plants north of Mexico. In: Richard I. Ford (ed.), *Prehistoric food production in North America*, Museum of Anthropology, University of Michigan, pp: 57-72. An Arbor, Michigan.

Heiser, C.B. Jr. 1988. Aspects of unconscious selection and the evolution of domesticated plants. *Euphytica*, 37: 77-81.

Heiser, C.B. Jr. 1990. New perspectives on the origin and evolution of New World domesticated plants: summary. *Economic Botany*, 44(3):111-116.

Henriquez Ureña, P. 1938. *Para la Historia de los indigenismos*. Papa y batata. El enigma del aje. Boniato. Caribe. Palabras antillanas. Facultad de Filosofia y Letras de la Universidad de Buenos Aires. Instituto de Filosofia. Biblioteca de Dialectologia Hispanoamericana. Anejo III. Buenos Aires.

Hernandez, F. 1943. *Historia de Las Plantas De Nueva España*. Imprenta Universitaria, Mexico.

Heywood, V.H. 1993. Broadening the basis of plant resource conservation. In: J.P. Gustafson, R. Appels, and P. Raven (eds.), *Gene conservation and exploitation*, pp: 1-14. Plenum Press, New York.

Hokanson, S.C., J.G. Isebrands, R.J. Jensen, and J.F. Hancock. 1993. Isozyme variation in oaks of the Apostle Islands in Wisconsin: genetic srtucture and levels of inbreeding in *Quercus rubra* and *Q. elllipsoidalis* (Fagaceae). *American Journal of Botany*, 80(11):1349-1357.

Horovitz, S. and H. Jimenez. 1967. Cruzamientos interespecificos e intergenericos en *Caricaceas* y sus implicaciones fitotecnicas. *Agronomia Tropical*, Volume XVII, No. 4:323-344.

Hubby, J.L. and R.C. Lewontin, 1966. A molecular approach to the study of genic heterozygosity in natural populations. I. The number of alleles at different loci in *Drosophila pseudoobscura*. *Genetics*, 54, 577-594.

Hunter, R.L. and C.L. Markert. 1957. Histochemical demonstration of enzymes separated by zone electrophoresis in starch gels. *Science*, 125:1294-1295.

Iezzoni, A.F. and M. P. Pritts. 1991. Applications of principal component analysis to horticultural research. *HortScience*, 26(4):334-338.

Irvine, F.R. 1961. *Wood plants of Ghana with special reference to their uses*. Oxford University Press. London.

Jaccard, P. 1908. Nouvelles recherches sur la distribution florale. *Bulletin Societe Vaudoise des Sciences Naturelles*, 44:223-270.

Jarret, R.L. and R.E. Litz. 1986. Isozymes as genetic markers in bananas and plaintains. *Euphytica*, 35:539-549.

Jensen, R.V., and M.J. McLeod, W.H. Eshbaugh, and S.I. Guttman. 1979. Numerical taxonomic analyses of allozymic variation in *Capsicum* (Solanaceae). *Taxon*, 28:315-327.

Jimenez de la Espada, M. 1897. *Relaciones geograficas de Indias*. Tomo III. Peru. Publicalas el Ministerio de Fomento. Madrid.

Kaneps, A. G. 1970. Late Neogene biostratigraphy (planktonic foraminifera), biogeography and depositional history. Columbia University. New York.

Kesseli, R.V. and R.W. Michelmore. 1986. Genetic variation and phylogenies detected from isozyme markers in species of *Lactuca*. *Journal of Heredity*, 7:324-331.

Kiang, Y.T. and M.B. Gorman. 1983. Soybean. In: S.D. Tanksley and T.J. Orton (eds.), *Isozymes in plant genetics and breeding*, Part B, pp: 295-328. Elsevier. Amsterdam.

Kirchoff, P. 1943. Mesoamerica. *Acta Americana*, I(I):92-107.

Ladizinsky, G. 1985. Founder effect in crop-plant evolution. *Economic Botany*, 39:191-199.

Ladizinsky, G. 1987. Pulse domestication before cultivation. *Economic Botany*, 41:60-65.

Lewontin, R.C. and J. Hubby. 1966. A molecular approach to the study of genic heterozygosity in natural populations. II. Amounts of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura*. *Genetics*, 54:595-609.

Linhart, Y.B. , J.B. Mitton, K.B. Sturgeon, and M.L.Davis. 1981. Genetic varaition in space and time in a population of ponderosa pine. *Heredity*, 46:407-426.

Little, T.M. and F.J. Hills. 1978. *Agricultural experimentation*. John Wiley and Sons. New York.

Litz, R.E. 1986. Papaya (*Carica papaya* L.). In: Y.P.S. Bajaj (ed.), *Biotechnology in Agriculture and Forestry*, Volume 1, pp: 220-232. Springer-Verlag. Berlin.

Lorrence, D.H. and R. Torres Colin. 1988. *Carica cnidoscoloides* (sp. nov.) and sect. *Holostigma* (sect. nov.) of Caricaceae from southern Mexico. *Systematic Botany*, 13(1):107-110.

Lothrop, S.K. 1950. Archaelogy of southern Veraguas, Panama. *Memoirs, Peabody Musuem, Harvard University*, Volume 9 no. 3. Cambridge.

Lush, W.M. 1979. Floral morphology of wild and cultivated cowpeas. *Economic Botany*, 33:442-447.

Manshardt, R. M. and T.F. Wenslaff. 1989a. Zygotic polyembryony in interspecific hybrids of *Carica papaya* and *C. cauliflora*. *Journal of American Society for Horticultural Science*, 114:684-689.

Manshardt, R.M. and T.F. Wenslaff. 1989b. Interspecific hybridization of papaya with other *Carica* species. *Journal of American Society for Horticultural Science*, 114:689-694.

Markert, C.L., and F. Moller. 1959. Multiple forms of enzymes:tissue, ontogenetic and species-specific patterns. *Proceedings of the National Academy of Science, USA*, 45:753-763.

Marshall, D.R. 1990. Crop genetic resources: Current and emerging issues. In: Brown, A.H.D., M.T. Clegg, A.L. Kahler and B.S.Weir (eds.), *Plant Population Genetics, Breeding, and Genetic Resources*, pp: 367-388. Sinauer Associates. Sunderland, Massachusetts.

Marshall, D.R., and A.H.D. Brown. 1975. Optimum sampling strategies in genetic conservation. In: O.H. Frankel and J.G. Hawkes (eds.), *Crop genetic resources for today and tomorrow*, pp: 53-80. Cambridge University Press, Cambridge.

Marshall, L.G., Webb, S.D., Sepkoski, J.J., Jr., and Raup, D.M. 1982. Mammalian evolution and the great American interchange. *Science*, 215:1351-1357.

Marty, L.T., D. O'Malley and R.P.Guries (eds.). 1984. *A manual for starch gel electrophoresis*. New microwave edition. Staff Paper Series No. 20. College of Agriculture and Life Sciences, School of Natural Resources, University of Wisconsin. Madison.

Mekako, H.U. and H.Y. Nakasone. 1975. Interspecific hybridization of papaya with other *Carica* species. *Journal of the American Society for Horticultural Science*, 100:237-242.

Mello, J.C. de and R. Spruce. 1869. Notes on Papayaceae. *Journal of the Linnean Society of Botany*, 10:1-15.

Mexico and Central American Handbook 1992. 1991. Second edition. Trade and Travel Publications. England.

Miksicek, C. H. 1983. Macrofloral remains of the Pulltrouser Area: Settlements and Fields. In: B.L. Turner II and P.D. Harrison (eds.), *Pulltrouser Swamp: Ancient Maya Habitat, agriculture, and settlement in Northern Belize*, pp: 94-104. University of Texas Press. Austin.

Morton, J.F. 1987. *Fruits of the warm climates*. Creative Resources Systems. Winterille, North Carolina.

Nakasone, H.Y. and W.B. Storey. 1955. Studies on the inheritance of fruiting height of *Carica papaya* L. *American Society For Horticultural Science*, 66:168-182.

National Academy of Sciences, Washington, D.C. 1972. *Genetic vulnerability of major crops*.

National Research Council. 1989. *Lost crops of the Incas: Little-known plants of the Andes with promise for worldwide cultivation*. National Academy Press. Washington D.C.

Neal, M.C. 1965. *In Gardens of Hawaii*. Bishop Museum Press. Honolulu.

Nei, M. 1972. Genetic distance between populations. *American Naturalist*, 106:283-293.

Nei, M. 1973. Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences*, 70:3321-3323.

Nei, M. 1977. F-statistics and analysis of gene diversity in subdivided populations. *Annals of Human Genetics*, 41:225-233.

Nevo, E., A.H.D. Brown and D. Zohary. 1979. Genetic diversity in the wild progenitor of barley in Israel. *Experientia*, 35: 1027-1029.

Nordenskiold, E. 1928. *Indianerna på Panamanäset*. Stockholm.

Ochse, J.J., M.J. Soule, M.J. Dijkman, and C. Wehlburg. 1961. *Tropical and subtropical agriculture*. Volume 1. MacMillan. New York.

Oviedo y Valdes, G.F. de 1959a. *Natural history of the West Indies*. Translated and edited by Sterling A. Stoudemire. The University of North Carolina Press. Chapel Hill.

Oviedo y Valdes, G.F. de 1959b. *Historia general y natural de las Indias*. Volume 1. Edicion y estudio preliminar de Juan Perez de Tudela Bueso. Biblioteca de Autores Espanoles. Continuacion de la Coleccion Rivadeneeira. Graficas Orbe. Madrid.

Owens, K.W., F.A. Bliss, and C.E. Peterson. 1985. Genetic analysis of fruit length and weight in two cucumber populations using the inbred backcross line method. *Journal of the American Society For Horticultural Science*, 110:431-436.

Patiño, V.M. 1963. *Plantas cultivadas y animales domesticos en America Equinoccial*. Edicion 1. Tomo I. Frutales. Imprenta Departmental. Cali.

274

Peirce, L.C. and J.L. Brewbaker. 1973. Applications of isozyme analysis in horticultural science. *Hortscience*, 8(1):17-22.

Pickersgill, B. 1968. The domestication of chili peppers. In: Ucko, Peter J. and G.W. Dimbleby (eds.), *The domestication and exploitation of plants and animals*, pp: 443-450. Aldine Publishing Company. Chicago.

Pindell, J. and J.F. Dewey. 1982. Permo-Triassic reconstruction of western Pangaea and the evolution of the Gulf of Mexico/Caribbean region. *Tectonics*, 1:1179-211.

Pitman, W.C. III, S. Cande, J. Labrecque, and J. Pindell. 1993. Fragmentation of Gondwana: The separation of Africa from South America. In: Peter Goldblatt (ed.), *Biological relationships between Africa and South America*, pp: 15-34. Yale University Press. New Haven.

Prance, G.T. 1984. The peibaje, *Guiliema gasipaes* (H.B.K.) Bailey, and the papaya, *Carica papaya* L. In: Stone, D. (ed.), *Pre-Columbian Plant Migration*, Papers of the Peabody Museum of Archaelogy and Ethnology, Volume 76, pp: 86-104. Harvard University Press. Cambridge.

Purseglove, J.W. 1974. *Tropical crops: dicotyledons*. Longman Group Ltd. Burnt Mill, Essex.

Raven, P.H. and D.I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden,* 61(3):539-673.

Rabinowitz, P.D. and J.L. LaBrecque. 1979. The Mesozoic South Atlantic Ocean and evolution of its continental margins. *Journal Geophysical Research*, 84:5973-6002.

Rick, C.M. 1976. Tomato. In: N.W. Simmonds (ed.), *Evolution of crop plants*, pp: 268-272. Longman. London.

Rick, C.M. 1983. Tomato (*Lycopersicon*). In: S.D. Tanksley and T.J. Orton (eds.), *Isozymes in plant genetics and breeding*, Part B, pp: 57-78. Elsevier. Amsterdam.

Rick, C.M and W.H. Dempsey. 1969. Position of the stigma in relation to fruit setting of the tomato. *Botanical Gazette*, 130:180-186.

Rick, C.M., R.W. Zobel, and J.F. Fobes. 1974. Four peroxidase loci in red-fruited tomato species: genetics and geographic distribution. *Proceedings of the National Academy of Science,* USA 71:835-839.

Rindos, D. 1980. Symbiosis, instability, and the origins and spread of agriculture: a new model. *Current anthropology*, 21(6):751-770.

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Rogers, J.S. 1972. *Measures of genetic similarity and genetic distance*. University of Texas Publication 7213:145-153.

Rolf, F.J. and R.R. Sokal. 1981. Comparing numerical taxonomic studies. *Systematic Zoology*, 30:459-490.

Roys, R.L. 1931. *The ethno-botany of the Maya*. The Tulane University of Louisiana. New Orleans.

Roys, R.L. 1933. *The book of Chilam Balam of Chumayel*. Carnegie Institution of Washington.

Roys, R.L. 1972. *The Indian background of Colonial Yucatan*. University of Oklahoma Press. Norman.

Sahagun, B. de. 1959. *General history of the things of New Spain*. Florentine Codex, Book 9-The Merchants. Translated by Charles E. Dibble and Arthur J.O. Anderson. The School of American Research and the University of Utah.

Sawant, A.C. 1958. Crossing relationships in the genus *Carica*. *Evolution*, 12:263-266.

Scholes, F.V. and R.L. Roys. 1968. *The Maya Chontal Indians of Acalan-Tixchel*. University of Oklahoma Press. Norman.

Schwanitz, F. 1967. *The origin of cultivated plants*. Harvard University Press, Cambridge.

Shaw, C.R. and R. Prasad. 1970. Starch gel electrophoresis of enzymes - a compilation of recipes. *Biochemical Genetics*, 4:297-320.

Simmonds, N.W. 1979. *Principles of crop improvement*. Longman Scientific and Technical. New York.

Simpson, B.B. and M. Conner-Ogorzaly. 1986. *Economic Botany*. McGraw-Hill. New York.

Simpson, G.G. 1980. *Splendid isolation: The curious history of South American mammals*. Yale University Press. New Haven.

Smith, C.E., Jr. 1987. Current archaeological evidence for the beginning of American agriculture. In: Linda Manzanilla (ed.), *Studies in the Neolithic and urban revolutions*, pp: 81-102. Bar International Series 349.

Smith, C.E., Jr. 1965. The archaeological record of cultivated crops of New World Origins. *Economic Botany*, 19:322-334.

Smith, N.J.H., J.T. Williams, D.L. Plucknett and J.P. Talbot. 1992. *Tropical forests and their crops*. Comstock Publishing Associates, Cornell University Press. Ithaca, New York.

Smithies, O. 1955a. Zone electrophoresis in starch gels: group variation in the serum proteins of normal human adults. *Biochemistry Journal*, 61:629-641.

Smithies, O. 1955b. Grouped variations in the occurrence of new protein components in normal human serum. *Nature*, 175:307-308.

Sneath, P.H.A. and R.R. Sokal. 1973. *Numerical Taxonomy*. W.H. Freeman. San Francisco.

Squier, E.G. 1851. *Nicaragua: Its people, scenery, monuments, and the proposed interoceanic canal*. Volume II. D. Appleton Publishers. New York.

Stebbins, G.L. 1957. Self-fertilization and population variability in the higher plants. *American Naturalist*, 91:337-354.

Storey, W.B. 1967. Theory of the derivations of the unisexual flowers of Caricaceae. *Agronomia Tropical* Volume XVII, No.4:273-322.

Stone, D. 1977. *Pre-Columbian man in Costa Rica*. Peabody Museum Press. Cambridge, Massachusetts.

Storey, W.B. 1976. Papaya. In: Simmonds, N. (ed.), *Evolution of Crop Plants*, pp: 21-24. Longman, London.

Stout, P.F. 1859. *Nicaragua: Past, present and future; A description of its inhabitants, customs, mines, minerals, early history, modern fillibusterism, proposed inter-oceanic canal and manifest destiny*. John E. Potter. Philadelphia.

Swofford, D.L. and R.B. Selander. 1989. *BIOSYS-1:a computer program for the analysis of allelic variation in population genetics and biochemical systematics*, release 1.7. Illinois Natural History Survey. Champaign, Illinois.

Tejera, E. 1951. *Palabras indijenas de la isla de Santo Domingo*. Con adiciones hechas por Emilio Tejera. Prologo de Pedro Henriquez Ureña. Ciudad Trujillo. Editora del Caribe.

Towle, M.A. 1961. *The ethnobotany of pre-Columbian Peru.* Aldine Publishing Company. Chicago.

Trujillo, D. de. 1948. *Relacion del descrubrimiento del Reyno del Peru.* Edicion, prologo y notas de Raul Porras Barrenechea. Escuela de Estudios Hispano-Americanos de Sevilla. XLVIII. Serie 7, No. 4. Sevilla. Imprenta de la Escuela de Estudios Hispano-Americanos.

Vavilov, N.I. 1939. The theory of the origin of cultivated plants after Darwin. Lecture presented at the Darwin session of the Academy of the Sciences on November 28, 1939. In: *Origin and geography of cultivated plants*, pp: 421-442. English edition 1992. Cambridge University Press, Cambridge.

Vavilov, N.I. 1951. The origin, variation, immunity and breeding of cultivated plants. *Chronica Botanica*, 13:1-364.

Vasquez de Espinosa, A. 1969. *Compendio y descripcion de Las Indias Occidentales.* Biblioteca de Autores Españoles. Madrid.

Velasco, J.L. de. 1971. *Geografia y descripcion universal de las Indias.* Biblioteca de Autores Españoles. Madrid.

Wassen, H. 1935. Notes on southern groups of Choco Indians in Colombia. *Etnologiska Studier*, 1:35-182.

Weir, B.S. 1990. Sampling properties of gene diversity. In: Brown, A.H.D., M.T. Clegg, A.L. Kahler, B.S. Weir (eds.), *Plant Population Genetics, Breeding, and Genetic Resources*, pp: 23-42. Sinauer Associates. Sunderland, Massachussetts.

Wendel, J.F., C.L. Brubaker, and A.E. Percival. 1992. Genetic diversity in *Gossyphium hirsutum* and the origin of upland cotton. *American Journal of Botany*, 79(11):1291-1310.

Whitmore, T.C. 1990. *An introduction to tropical rain forests*. Oxford University Press. Oxford.

Williams, J.T. 1984. A decade of crop genetic resources research. In: J.H.W. Holden and J.T. Williams (eds.), *Crop Genetic Resources Conservation and Evaluation*, pp: 1-17. George Allen and Unwin. London.

Williams, J.T. 1993. Scientific issues affecting gene conservation and exploitation of some tropical perennials. In: J. Perry Gustafson, R. Appels, and P. Raven, *Gene conservation and exploitation*, pp: 15-28. Plenum Press. New York and London.

Woodland, D.W. 1991. *Contemporary plant systematics*. Prentice-Hall. New Jersey.

Wright, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. *Evolution*, 19:395-420.

Wright, S. 1978. Variability within and among natural populations. *Evolution and the genetics of populations*, Volume 4. University of Chicago Press. Chicago.

Yee, W., E.K. Akamine, G.M. Aoki, R.A. Hamilton, F.H. Haramoto, R.B. Hine, O.V. Holtzmann, J.T. Ishida, J.T. Keeler and H.Y. Nakasone. 1970. Papayas in Hawaii. *University of Hawaii Cooperative Extension Service*, Circular 436.

Zee, F.T.P. 1985. Breeding for papaya ringspot virus tolerance in Solo papaya, *Carica papaya* L. Doctoral dissertation. University of Hawaii, Honolulu.

Zerpa, D. M. de. 1967. Informe sobre resultados de inoculaciones sobre lechosa (*Carica papaya* L.) con virus de la "deformacion foliar y mancha en anillo" (Distortion Ringspot) en condiciones diversas. *Agronomia Tropical*, Volume XVII, No. 4:361-370.

Zohary, D. 1969. The progenitors of wheat and barley in relation to domestication and agricultural dispersal in the Old World. In: Peter J. Ucko and G.W. Dimbleby (eds.), *The domestication and exploitation of plants and animals*, pp: 47-66. Aldine Publishing Company. Chicago.