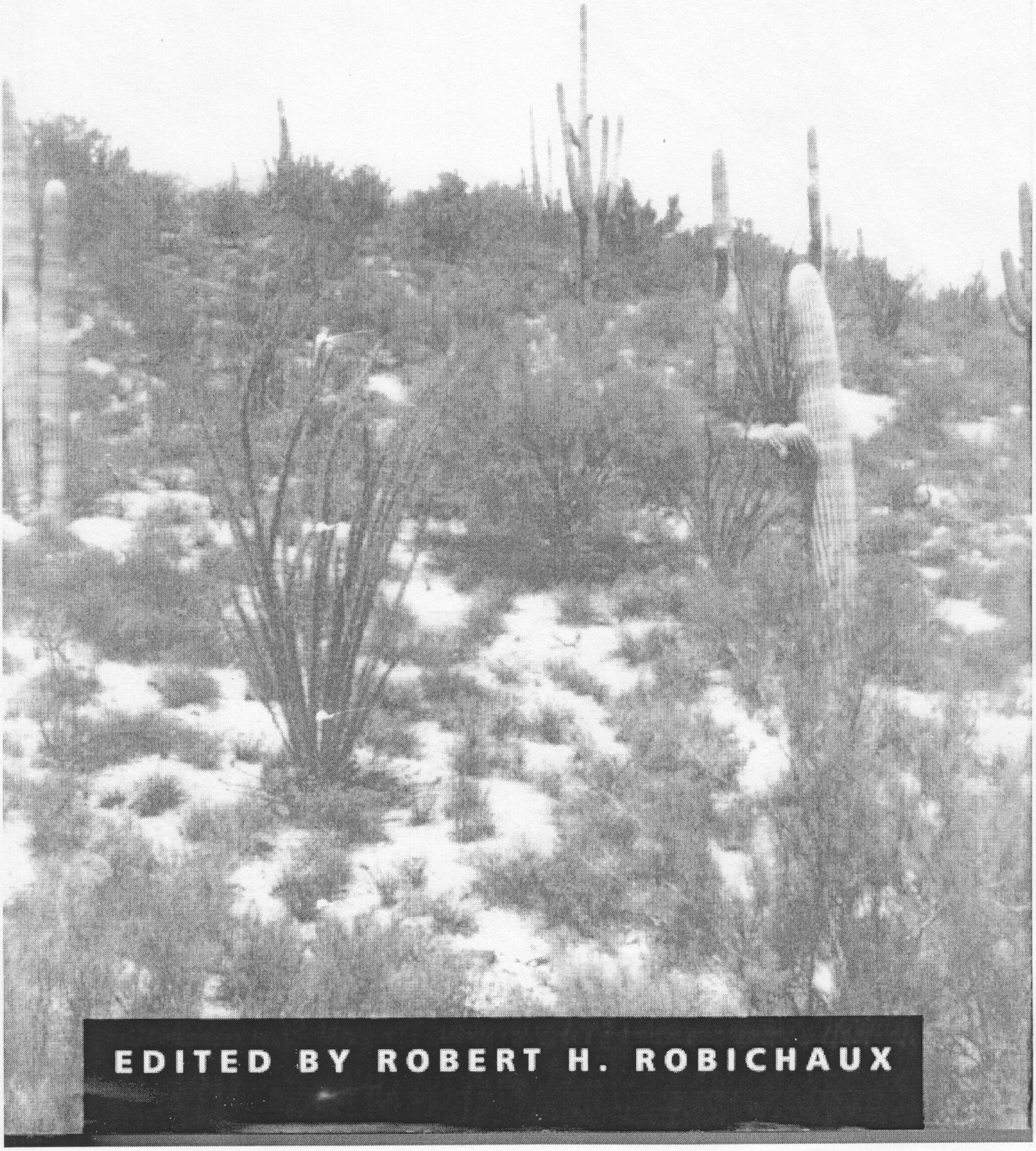
Ecology of Sonoran Desert Plants and Plant Communities



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6 Ecological Genetics of Cactophilic *Drosophila*

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This paper is dedicated to the most steadfast member of the desert *Drosophila* group, Ms. Jean S. Russell.

The large number of cactus species in the deserts and semideserts of North and South America is one of the most remarkable aspects of these arid lands. Their presence has shaped a wide variety of animal-plant associations, including that between cacti and many insect species that have become intricately dependent on either their living or dead tissues. Most cacti are well armed with spines that fend off herbivory and affect surrounding microclimatic characteristics (Nobel and Loik, chapter 5, this volume). Senescence or injury may cause the death of older tissues or, at times, the entire plant. The decaying tissues attract and contain an interesting community of saprophytic organisms that ingest the available nutrients and moisture released from the plant cells. This community consists chiefly of opportunistic bacteria and yeasts as well as immature stages of insects, including the larvae of various species of flies of the order Diptera. The larvae feed on the bacteria, the yeasts, and the plant cells, including the cell sap of the depleted tissues. These invading organisms are not among the more obvious arid land inhabitants, yet studies of *Drosophila*/microorganism/cactus relationships have provided enormous insight into their ecology and evolution. For reviews of this subject, see Barker and Starmer (1982), Heed and Mangan (1986), Fogleman and Heed (1989), and Barker et al. (1990).

For ecological geneticists who work with *Drosophila* (pomace flies) and are interested in the processes that change gene and chromosomal frequencies within and between species, the community inhabiting a "rot pocket" is a wellspring of information just waiting to be tapped. In the Sonoran Desert, two of the four species of *Drosophila* that are endemic to the desert and whose larvae and adults live in and around these fermenting tissues, have variable polytene chromosomes (inversions of gene order) that differ in frequency from one area to another. These chromosomes can be easily studied by dissecting out the salivary glands of the larvae just about to enter pupation. The tissues are then histochemically stained and squashed under a cover glass on a microscope slide to allow chromosome identification. The larvae may be obtained directly from the cactus rot pocket or adult flies may be aspirated from the rot, where they are feeding, mating, and laying eggs, and transferred to the laboratory where they continue the same activities on artificial media in glass vials.

The chief goal of this chapter is to compare the degree of the polytene chromosomal variability in *Drosophila pachea* and *Drosophila mojavensis* in relation to the host cacti used for feeding and breeding within the relevant vegetational subdivisions of the Sonoran Desert and adjacent regions as described by Gentry (1942), Shreve (1951, 1964), Brown and Lowe (1980), and Brown (1982). These subdivisions have been made with reference strictly to vegetation, which consists of the character and organization of communities (fig. 6.1). Even though the host cacti for the two *Drosophila* species traverse many of the subdivisions, it seems reasonable to infer that environmental conditions that differ somewhat between these areas could affect gene and chromosomal frequencies of the flies inhabiting their respective hosts. In fact, data on mean temperature plotted against mean precipitation for five of the six subdivisions, and including the Mojave desertscrub, has been presented as "climatographs" by Turner and Brown (1982). Even though there is a strong degree of overlap of the climatographs in certain seasons, representing shared environmental conditions, each subdivision also has its own characteristics. Variable edaphic conditions throughout the desert undoubtedly complicate any analysis of climatic factors by contracting or extending the limits of various species of cacti and/or the vegetational subdivisions themselves in certain cases, but this has not been taken into account in our analyses.

The Flies and Their Chromosomes

The polytene chromosomes of *Drosophila* have been a tool for geneticists in gene mapping and gene action since they were first discovered by

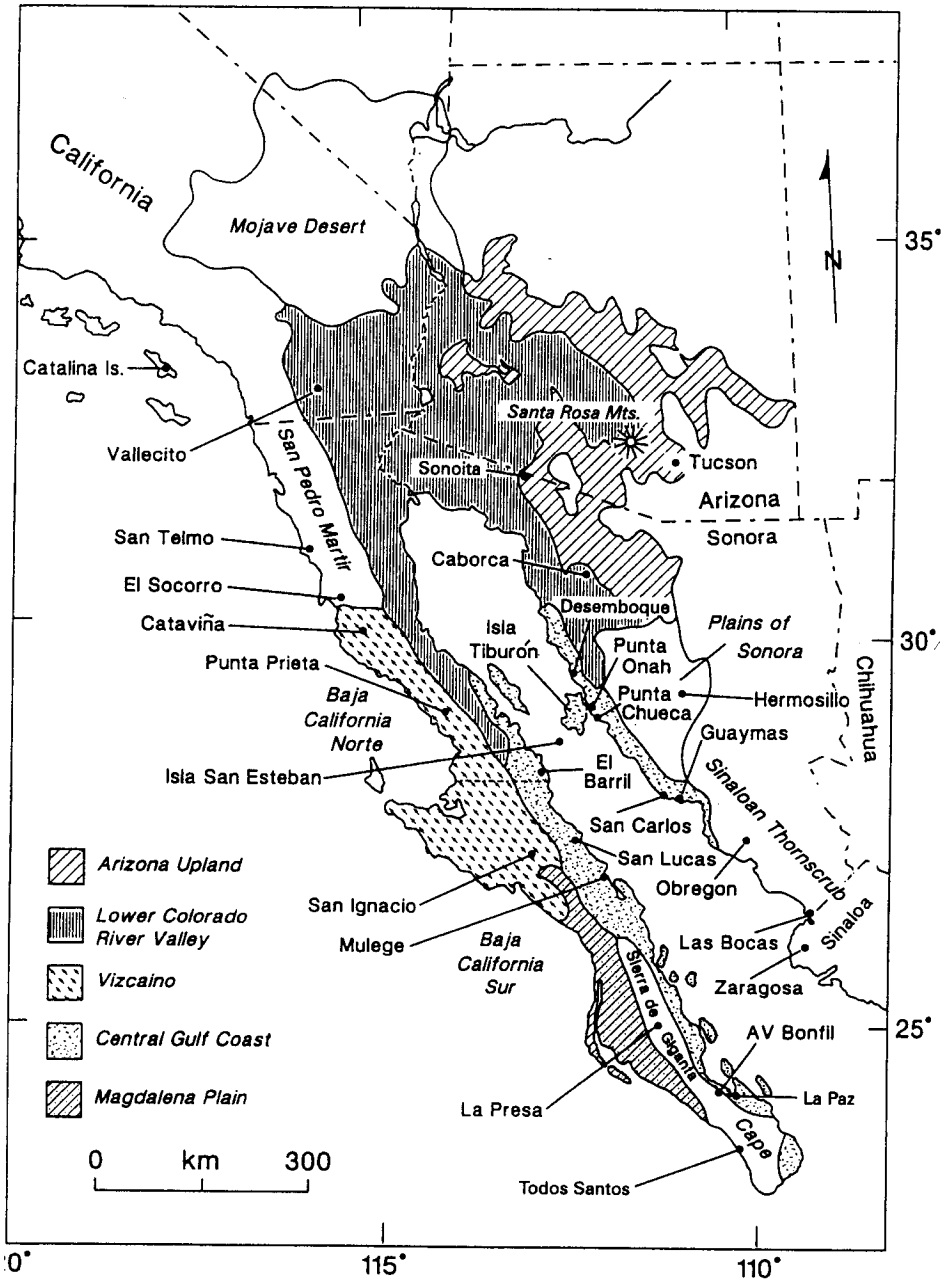

Figure 6.1 *(opposite page)* Map of the major vegetational subdivisions of the Sonoran Desert as presently envisioned (Turner and Brown 1982). Five subdivisons are listed whereas the sixth one (Plains of Sonora) is designated on the map. Adjacent vegetational regions (from Brown 1982) are indicated as the Cape region (San Lucan deciduous scrub), San Pedro Martir (Californian coastal scrub and chaparral), Mojave Desert, and Sinaloan thornscrub. Major landscape features and several place names referred to in the text are included.

Kostoff (1930) and elaborated upon by T. S. Painter (1933) at the University of Texas. The first significant analysis of salivary chromosome evolution was made by Sturtevant and Dobzhansky (1936). Since then many studies have been made of natural populations of *Drosophila* (Patterson and Stone 1952; Krimbas and Powell 1992; Powell 1997), but none of them include an in-depth analysis of host plants as possible factors that could affect inversion frequencies.

Inversion rearrangements, as well as other chromosomal mutations, can be detected in polytene chromosomes because of their large size, visible complexity, and a very defined aperiodic structure. Polytene chromosomes, which are found throughout the evolutionarily more advanced Diptera, consist of band sequences that correspond to the organization of particular genes. The bands vary in width, detail, and density of staining, the sequence of which is rarely repeated anywhere, except as short duplications. Therefore all chromosomes of an individual, as well as subunits of a single chromosome, may be separately identified. Between individuals within a species the banding sequences are often identical, while other individuals may differ by one or more inversion rearrangements. Also, closely related species usually have completely identifiable sequences that are similar or differ by one or more gene arrangements. Thus any number of genes may differ between related species, but this does not necessarily affect the visible structure of the chromosome. Therefore, the fingerprint of the polytene chromosome may be considered a living fossil record. In the simplest case, when two or more species have the same inversion fixed (homozygous), we know that their lineages trace back to a common ancestor. All inversions are thought to arise by unique mutational events (Aquadro et al. 1991; Krimbas and Powell 1992).

Another advantage of the polytene chromosome derives from its property of somatic pairing. When there are differences in gene order between

homologous chromosomes, the only way they can pair is in the form of a loop. The loop represents the pairing of inverted and noninverted homologous chromosomes in the heterozygous state. In *Drosophila pachea,* there are three possible karyotypes with a single inversion in gene order: 7 +/+, 7 +/A, and 7 A/A. This is the only inversion polymorphism in the species. The Sonoran part of the distribution of inversion 7 A has been reported earlier (Ward et al. 1975). The Baja California part of the distribution, analyzed chiefly by Duncan (1979), will be presented here and a summary of the total distribution will be made. Inversions in *D. mojavensis* have been recently described by Ruiz et al. (1990). However, most of the quantitative data on inversion frequency variation in this species was presented by Johnson (1980) and is reviewed and updated in the present text.

The significance of inversion heterozygotes is that they rarely allow the recombination that occurs within them to be incorporated into the next generation, so the genes associated within the inverted sequence are usually inherited as a unit. When inversions rise in frequency in populations due to their effects on fitness, the genes contained within them are considered coadapted. Thus, inversions may have various levels of adaptive significance depending on the coadaptedness of the genes within them. Inversions have significant effects on fitness characters important in the life cycle of their carriers, such as longevity, fecundity, viability, speed of development and mating, and mating success (Dobzhansky 1955; Dobzhansky et al. 1964; Anderson and Watanabe 1974; Prakash 1967; Spiess and Spiess 1967; Ruiz et al. 1986; Etges 1989a; Salceda and Anderson 1988; Etges 1996). However, inversions are also very useful for the study of population structure, and it is in this context that we analyze the various gene orders discovered in the two desert species. The comparison of degrees of differentiation within and between local populations and larger geographical areas may be made in a hierarchical fashion with fixation indices following the pioneering work of Sewall Wright, which he summarized in volumes 2 and 4 of *Evolution and the Genetics of Populations* (Wright 1969, 1978). The fixation indices for each chromosome may then be compared in a general way to degrees of differentiation in other species in different geographical areas with different ecologies, as was done for *Drosophila pseudoobscura* in western North America (Wright 1978) and *D. subobscura* in Europe (Ferrari and Taylor 1981). In addition, historical factors certainly contribute to the variation of inversion frequency distributions. We have the added advantage in this context that the ancestral sequence of gene arrangements is known with high certainty in both *D. mojavensis* and *D. pachea.*

The Flies and Their Ecology

The phylogenetic lineages of *Drosophila mojavensis* and *D. pachea* have been separated by millions of years of evolution.[1] To make this clear, the species were assigned to different "species groups." *D. pachea* is classified as a member of the nannoptera species group with relatives in central and southern Mexico (Ward and Heed 1970; Pitnick and Heed 1994), and *D. mojavensis* is a member of the large repleta species group (Patterson and Crow 1940; Wasserman 1992). Furthermore, the host plants of the two species are very distinct. *D. pachea* breeds in the fermenting tissues of the senita cactus (*Lophocereus schottii*). This species contains unique phytosterols that are necessary for the larvae to complete development and for adults to lay fertile eggs (Heed and Kircher 1965; Fogleman et al. 1986). In addition, the presence of certain toxic alkaloids in senita excludes most other drosophilids, including *D. mojavensis,* from this host (Kircher et al. 1967; Fogleman et al. 1982). Figure 6.2 shows the distribution of *L. schottii* and its subdivision into three subspecies (Lindsay 1963). It is axiomatic that wherever senita is found in the desert, in associated thornscrub areas, or in deciduous scrub, *D. pachea* is present also. So the distribution of senita determines that of *D. pachea. Drosophila pachea* (strain A202) has also been reared once from *L. gatesii,* a species closely related to senita, found in allopatry in a small area of southwestern Baja California (Lindsay 1963). It is most probable that *L. gatesii,* which is not included in fig. 6.2, also contains the required sterols for larval growth and adult fecundity.

In contrast, *Drosophila mojavensis* uses a variety of different cacti, as shown in figure 6.3 (Heed and Mangan 1986). Pitahaya agria (*Stenocereus gummosus*) is the primary host for the entire peninsula of Baja California where the plant occurs, as well as for the midriff islands and other islands in the Gulf of California and the coastal area between Bahía Kino and Desemboque del Rio San Ignacio in Sonora, Mexico. A few records exist of *D. mojavensis* using organ pipe cactus (*S. thurberi*), cochal (*Myrtillocactus cochal*), and *Opuntia* in peninsular Baja California, but these records are rare. The principal host for *D. mojavensis* in mainland southern Arizona and northern Sonora is the organ pipe cactus. In southern

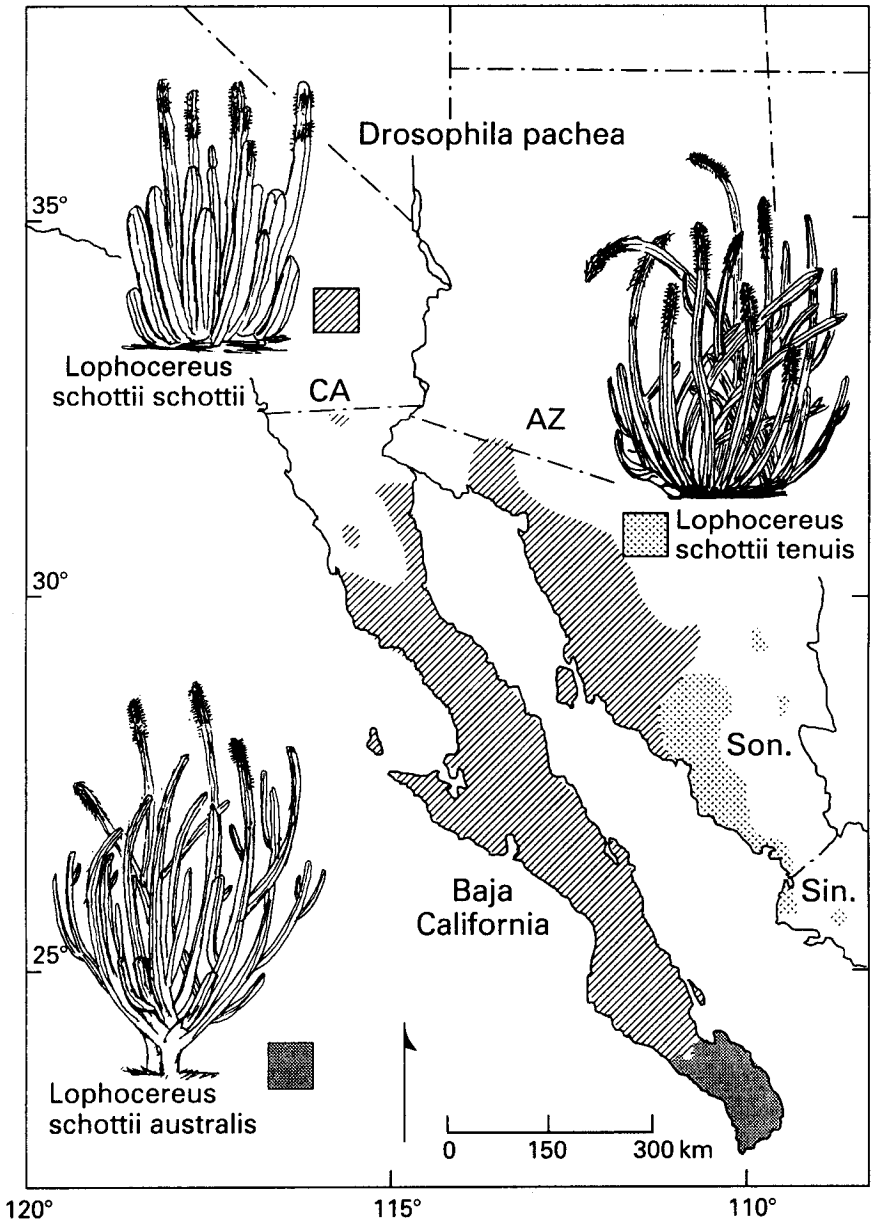

Figure 6.2 *(opposite page)* The distribution of senita cactus, the main host plant used by *Drosophila pachea*. The approximate distributions of the three subspecies in Mexico and the United States are shown, following Lindsay (1963) and Hastings et al. (1972). *Lophocereus schottii* var. *schottii* occurs in Baja California and the mainland (Arizona and Sonora), *L.s.* var. *tenuis* occurs in southern Sonora and northern Sinaloa, and *L. s.* var. *australis* occurs in the Cape region of Baja California.

Sonora and northern Sinaloa, the hosts are organ pipe and sina (*S. alamosensis*; Ruiz and Heed 1988). In the Lower Colorado subdivision of the Sonoran Desert, the Mojave Desert, and the Grand Canyon, *D. mojavensis* uses the California barrel cactus (*Ferocactus cylindraceous* [= *acanthodes*]; Taylor 1979; Turner et al. 1995). On Santa Catalina Island near Los Angeles, California, the host is *Opuntia demissa* (mostly the fruit). Thus *D. mojavensis* is oligophagous in its choice of hosts, and its distribution is neither limited by one plant nor is it limited to the Sonoran Desert (fig. 6.3). Since the senita cactus is sympatric with the pitahaya agria in the lower three quarters of Baja California and with organ pipe and sina cacti in Sonora, Mexico, we can determine whether the chromosome polymorphisms are responding similarly to environmental factors that should be common to both *Drosophila* species, such as temperature and humidity, in addition to the various host cacti to which each species is restricted[2] or whether they are the result of random forces.

Collecting Methods and the Chromosomes

Adult flies from natural populations of *Drosophila mojavensis* and *D. pachea* were obtained from 51 and 47 localities, respectively, in southern Arizona, California, and Sonora, Sinaloa, and Baja California, Mexico (appendix 6.1; appendix 6.2). Most of the collections were made from 1968 to 1980 (Johnson 1980; Duncan 1979), and in 1984 and 1985. A majority of the population samples were collected by locating rot pockets in agria, organ pipe, or senita cacti and aspirating the adult flies from the rots in the morning and evening hours. If sufficient numbers of adults were not present, intact cactus arms containing the fermenting tissues were carefully cut from the plant, wrapped in newspaper, and returned to the laboratory, where flies eclosed from the rots. Inversion frequencies

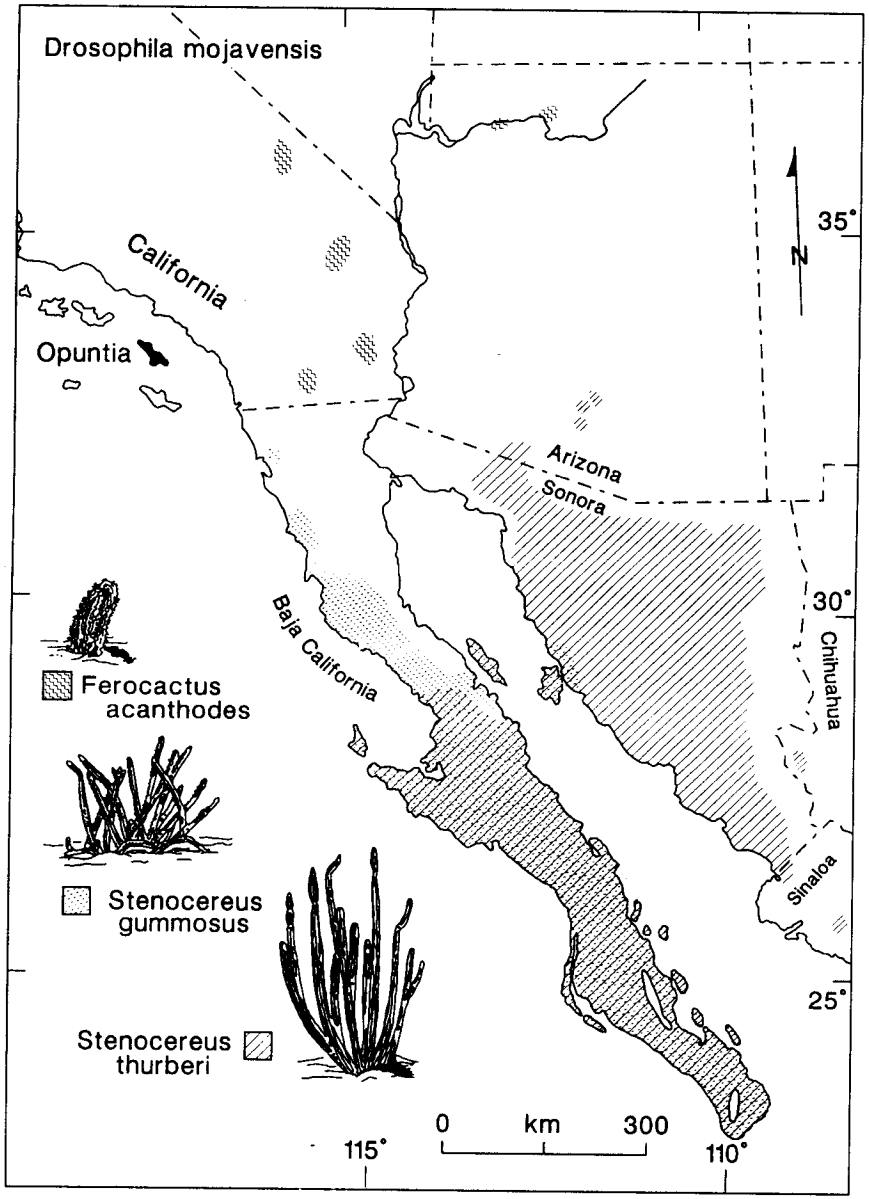

Figure 6.3 *(opposite page)* The distribution of the major host cacti of *Drosophila mojavensis* (modified from Heed and Mangan 1986, with permission). Pitahaya agria (*Stenocereus gummosus*) and organ pipe (*S. thurberi*) cacti occur together in the lower one half of Baja California and across the midriff islands to the mainland of Sonora, Mexico. Pitahaya agria extends beyond the desert in Baja California into the San Pedro Martir region in the north and into the Cape region in the south. Organ pipe cacti on the mainland extend beyond the desert eastward into the foothills of the Sierra Madre Occidental and southward into the Sinaloan thornscrub (Hastings et al. 1972). *D. mojavensis* may be found in all these areas. The distribution of the California barrel cactus, *Ferocactus cylindraceous* (labelled *acanthodes*) is shown only where collections of *D. mojavensis* have been made in association with it (Lower Colorado Valley subdivision and Mojave Desert, including the Colorado River in Arizona). *D. mojavensis* has also become established on Santa Catalina Island, where it breeds chiefly in the fruits of *Opuntia demissa*.

were calculated from the numbers of observed karyotypes for each population sample.[3]

All populations of *Drosophila pachea* were scored for chromosome seven karyotypes involving the 7 A and 7 + gene arrangements (Ward and Heed 1970). Gene arrangement designations for *D. mojavensis* for the second chromosome are ST = Standard, LP = La Paz, BA = Baja, and SL = San Lucas (Mettler 1963), which correspond to 2s, $2q^5$, $2r^5$, and $2v^7$, respectively (Ruiz et al. 1990; Wasserman 1992). ST is a single inversion removed from a hypothetical 2 abcfghqr arrangement. LP is derived from and overlaps ST. The two shorter inversions, BA and SL, are derived from and included within LP. However, BA and SL have not been recorded to be on the same homologue; therefore, the four gene arrangements may be treated statistically as though they were alleles at a single locus. On the third chromosome, ST (Standard, 3d) is the ancestral arrangement, and MU (Mulegé, 3y) is a centrally located, medium-length inversion derived from ST. Of 10 possible karyotypes expected from the four arrangements on the second chromosome (ST, LP, BA, and SL) and three possible from the third chromosome, all were identified in natural populations, except SL in the homozygous state (SL/SL). This previously undescribed short basal inversion has been found in eight localities in Baja California and on Tiburón Island and appears to be restricted to the Gulf Coast region. For *D. mojavensis*, all scoring was made simultaneously with the particular gene arrangements on both the second and third chromosomes.

Another chromosome, SI (San Ignacio), was discovered by M. Wasserman (1976, personal communication) in a laboratory culture (A367) derived from a collection made in March 1972 near San Ignacio, Baja California. When this culture was initially analyzed for chromosome frequencies, the chromosome was not observed, but when other cultures from early collections were reanalyzed, the chromosome was found in one from San Lucas, Baja California (A422). Collections from the same area (A566, San Ignacio) also indicated the presence of the chromosome in very low frequencies (1%). Recent assays of these stocks kept in the laboratory showed that SI was still present after eight years in culture (Etges, unpublished data). This chromosome is interesting in that it is derived via three paracentric inversions ($2s^7$, $2t^7$, and $2u^7$) from the ancestral, hypothetical chromosome (2abcfghqr), which also gave rise to the ST arrangement via one paracentric inversion. For a phylogeny of the arrangements of the second chromosome, see Ruiz et al. (1990). The SI chromosome was not included in the analysis which follows.

Patterns of Karyotypic Variation

Drosophila pachea

Inversion polymorphism in natural populations of *Drosophila pachea* in Baja California is comparable to that described for mainland populations (Ward et. al. 1975). We recognize that some of the frequency data may be biased due to incomplete sampling of larvae for karyotyping using the PM7 and FCF7 methods (see appendix 6.2), but here we are concerned with the overall pattern of variation in relation to the vegetational subdivisions. In Baja California, the 7 + gene arrangement was not found north of Mulegé (approximately 27° N lat.), unlike in mainland populations, where 7 + has been found in low frequencies as far north as Sonoita, Sonora (approximately 31°45′ N lat.). A cline is apparent in Baja California, as 7 + increases in frequency southward to its highest frequency of 0.74 north of La Paz (appendix 6.2; fig. 6.4). Thus, clinal variation in Baja California parallels that on the mainland but is shifted 3° to 4° southward on the peninsula. South of 24°15′ N lat. in Baja California, the 7 + gene arrangement decreases in frequency, unlike on the mainland where 7 + continues to increase southward until all populations are karyotypically 7 +/+. Therefore, the 7 A arrangement in Baja California is not only the most common in the north, but it is also the most common gene arrangement in the far south in the Cape region. We consider the populations of *D. pachea* that inhabit southern Sonora to be ancestral for the species, because they are homozygous 7 +/+, as are all three nannoptera group species in southern Mexico (Ward and Heed 1970).

Drosophila mojavensis

Gene arrangement frequencies varied throughout the range of *Drosophila mojavensis* showing a classical central-marginal pattern of variation (Carson 1959; Heed 1981; Brussard 1984), where populations near the center of the species' range exhibited greater inversion heterozygosity than those at the periphery of the range as well as distinctive clines along peninsular Baja California (appendix 6.1; fig. 6.5; fig. 6.6). At least five categories of second chromosome inversion polymorphism are apparent: (1) Highly heterozygous populations occupy the Central Gulf Coast of Baja California. (2) Inversion LP predominated in populations occupying the Cape region south of La Paz and decreased in frequency in the Magdalena Plains where inversion ST is most common. (3) There was a gradual exchange of predominantly ST populations in the Magdalena Plains northward through heterozygous LP, ST, and BA populations in the Vizcaíno region to predominantly LP populations in the San Pedro Martir region. These more southern populations are topographically separated from the Central Gulf Coast populations by the Sierra de Giganta. (4) Homozygous LP populations occupied southern Arizona, Sonora, and Sinaloa, with the exception of several populations in the Desemboque area, including Tiburón Island. (5) Homozygous ST populations were found in the Lower Colorado River subdivision of southern California, on Santa Catalina Island, and in the Grand Canyon, Arizona (Ruiz et al. 1990). These populations are apparently discontinuous with the northern Baja populations due to high mountain ranges and the lack of suitable host cacti.

In contrast to the widespread distribution and high frequencies of LP and ST, BA and SL have more localized distributions and were sometimes quite rare. BA was most abundant (0.02 to 0.38) in the San Pedro Martir and Vizcaíno regions, decreasing in frequency southwards. BA was found again in the narrow isthmus north of the Cape region and on Isla San Jose. From these population samples, it appears that the distribution of BA is discontinuous east of the Sierra de Giganta, but it is possible that it is continuous along the Pacific Coast. BA was also present in some populations in the Desemboque region in Sonora.

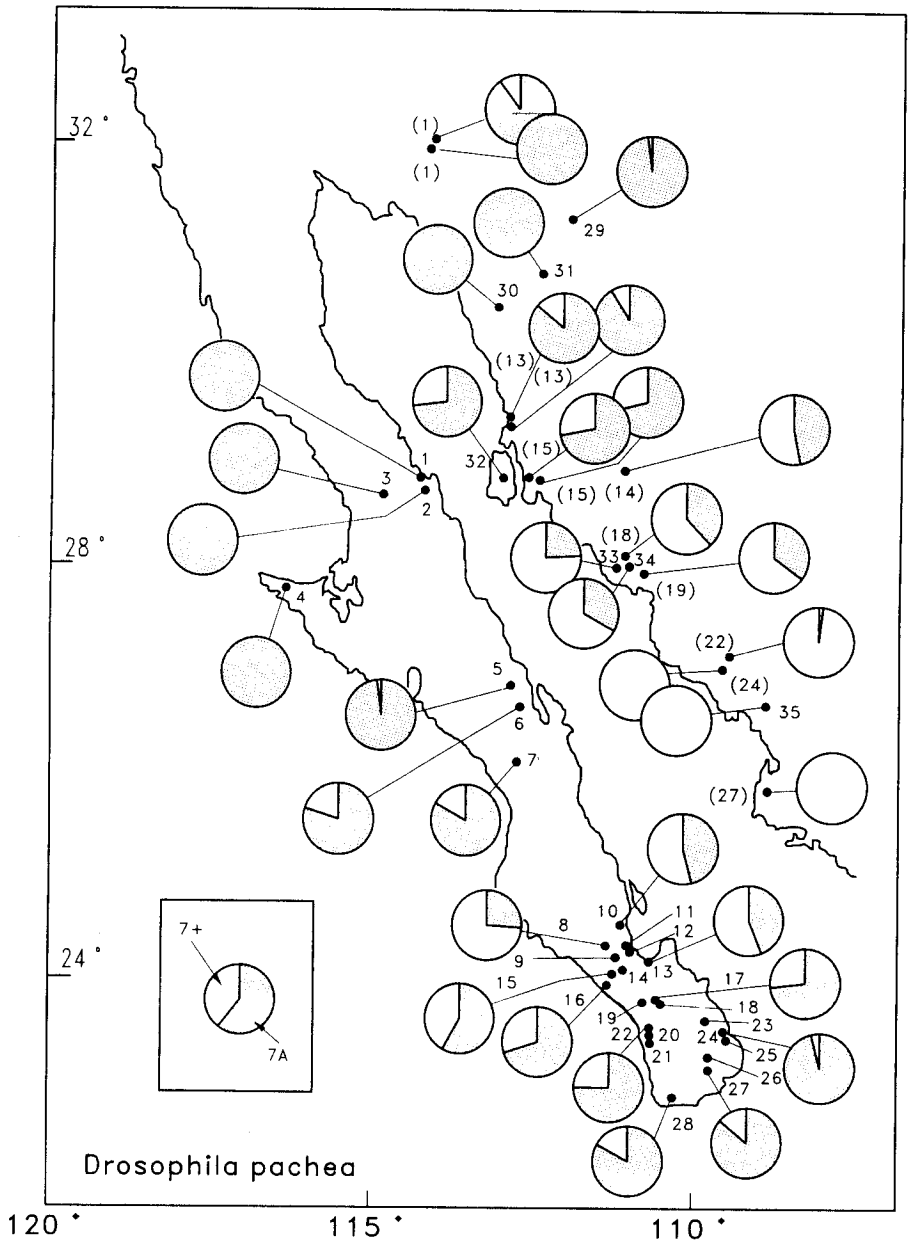

Figure 6.4 *(opposite page)* Geographical variation in chromosome 7 gene arrangement frequency in populations of *Drosophila pachea*. Population localities in parentheses are numbered according to table 1 in Ward et al. (1975). They represent 12 of the 24 localities listed in that table. The others correspond to appendix 6.2 in the present report. Not all populations are plotted for inversion frequencies, but their locations are numbered as in appendix 6.2.

SL was present in Santiago, in the Cape region, in the Central Gulf Coast region of the peninsula north of La Paz to El Barril, and on Tiburón Island. This short inversion was not discovered until the spring of 1974 even though four previous collections were made in this region (Johnson 1973).

The geographic pattern exhibited by third chromosome gene arrangements of *Drosophila mojavensis* was similar to the pattern for chromosome 2 (fig. 6.6; appendix 6.1). The important similarities are the complementary karyotypes between the Cape and the lower Magdalena Plain regions (MU decreases and ST increases in frequency), similar frequency changes with latitude in Baja California, and near fixation or fixation of ST in southern California, northern Baja California, Sonora, and southern Arizona. The important distinctions are (1) little east-west differentiation across the Sierra de Giganta, (2) replacement of karyotypes between the Vizcaíno and the San Pedro Martir regions, in contrast to the replacement occurring between the San Pedro Martir region and southern California as observed in the second chromosome, and (3) presence of heterokaryotypes in populations not using agria along coastal Sonora.

Hierarchical Analysis of Karyotypic Variation

The Method

In both *Drosophila mojavensis* and *D. pachea,* we partitioned karyotypic variation into within-population, between-population within regions (the vegetational subdivisions and adjoining regions), and between regions. We used the Analysis of Molecular Variance (AMOVA, ver. 1.53) described by Excoffier et al. (1992) to produce variance components and associated Φ (phi) statistics[4] for each level of geographic variation and Wright's F statistics (Wright 1951). We were most interested in comparing the hierarchical structures of *D. mojavensis* and *D. pachea* populations based on

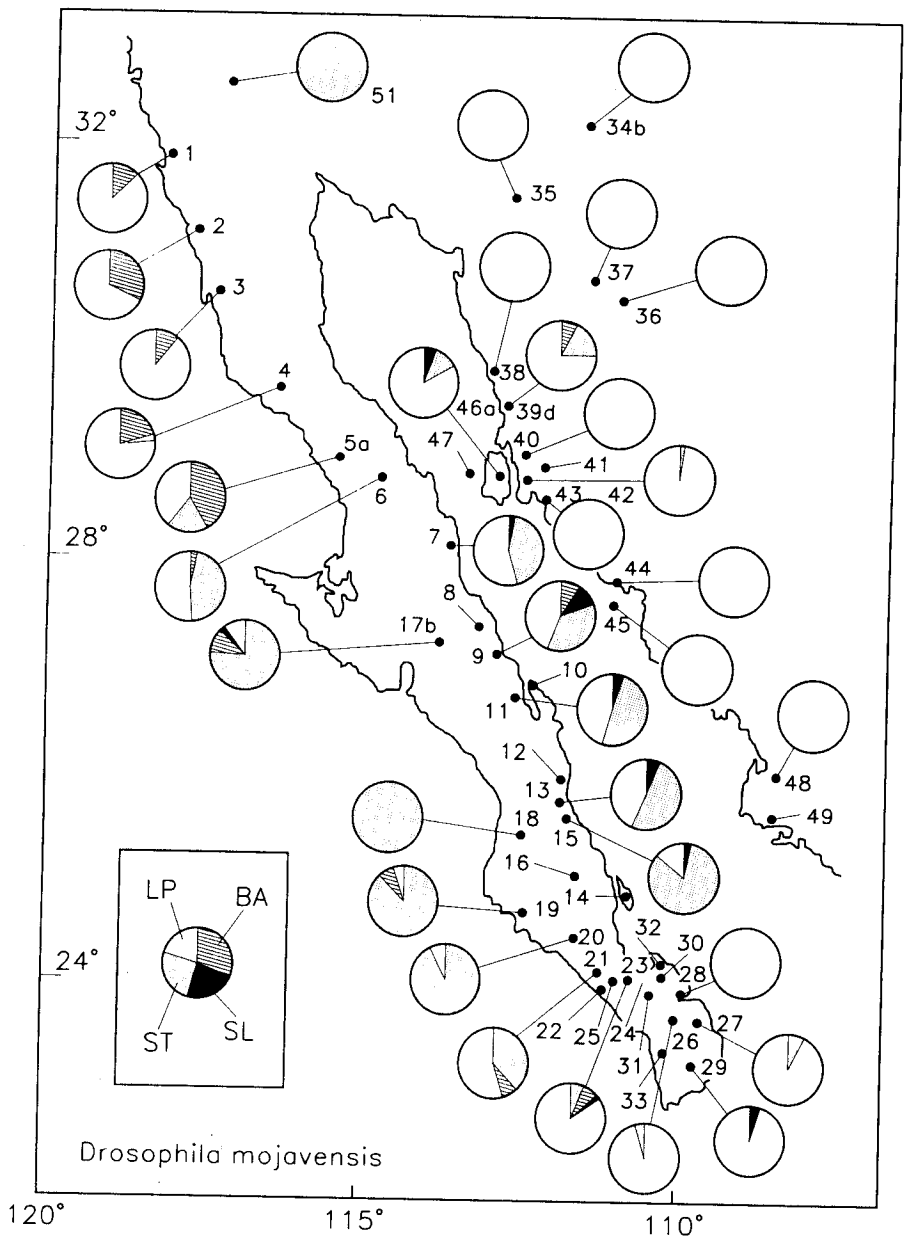

Figure 6.5 *(opposite page)* Geographical variation in chromosome 2 gene arrangement frequency in the majority of the sampled populations of *Drosophila mojavensis*. Numbers refer to localities in appendix 6.1. Locality 50, Santa Catalina Island, is not included in the figure. The remaining sampled populations are found in Ruiz et al. (1990).

the nonarbitrary grouping of populations within the vegetational subdivisions, as well as comparing these results with previous analyses of population structure in *D. pseudoobscura* and *D. subobscura* (Wright 1978; Ferrari and Taylor 1981).

Populations were grouped into the vegetational subdivisions as objectively as possible, even when obvious transition zones were apparent (Johnson 1980). The Central Gulf Coast populations were separated into either peninsular (including the islands in the Gulf of California close to the peninsula) or mainland (including the islands of Tiburón and San Pedro Nolasco) regions. This was done because of the large differences between populations in these regions due to isolation caused by the Gulf of California. The Santa Catalina Island population was grouped with the southern California population because these populations share similar chromosomal constitutions. Later, however, the island was found to have closer vegetational affinities with the San Pedro Martir subdivision and was designated Coastal Sage (Axelrod 1978), even though the karyotypic affinity of *Drosophila mojavensis* on the island lies with the Vallecito sample and other collections in southern California and not with the San Pedro Martir populations (see fig. 6.1; fig. 6.5; appendix 6.1; Ruiz et al. 1990).

We also estimated the extent of population structure using host cacti as natural groups. For *Drosophila pachea,* the three subspecies of senita were used, *Lophocereus schottii schottii, L. s. tenuis,* and *L. s. australis.* For *D. mojavensis,* these groups were agria, organ pipe, California barrel, and *Opuntia* cacti.

Relation to the Vegetational Subdivisions

Both *Drosophila mojavensis* and *D. pachea* populations exhibited significant levels of karyotypic variation at all levels of the hierarchical analysis (table 6.1; table 6.2). Even though population sampling was carried out in different years by different investigators, and in many cases different populations were sampled within subdivisions (appendix 6.1; appendix 6.2),

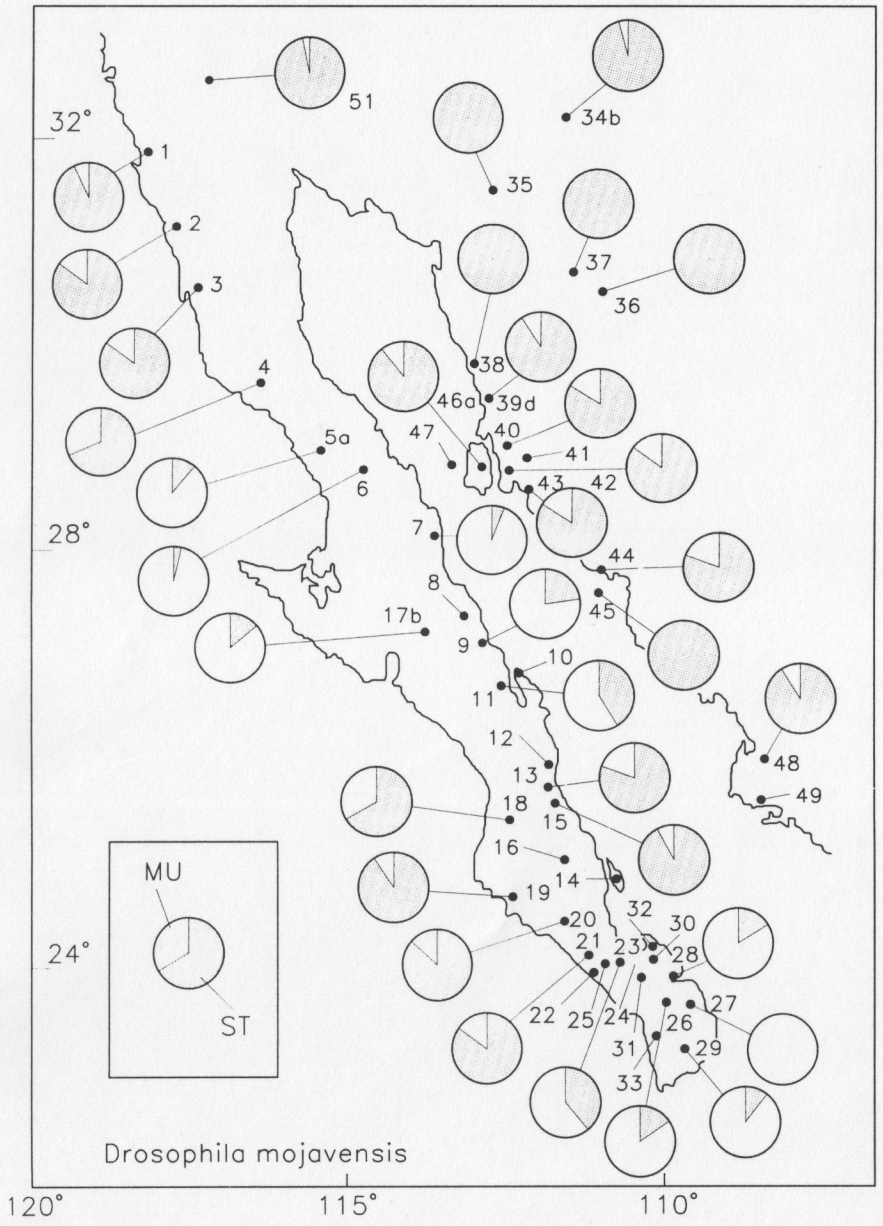

Figure 6.6 *(opposite page)* Geographical variation in chromosome 3 gene arrangement frequency in the majority of the sampled populations of *Drosophila mojavensis*. Numbers refer to localities in appendix 6.1. Locality 50, Santa Catalina Island, is not included in the figure. The remaining sampled populations are found in Ruiz et al. (1990).

both species showed significant within-population, among-population-within-subdivision, and among-subdivision variation in karyotype frequency. We were most interested in the among-subdivision levels of variation (Φ_{ct}), for at this level we can investigate the effects of the vegetational subdivisions on karyotype variation relative to other levels. Only qualitative comparisons can be made between variance components because confidence intervals around them are currently unavailable, yet these comparisons lead to some intriguing insights. When all populations were included, *D. pachea* exhibited greater genetic variance between subdivisions (61.47% of the variance, $\Phi_{ct} = 0.615$) than *D. mojavensis* (27.88% of the variance, $\Phi_{ct} = 0.279$). At first, this result suggested that populations of *D. pachea* were much more structured around the ecological pattern of the vegetational subdivisions than those of *D. mojavensis,* whether or not the Central Gulf Coast (CGC) populations were separated into Baja and mainland groups (table 6.1; table 6.2). However, after removing the Sinaloan thornscrub (STS) subdivision and reanalyzing the remaining data, estimates of Φ_{ct} and F_{rt} for *D. pachea* approached those of *D. mojavensis*. Populations of *D. pachea* in the STS subdivision are all homokaryotypic for 7 + except for three 7 +/A heterokaryotypes found near Ciudad Obregon (Ward et al. 1975). Therefore, much of the apparent intersubdivision structure was due to the influence of these STS populations.

We sequentially removed other subdivisions in a similar fashion and reanalyzed the remaining data. Removal of the Lower Colorado populations further decreased Φ_{ct} and F_{rt} and when populations from Baja California were reanalyzed by themselves, no significant difference among subdivisions was apparent (all data [STS, LC, PLS, ARIZ] analysis, table 6.2). A similar approach was used for *Drosophila mojavensis* and a negligible reduction in among-subdivision variation was detected after removing all mainland populations except the mainland CGC populations (table 6.1). Therefore, both species exhibited low, but significant, karyotypic variation between vegetational subdivisions in the Sonoran Desert. The

Table 6.1 Results of hierarchical population structure analyses in *Drosophila mojavensis* for both AMOVA analyses and Wright's F statistics for karyotypic variation within and between 51 populations.

Variance Components	df	Variance	% Total	P[a]	Φ Statistics[b] F Statistics
A. Among Subdivisions					
All data $-\sigma^2_a$	9	0.761	27.88	< 0.02	$\Phi_{ct} = 0.279$
	9	0.098	22.89	< 0.02	$F_{rt} = 0.229$
All data (STS, LC, ARIZ)[c] $-\sigma^2_a$	6	0.744	25.39	< 0.02	$\Phi_{ct} = 0.254$
	6	0.081	18.28	< 0.02	$F_{rt} = 0.183$
Among Populations within Subdivisions					
All data $-\sigma^2_b$	41	0.783	28.69	< 0.02	$\Phi_{sc} = 0.398$
	41	0.103	24.22	< 0.02	$F_{dr} = 0.314$
All data (STS, LC, ARIZ) $-\sigma^2_b$	36	0.801	27.31	< 0.02	$\Phi_{sc} = 0.254$
	36	0.102	22.87	< 0.02	$F_{dr} = 0.280$
Among Individuals within Populations					
All data $-\sigma^2_c$	2289	1.185	43.44	< 0.02	$\Phi_{st} = 0.566$
	2289	0.226	52.89	< 0.02	$F_{id} = 0.471$
All data (STS, LC, ARIZ) $-\sigma^2_c$	1951	1.387	47.30	< 0.02	$\Phi_{st} = 0.527$
	1951	0.262	58.85	< 0.02	$F_{id} = 0.411$
B. Among Host Plants[d]					
All data $-\sigma^2_a$	3	0.615	20.26	< 0.02	$\Phi_{ct} = 0.203$
	3	0.128	25.57	< 0.02	$F_{rt} = 0.256$
Among Populations within Cactus Species					
All data $-\sigma^2_b$	47	1.237	40.73	< 0.02	$\Phi_{sc} = 0.511$
	47	0.145	29.13	< 0.02	$F_{dr} = 0.391$
Among Individuals within Populations					
All data $-\sigma^2_c$	2289	1.185	39.01	< 0.02	$\Phi_{st} = 0.610$
	2289	0.226	45.30	< 0.02	$F_{id} = 0.547$

Note: The 51 populations are grouped according to (A) the vegetational subdivisions in and around the Sonoran Desert, and (B) the major host plants used by *D. mojavensis*. The data are from appendix 6.1. See text for details.

[a] The probability that the observed variance components, Φ statistics, and F statistics would be larger by chance alone. Following Excoffier et al. (1992), Φ_{ct} and σ^2_a were tested by 50 random permutations of populations across regions, Φ_{sc} and σ^2_b were tested by 50 random permutations of individuals across populations but within the same region, and Φ_{st} and σ^2_c were tested by 50 random permutations of individuals across populations without specifying populations or regions.

[b] For each level of analysis, results of the AMOVA analyses are listed in the first line of each pair, with Wright's F statistics listed in the second line. Subscripts for Φ statistics are consistent with Excoffier et al. (1992). Subscripts for F statistics are consistent with Wright (1978), except for F_{id}, which is used here because these analyses are based on karyotypes rather than inversion frequencies. F_{rt} is the correlation between randomly chosen karyotypes within a group of populations relative to the entire species, F_{dr} is the correlation between randomly picked karyotypes within populations relative to that of the region, and F_{id} is the correlation of random karyotypes within populations relative to the entire species.

[c] Abbreviations in parentheses refer to the vegetational subdivisions that were excluded in each analysis. See appendix 6.1 for abbreviations.

[d] In this analysis, host cactus replaces subdivision: the host cacti are *Stenocereus gummosus*, *S. thurberi*, *Ferocactus cylindraceous*, and *Opuntia demissa*.

steep transition across the STS into the Sonoran Desert in southern Sonora almost entirely coincident with a shift in host subspecies use is the most notable aspect of karyotype variation in *D. pachea*.

It would not be possible to infer causes for the subdivision-related karyotype differences between *Drosophila mojavensis* and *D. pachea* if other independent genetic data were unavailable. However, Rockwood-Sluss et al. (1973) suggested that little population structure existed across the range of *D. pachea* based upon an absence of allelic variation at four protein encoding loci among eleven mainland populations. Furthermore, they found that a single population from Guaymas, Sonora (fig. 6.4, population 34) contained as much genetic variability as all the populations taken together. Such genetic uniformity among partially isolated populations is most parsimoniously explained as the result of gene flow, which homogenizes gene frequencies, particularly at enzyme encoding loci. *Drosophila pachea* adults must therefore be capable of dispersing long distances. In fact, Johnston (1974) concluded, based on intensive mark-recapture studies, that the size of mainland populations of *D. pachea* are on average smaller than those of *D. mojavensis* and that *D. pachea* individuals migrate further. The population structuring based on karyotype variability at the level of vegetational subdivisions in *D. pachea* must therefore result from forces strong enough to overcome gene flow, i.e., natural selection shaping karyotypic frequencies in response to local ecological conditions. Similar patterns exist for *D. mojavensis* based on allozyme variation (Zouros 1973), particularly at the Adh-2 locus (Starmer et al. 1977), but mainland *D. mojavensis* populations are nearly homokaryotypic for second chromosome gene arrangements, except for several that use agria (*Stenocereus gummosus*) and exhibit limited third chromosome polymorphism (fig. 6.3; fig. 6.5; fig. 6.6).

For *Drosophila mojavensis*, 43.44% of the overall variability (Φ_{st} = 0.566) was found within populations, contrasting with 22.86% (Φ_{st} = 0.771) in *D. pachea*. Φ_{st} is an estimate of the correlation between karyotypes within the same population relative to randomly chosen karyotypes across the entire species. The magnitude of Φ_{st}, as well as F_{id} (among individuals within demes), decreased somewhat and the percent of the total variance increased as mainland groups were removed, as described above. In local populations, these large Φ_{st} are expected simply on the basis of local panmixia relative to the karyotypic variation in *D. mojavensis* and *D. pachea* populations throughout their respective ranges. There is

Table 6.2 Results of hierarchical population structure analyses in *Drosophila pachea* for both AMOVA analyses and Wright's F statistics for karyotypic variation within and between 58 populations.

Variance Components	df	Variance	% Total	P[a]	Φ Statistics[b] F Statistics
A. Among Subdivisions					
All data — σ^2_a	8	0.515	61.47	< 0.02	$\Phi_{ct} = 0.615$
	8	0.144	45.09	< 0.02	$F_{rt} = 0.451$
All data (CGC combined)[c] — σ^2_a	7	0.520	60.69	< 0.02	$\Phi_{ct} = 0.607$
	7	0.146	44.92	< 0.02	$F_{rt} = 0.449$
All data (STS)[d] — σ^2_a	7	0.170	31.23	< 0.02	$\Phi_{ct} = 0.312$
	7	0.061	23.08	< 0.02	$F_{rt} = 0.231$
All data (STS, LC)[d] — σ^2_a	6	0.149	24.46	< 0.02	$\Phi_{ct} = 0.245$
	6	0.052	17.49	< 0.02	$F_{rt} = 0.175$
All data (STS, LC, PLS, ARIZ)[d] — σ^2_a	4	0.095	14.82	ns	$\Phi_{ct} = 0.148$
	4	0.027	8.66	ns	$F_{rt} = 0.087$
Among Populations within Subdivisions					
All data — σ^2_b	49	0.131	15.67	< 0.02	$\Phi_{sc} = 0.407$
	49	0.040	12.42	< 0.02	$F_{dr} = 0.226$
All data (CGC combined) — σ^2_b	50	0.145	16.97	< 0.02	$\Phi_{sc} = 0.432$
	50	0.043	13.31	< 0.02	$F_{dr} = 0.242$
All data (STS) — σ^2_b	44	0.152	27.82	< 0.02	$\Phi_{sc} = 0.405$
	44	0.047	17.27	< 0.02	$F_{dr} = 0.225$
All data (STS, LC) — σ^2_b	35	0.191	31.28	< 0.02	$\Phi_{sc} = 0.414$
	35	0.057	19.08	< 0.02	$F_{dr} = 0.231$
All data (STS, LC, PLS, ARIZ) — σ^2_b	28	0.230	35.82	< 0.02	$\Phi_{sc} = 0.421$
	28	0.069	21.67	< 0.02	$F_{dr} = 0.237$
Among Individuals within Populations					
All data — σ^2_c	2227	0.192	22.86	< 0.02	$\Phi_{st} = 0.771$
	2227	0.135	42.50	< 0.02	$F_{id} = 0.575$
All data (CGC combined) — σ^2_c	2227	0.192	22.34	< 0.02	$\Phi_{st} = 0.777$
	2227	0.135	41.77	< 0.02	$F_{id} = 0.582$
All data (STS) — σ^2_c	1893	0.224	40.95	< 0.02	$\Phi_{st} = 0.591$
	1893	0.158	59.65	< 0.02	$F_{id} = 0.404$
All data (STS, LC) — σ^2_c	1522	0.270	44.26	< 0.02	$\Phi_{st} = 0.557$
	1522	0.188	63.42	< 0.02	$F_{id} = 0.366$
All data (STS, LC, PLS, ARIZ) — σ^2_c	1255	0.317	49.35	< 0.02	$\Phi_{st} = 0.506$
	1255	0.221	69.66	< 0.02	$F_{id} = 0.303$
B. Among Senita Cactus Subspecies[e]					
All data — σ^2_a	2	0.742	72.74	< 0.02	$\Phi_{ct} = 0.727$
	2	0.181	50.25	< 0.02	$F_{rt} = 0.502$
Among Populations within Cactus Subspecies					
All data — σ^2_b	55	0.087	8.49	< 0.02	$\Phi_{sc} = 0.311$
	55	0.044	12.21	< 0.02	$F_{dr} = 0.245$
Among Individuals within Populations					
All data — σ^2_c	2227	0.192	18.77	< 0.02	$\Phi_{st} = 0.812$
	2227	0.135	37.54	< 0.02	$F_{id} = 0.625$

Table 6.2 continued

Note: The 58 populations are grouped according to (A) the vegetational subdivisions in and around the Sonoran Desert, and (B) the three subspecies of senita cactus. The data from appendix 6.2 were combined with all published (Ward et al. 1975) and unpublished *D. pachea* karyotype data. See text for details.

[a] The probability that the observed variance components, Φ statistics, and F statistics would be larger by chance alone. Following Excoffier et al. (1992), Φ_{ct} and σ^2_a were tested by 50 random permutations of populations across regions, Φ_{sc} and σ^2_b were tested by 50 random permutations of individuals across populations but within the same region, and Φ_{st} and σ^2_c were tested by 50 random permutations of individuals across populations without specifying populations or regions.

[b] For each level of analysis, results of the AMOVA analyses are listed in the first line of each pair, with Wright's F statistics listed in the second line. Subscripts for Φ statistics are consistent with Excoffier et al. (1992). Subscripts for F statistics are consistent with Wright (1978), except for F_{id}, which is used here because these analyses are based on karyotypes rather than inversion frequencies. F_{rt} is the correlation between randomly chosen karyotypes within a group of populations relative to the entire species, F_{dr} is the correlation between randomly picked karyotypes within populations relative to that of the region, and F_{id} is the correlation of random karyotypes within populations relative to the entire species.

[c] All Central Gulf Coast populations from both sides of the Gulf of California combined into one group.

[d] Abbreviations in parentheses refer to the vegetational subdivisions that were excluded in each analysis. See appendix 6.2 for abbreviations.

[e] In this analysis, cactus subspecies replace subdivisions: the subspecies are *Lophocereus schottii* var. *schottii*, *L. s.* var. *tenuis*, and *L. s.* var. *australis*.

no commonly used F statistic at this level because our analyses are based on karyotype frequencies, not inversion frequencies.

Estimates of Φ_{sc} and F_{dr}, reflecting karyotypic correlations among populations within subdivisions relative to the correlation between randomly picked karyotypes, were similar in both species. At this level of population structuring, overall karyotypic variation within vegetational subdivisions was not markedly different between species.

Comparisons with Other Species

Comparisons of population structure with other *Drosophila* species are potentially difficult to interpret because of differences in absolute sizes of species' ranges and the lack of breeding site data. Other studies involve large-scale differentiation over continent-wide ranges in North American *D. pseudoobscura* (Wright 1978) and European and northwest African *D. subobscura* (Ferrari and Taylor 1981) that were collected by trapping; i.e., breeding sites for these species are not known except in a few cases (Carson 1951; Begon 1976). There has been no analysis of how breeding site variation (as opposed to meteorological variation) in these species might influence inversion polymorphism or gene flow in natural populations.

Trapping (or baiting) can significantly distort estimates of dispersal and, thus, population structure, because movement is strongly correlated with the distance between traps (Johnston and Heed 1975). Also, grouping into regions in such large-scale studies has been somewhat subjective, based on geographic proximity (Wright 1978) and "proximity and the probable paleolithic distribution of the species" (Ferrari and Taylor 1981).

Nevertheless, extensive population structuring has been reported across the ranges of *Drosophila pseudoobscura* and *D. subobscura* based on inversion frequencies. We can compare only two levels of population structure given the AMOVA results: F_{rt}, variation among regions within a species, and F_{dr}, variation among populations within regions. For *D. pseudoobscura*, $F_{rt} = 0.322$ and $F_{dr} = 0.075$, based on 87 populations grouped into 15 regions. For *D. subobscura*, $F_{rt} = 0.208$ and $F_{dr} = 0.149$, based on 38 populations grouped into 10 regions. Both studies also included groupings of regions in the hierarchy that we did not. Judging by the reported variation across the ranges of each species, the vegetational subdivisions in and around the Sonoran Desert are most similar to the regions, in terms of scale, used by Wright (1978) and Ferrari and Taylor (1981). *Drosophila pachea* showed the highest degree of variation among regions, but we have already demonstrated that this is due to the large effect of the STS populations. With this region removed from the analysis, F_{rt} declined from 0.451 to 0.231. It is striking to us that this single region has such a large effect on population structure in *D. pachea*, lowering the magnitude of the among-region variation to below that calculated for *D. pseudoobscura*, which included populations from British Columbia and northwestern California to Guatemala and Colombia. When Wright (1978) considered only populations north of Mexico, F_{rt} decreased to 0.213. Thus, genetic differentiation of populations of *D. mojavensis* and *D. pachea* among the smaller-scaled vegetational subdivisions of the desert and adjacent areas is similar to that of all European populations of *D. subobscura* and United States and Canadian populations of *D. pseudoobscura*.

The degree of interdemic variation within regions, F_{dr}, was lower in both widespread species, particularly *Drosophila pseudoobscura*. F_{dr} was approximately twice the value in the desert species than in the others, showing a much finer scale of variation even among populations within subdivisions. This is probably the result of the method of measurement, i.e., *D. pseudoobscura* and *D. subobscura* were grouped according to regional similarity of inversion frequencies while among-population-within-subdivision structuring in *D. mojavensis* and *D. pachea* was measured independently of karyotypic similarity and in accordance with the vegetational subdivisions. There is also the potential that host plant effects have played a major role in the level of local population structuring in the desert species.

Variation Correlated with Substrate

Drosophila pachea

Since *Drosophila pachea* can essentially use only senita cactus as a host plant, the three subspecies were partitioned to determine any effect they may have on karyotype frequencies. Results of this AMOVA analysis for populations grouped by subspecies revealed large Φ_{ct} and F_{rt}, indicating strong karyotypic differences associated with them (table 6.2B).

The average frequency of the 7 + chromosome among *Drosophila pachea* populations associated with the three cactus subspecies was 0.060 for *Lophocereus schottii schottii*, 0.258 for *L. s. australis*, and 0.804 for *L. s. tenuis*. There were no significant karyotypic differences between populations using *L. s. schottii* in Baja California and those from Sonora, so the two areas have been treated as a unit. An analysis of variance testing for the differences among populations that use the different host plant subspecies was also highly significant ($F = 99.99$, $P < .001$). Host plant use accounted for 80.64% of the total variance in inversion frequencies among *D. pachea* populations. These large differences are a reflection of the high values of $\Phi_{ct} = 0.727$ and $F_{rt} = 0.502$ mentioned above and found in table 6.2B.

On the mainland, the steep transition in inversion frequency from the midpart of the Central Gulf Coast subdivision in the vicinity of Bahía Kino into the Sinaloan thornscrub is coincident in the Guaymas region with the replacement of *Lophocereus schottii schottii* with *L. s. tenuis* (fig. 6.2; fig. 6.4). This apparent coincidence is a problem for disentangling the effects of host plants and subdivisions on inversion frequencies. However, the Guaymas–San Carlos–Empalme area lies within the Central Gulf Coast subdivision and is inhabited by the westward extension of *L. s. tenuis* from the Sinaloan thornscrub (Lindsay 1963). This subspecies also extends directly north into the Plains of Sonora as far as Hermosillo (Lindsay 1963).

A total of 236 karyotypes analyzed from the Hermosillo and Guaymas areas (appendix 6.2) exhibited the highest heterozygosity, 0.453, of chro-

mosome 7 in *Drosophila pachea* on the mainland. The average frequency of the 7 + arrangement was 0.669 in these populations. It is the abrupt step from this frequency to an average frequency of 0.996 (n = 170 individuals) in the Sinaloan thornscrub that has probably given the STS its large effect in the analyses of population structure (table 6.2).

In summary, the shift from *Lophocereus schottii schottii* to *L. s. tenuis* in the Guaymas region was accompanied by high heterozygosity for chromosome 7 in *Drosophila pachea* populations (see also Ward et al. 1975). Similarly, *L. s. schotti* merges with *L. s. australis* near La Paz in and around the Cape region in Baja California (Lindsay 1963), and these populations are characterized by the highest heterozygosities for *D. pachea* in the peninsula (0.489, n = 91 individuals). The average frequency of the 7 + gene arrangement in these populations (nos. 8 to 16, appendix 6.2) was 0.505. Notice that San Agustin and La Aguja are listed in the Magdalena Plain subdivision while E. La Paz is located within the Central Gulf Coast subdivision. Thus *L. s. australis* extends beyond the Cape Region, analogous to the extension of *L. s. tenuis* in the Guaymas area on the mainland. Shreve (1937) characterized the transition from the desert to the Cape as an interdigitation of the two regions over rugged and varied country rather than a gradual transition over many kilometers, as occurs with the merging of the desert with the thornscrub in Sonora.

South of La Paz the samples in appendix 6.2 may be readily pooled into groups according to similarity in gene arrangement frequencies within similar geographic areas. A cline in frequencies of the 7 + gene arrangement was also present west of the Sierra La Laguna from the San Pedro area (frequency of 7 + = 0.186), directly south to the tip of the peninsula at Cabo San Lucas and then north on the east side of the sierras (frequency of 7 + = 0.138) to San Bartolo (frequency of 7 + = 0.037). Other interpretations for the Cape region must include a varied and patchy distribution of the 7 + gene arrangement. Even so, the difference in frequencies between the latter two areas mentioned is significant (G = 12.674, $P < .005$) and they are only 25 km apart.

Collection records north of La Paz indicate a gradual increase of the 7 + gene arrangement until ca. 27° N lat. where it decreases to zero. Up to this point the frequencies north and south of La Paz are mirror images, except the distances involved are much less in the Cape region.

The overall characteristics of the two major tropical subspecies, *Lophocereus schottii tenuis* and *L. s. australis*, are the presence of more and thinner stems with a correspondingly higher number of ribs (Borg 1937; Lindsay 1963). In addition, *L. s. australis* has a noticeable trunk, which makes it more treelike than the others (Lindsay 1963; Cody 1984; fig. 6.2). Cody (1984) also recorded a significantly greater amount of stem branching in *L. s. australis* than in *L. s. schottii* in Baja California.

That changes in the diameter of the stems are gradual, at least on the mainland, has been observed by Felger and Lowe (1967) and Nobel (1980). Felger and Lowe (1967) reported a cline in surface-volume ratio of the stems. The ratio increased gradually southward from Sonoita to Bahía Kino and then more abruptly from there and from Hermosillo to the Playa Cochorit-Potam area south of Guaymas. The correlation of the transformed clinal frequency of the 7 + gene arrangement of *Drosophila pachea* to this ratio, and also the increasing rib number, was shown to be significant in both cases (Ward et al. 1975).

Nobel (1980) measured midstem diameter of senita populations along approximately the same transect as Felger and Lowe (1967). His data illustrate that plants in the three northern localities have significantly greater mean stem diameters, in both mature and immature stems, than the plants in the three more southern localities (mature stems: t = 14.41; $P < .01$; $n_1 = n_2 \cong 50$; immature stems: t = 12.51; $P < .01$; $n_1 = n_2 \cong 50$). Furthermore, the rate of change in relation to latitude increased from Hermosillo to San Carlos and then to Obregon, the southern localities, as did the rate of change in the frequency of the 7 + gene arrangement.

From these two sets of data it appears that *Lophocereus schottii tenuis* responds to a change in latitude to a greater degree than *L. s. schottii*. The important characteristic of senita cacti in regard to the larvae of *Drosophila pachea* is probably the diameter of the stem, because it could indirectly influence larval development time. The fermenting tissues in thicker stems should ultimately allow for slower developmental rates since these rots, on average, should be longer lived.

This scenario is in agreement with the data for the mainland, yet it is only partially in agreement in the Cape region where there is a decrease in frequency of the 7 + gene arrangement southeast from La Paz. The Cape region exhibits a cline in the reverse direction compared to the mainland as previously discussed. Duncan (1979) also found a reverse cline in rib number for the Cape and that the correlation with the 7 + arrangement was positive and significant. Duncan recorded the lowest rib number on all plants scored with a mean of nine ribs in the La Paz region, which

gradually declined to a mean of six ribs near Cabo San Lucas at the tip of the peninsula. However, since senita stem diameter has not been directly measured in the Cape region, to our knowledge, this correlation only suggests senita stems increase in width to the southeast. A possible regulating factor in this context is the presence of an isolated section of the Central Gulf Coast subdivision of the desert in the southeast corner of the Cape north of 23° N lat. Shreve (1964) noted the similarity in aspect and composition of this area to the region around Bahía Concepción between 26° and 27° N lat. The frequencies of the 7 + gene arrangement are similar near both areas.

Drosophila mojavensis

The host plants and their distribution have been described earlier in this chapter for *Drosophila mojavensis*. It is clear that karyotypic variation is host plant related; without exception, all heterozygosity on the second chromosome has been found in pitahaya agria–inhabiting *D. mojavensis* populations. This association is epitomized by two samples separated by 50 km of uninterrupted desert in coastal Sonora. One collection taken from pitahaya agria (locality 39d, appendix 6.1) was polymorphic with the frequencies of LP = 0.78, ST = 0.18, and BA = 0.04, while the sample from an organ pipe population (locality 40) was homozygous for LP. ST/ST homokaryotypes are found throughout southern California and the Grand Canyon in barrel cactus–breeding populations and in Santa Catalina Island populations that use *Opuntia*. LP is fixed throughout the organ pipe–breeding and sina-breeding populations in southern Arizona, Sonora, and Sinaloa. Genetic differentiation mediated by the cacti has also been proposed by Richardson et al. (1977) for allozyme frequencies. This substrate correlation does not hold true, however, for heterozygosity on the third chromosome of *D. mojavensis* because of the presence of MU in many of the populations along coastal Sonora where agria is not present.

The AMOVA results confirm this host-karyotype association (table 6.1B) as well as significant variation between populations using the same host, and a large within-population correlation among karyotypes as seen when the populations were grouped according to the vegetational subdivisions. Significant Φ_{sc} and F_{dr}, indicative of significant variation among populations using particular hosts, were due to the degree of polymorphism among populations using the same hosts. Several Baja California populations of *Drosophila mojavensis* are homokaryotypic for both second and third chromosome gene arrangements, and some organ pipe–breeding populations are polymorphic for the third chromosome while others are not (fig. 6.5; fig. 6.6). Thus, other factors, particularly plant density and host preference behavior, as well as direct climatic influences have been included as factors controlling inversion polymorphism.

A large portion of southern Baja California, most of the islands in the Gulf, and the Desemboque region on the mainland are occupied by both agria and organ pipe cacti. However, our rearing records from these areas, which extend beyond 30 years, show very few instances of the use of organ pipe in this region of overlap. Adult *Drosophila mojavensis* also tend to prefer the volatile profiles of agria over organ pipe cacti in choice tests (Downing 1985; Fogleman and Heed 1989; Newby and Etges 1998). *D. mojavensis* probably uses agria to a greater degree because it is consistently a more abundant and uniform trophic resource. Pitahaya agria plants frequently grow in large thickets of interconnected stems that reproduce themselves mainly by vegetative growth. Organ pipe cacti rely entirely on fruiting and animal dispersion of seeds and therefore grow as individual plants. The density of agria stems can exceed that of organ pipe stems by seven times, yet agria stems are on average half the diameter of organ pipe stems. Most significantly, rot densities can be approximately 40 times higher in agria than in organ pipe cacti in certain localities (Mangan 1982). Therefore, agria is a more predictable resource for ovipositing adults, but organ pipe rots last longer when they occur, due to larger stem diameters (Heed 1981; Heed and Mangan 1986; Etges and Heed 1987).

Rot density, or trophic predictability, is probably the most significant factor influencing population structure, as it will determine levels of rot-to-rot dispersal and, therefore, gene flow among demes (Endler 1979). Studies of dispersal, similar to Johnston (1974), have yet to be undertaken in Baja, where inter-rot migration in agria-inhabiting populations of *Drosophila mojavensis* is suspected to be lower than in organ pipe–inhabiting populations because of the higher abundance of agria rots. Higher density and aggregation of rots in agria patches vs. organ pipe patches represents a major shift in trophic predictability and has influenced the evolution of life history differences between Baja and mainland *D. mojavensis* (Etges and Heed 1987). Baja California populations have shorter egg-to-adult development times and show greater genetic homeostasis (more constant expression of life history traits), with increasing larval densities, than mainland populations. This is associated with higher

rates of tissue fermentation in agria than in organ pipe cacti (Etges 1989b). Longer development times, on the other hand, usually engender larger adult body size and reproductive potential in *Drosophila;* this is also the case in *D. mojavensis* (Etges and Heed 1992). Therefore, the longer egg-to-adult development times of mainland *D. mojavensis* are probably an adaptation resulting from the greater longevity of breeding sites that produce larger adults better able to disperse between the comparatively rarer, but larger, organ pipe rots (Etges 1993).

In summary, the switch to organ pipe from pitahaya agria has caused a number of shifts in the life history, physiology, and behavior of *Drosophila mojavensis* with a concomitant loss of significant heterozygosity for chromosomal inversions. For these reasons, *D. mojavensis* is considered to consist of at least two host races (Etges 1990).

Variation Correlated with Climate

A direct assessment was made of covariation of inversion heterozygosity and annual temperature fluctuation for populations of *Drosophila mojavensis* and *D. pachea.* The rationale for this approach is as follows: heterozygosity is a convenient measure of karyotypic variability within populations of *Drosophila* that frequently results from balancing selection (Lewontin et al. 1981). This approach does not assume that there is selection for heterozygosity per se, only that polymorphism is retained because of variable selection (see Orzack 1985; Etges 1989b for further details). Because precipitation and average temperature fluctuation through the year are among the principal causes for the formation of the vegetational subdivisions (Hastings and Turner 1965; Turner and Brown 1982), we calculated average annual temperature range, TMR, by taking the difference between the highest average monthly temperature and lowest average monthly temperature recorded at the nearest weather station (Hastings and Humphrey 1969a, 1969b). Inversion heterozygosity was calculated using $h_x = 1 - \Sigma x_i^2$, where x_i is the frequency of the i^{th} gene arrangement (appendix 6.1; appendix 6.2). Correlations were calculated between arcsine transformed heterozygosity values and TMR, degrees latitude, degrees longitude, and elevation above sea level of the weather station nearest to each population. Populations were separated into mainland and Baja groups prior to analysis.

Inversion heterozygosity was negatively correlated with TMR and elevation in *Drosophila pachea* on the mainland and marginally so on the peninsula (table 6.3). Levels of chromosome polymorphism in *D. pachea* were therefore lowest in populations experiencing the greatest annual temperature fluctuations, such as in the Lower Colorado and Arizona Upland subdivisions. Heterozygosity increased along Baja California to the south near La Paz and then decreased in the southern Cape region as the frequency of 7 A increased (fig. 6.4). Thus the possibility of finding a basis for variable selection due to temperature variation has not been realized. In fact, the response of average heterozygosity (HBAR) on the mainland compared to Baja was quite different. Significant correlations, all negative, were found for latitude and longitude in Baja California but with TMR and elevation on the mainland. TMR was strongly correlated with latitude, longitude, and elevation on the mainland, but less so on the peninsula due to the prevailing maritime conditions and the lack of weather stations at consistently higher elevations.

Duncan (1979) suggested that the pattern of heterozygosity in Baja California resulted from secondary contact of isolated populations after the Cape region was rejoined to the peninsula during the Pleistocene, prior to which it was an island. However, the area of highest heterozygosity on the mainland is localized in the Guaymas region and thus resembles the region around La Paz with respect to placement on the southern edge of the desert. It is this phenomenon which could be most significant. In sum, inversion polymorphism in *Drosophila pachea* seems unrelated to local temperature fluctuations that could cause fluctuating selection, suggesting that host plant use is a major determinant of the degree of inversion polymorphism in this species (but see Ward et al. 1975).

Because of the disparity in the distribution of polymorphism between mainland and Baja populations of *Drosophila mojavensis,* most of the correlations with heterozygosity were found for Baja populations. TMR was uncorrelated with heterozygosity of either chromosome. Both latitude and longitude were positively associated with heterozygosity on the second chromosome due to the number of populations close to fixation in southern Baja and the Cape region. Throughout the range of *D. mojavensis,* levels of second and third chromosome heterozygosity were uncorrelated (table 6.3), suggesting these polymorphisms are influenced by other factors.

Environmental variables in *Drosophila pachea* and *D. mojavensis*.

	HBAR	TMR	LAT	LONG	ELEV
D. pachea					
HBAR	–	−0.453***	−0.223	0.067	−0.416**
		(50)	(49)	(44)	(44)
TMR	−0.360+	–	0.756***	0.686***	0.434***
	(28)		(81)	(76)	(76)
LAT	−0.508**	0.409**	–	0.832***	0.742***
	(28)	(60)		(76)	(76)
LONG	−0.450*	0.218+	0.966***	–	0.333**
	(28)	(60)	(60)		(76)
ELEV	−0.247	0.281*	0.303*	0.264*	–
	(28)	(59)	(59)	(59)	
D. mojavensis					
	H2BAR	H3BAR	HBAR	TMR	LAT	LONG	ELEV
H2BAR	–	0.208	0.776***	0.198	−0.010	0.025	0.241
		(21)	(21)	(19)	(21)	(21)	(15)
H3BAR	0.0516	–	0.764***	0.093	−0.199	−0.073	−0.481+
	(37)		(21)	(19)	(21)	(21)	(15)
HBAR	0.813***	0.622***	–	0.219	−0.115	−0.021	−0.476+
	(37)	(37)		(19)	(21)	(21)	(15)
TMR	0.186	0.150	0.228	–	0.244+	−0.032	0.022
	(37)	(37)	(37)		(61)	(61)	(55)
LAT	0.576***	−0.102	0.395*	0.230+	–	−0.128	0.602***
	(37)	(37)	(37)	(71)		(63)	(55)
LONG	0.433**	−0.092	0.290+	0.042	0.949***	–	0.107
	(37)	(37)	(37)	(71)	(71)		(55)
ELEV	−0.043	−0.039	−0.056	0.176	0.195	0.173	–
	(28)	(28)	(28)	(62)	(62)	(62)	

Note: TMR is defined in Appendix 6.1, LAT is degrees latitude, LONG is degrees longitude, and ELEV is distance above sea level. HBAR is average heterozygosity. For *D. mojavensis*, H2BAR is observed second chromosome heterozygosity, and H3BAR is observed third chromosome heterozygosity. Values above the diagonal refer to mainland populations, and those below the diagonal to Baja California populations. Values in parentheses are sample sizes. See Appendices 6.1 and 6.2 for those populations included in the analyses. Additional meteorological data were taken from weather stations listed in Hastings and Humphrey (1969a, 1969b). Some data were missing.

+ $0.10 \leq p \geq .05$. * $p \leq .05$. ** $p \leq .01$. *** $p \leq .001$.

Inversion Phylogeny and the History of the Sonoran Desert

Distance trees were constructed based on the inversion frequencies in *Drosophila mojavensis* using PHYLIP (ver. 3.51c; Felsenstein 1993) to further scrutinize population structuring. We were most interested in assessing the shape of the tree with respect to the clustering of populations in the phytogeographic subdivisions. Inversions were considered "alleles" of the second and third chromosomes, while the latter were considered "loci" for a subset of the 51 populations (appendix 6.1). We used the neighbor-joining method (Saitou and Nei 1987) to explore the sensitivity of this technique with our rather restricted data set, which consisted of the frequencies of two polymorphic chromosomes in 43 populations. The analyses were used to order populations based on genetic distances and to form heuristic population clusters.

The inversion phylogeny for *Drosophila mojavensis* and its relatives is well known (Ruiz et al. 1990; Wasserman 1992). The ST and SI second chromosomes are derived from a hypothetical ancestor that gave rise to *D. mojavensis* and its closest relative *D. arizonae*. All of the other second chromosome inversions arose from the ST chromosome. Therefore, the genetic distance tree based on inversion frequency similarity among populations has an evolutionary basis (fig. 6.7). This analysis revealed a different degree of structuring than that explained by the presence of the vegetational subdivisions. This tree also provides more evidence for the proposed history of divergence of *D. mojavensis* throughout the Sonoran Desert (Heed 1982), despite the difficulties of using gene arrangements in this instance that are usually not selectively neutral characters. Of the 51 populations, eight were deleted because they were all homokaryotypic populations from the mainland and added no information to the pattern of relationships (Felsenstein 1993). These are grouped under a single label, Arizona/Sonora. We decided to use a presumed ancestral population from Vallecito in southern California (Ruiz et al. 1990) as an outgroup even though the neighbor-joining method does not produce a rooted tree.

Population clusters in the genetic distance tree relate only marginally to the vegetational subdivisions discussed above (fig. 6.7; fig. 6.8). Whereas the vegetational subdivisions are predominantly an east-west division on the peninsula, the genetic distance clusters are entirely subdivided along the axis of the peninsula in a northwest-southeast direction. The result is a mosaic of disjunctions that are difficult to interpret without

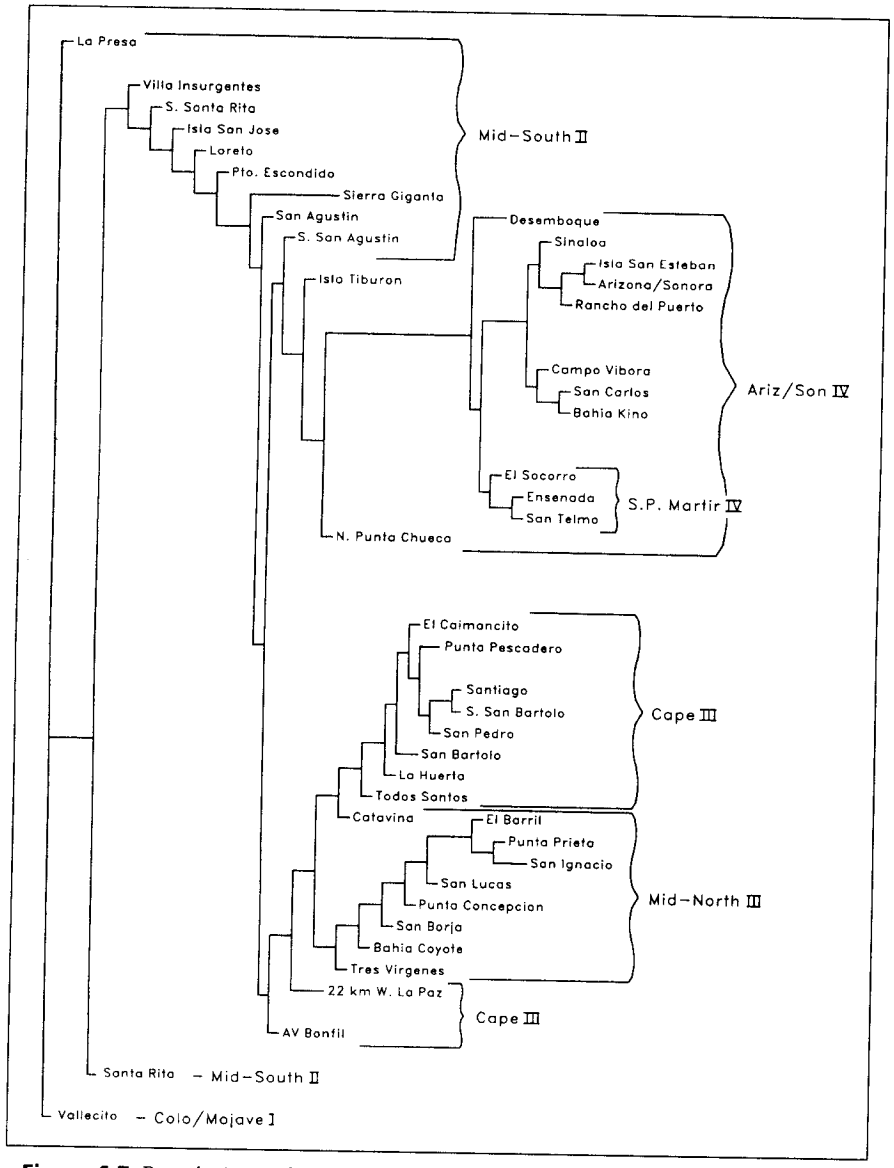

Figure 6.7 Populations of *Drosophila mojavensis* are clustered by their genetic distances using the neighbor-joining method (Saitou and Nei 1987). The ancestral Colorado/Mojave cluster, represented by the Vallecito population, was used as the "outgroup." Clusters are labelled according to their approximate geographic region.

either invoking convergence in inversion frequencies due to natural selection or a series of migrations (dispersals) and extinctions in the history of the species. In any event, there is evidence in the tree that an ancestral condition for *Drosophila mojavensis* exists in Baja California. The mid-south cluster in Baja California is positioned as the ancestral group that gave rise to the diversification of all Baja and mainland Mexico and Arizona populations.

The history of diversification of *Drosophila mojavensis* into its present range has also been inferred from other comparative data. Johnson (1980) suggested that the central-marginal pattern of population structure in *D. mojavensis* resulted from the divergence of Baja populations into mainland Mexico by dispersing across the midriff islands in the Gulf of California at about 29° N lat. Cody et al. (1983) suggested that the spread of plants across these islands, mostly from west to east, including pitahaya agria, occurred about 15 000 years ago when aridity became the dominant climatological factor in the region. Johnson (1980) also observed that all of the present-day gene arrangements can be found in Baja, including the rare S1 chromosome found only in San Ignacio and San Lucas, Baja California Sur. These localities are located in the southern part of the Mid-North group (fig. 6.7; fig. 6.8). Since S1 contains three inversions and is derived from the same hypothetical ancestral chromosome as ST, it may be considered a relictual survivor of events described above. All of the host plants used by *D. mojavensis* are present in Baja, except sina, yet agria is the most widespread and it appears to be the most important host plant in the region. Divergence onto the mainland eventually resulted in a host plant switch to organ pipe and sina cacti. Mainland populations have lost most of the inversion heterozygosity (fig. 6.5; fig. 6.6), have shifted in allele frequencies at several enzyme loci (Zouros 1973; Heed 1978), and have undergone evolution in life history, morphological and physiological traits associated with adaptation to organ pipe cacti (Starmer et al. 1977; Etges and Heed 1987; Etges 1989c; Etges and Klassen 1989; Etges 1990; Etges 1993).

The origin of *Drosophila mojavensis* is thought to have occurred in Baja California as the peninsula formed. The movement north of what is now Baja California from mainland Mexico resulted from tectonic drift starting four to six million years ago (Gastil et al. 1975). This split the proto-*D. mojavensis* from its mainland ancestors that evolved into *D. arizonae* and provided the isolation required for *D. mojavensis* to speciate.

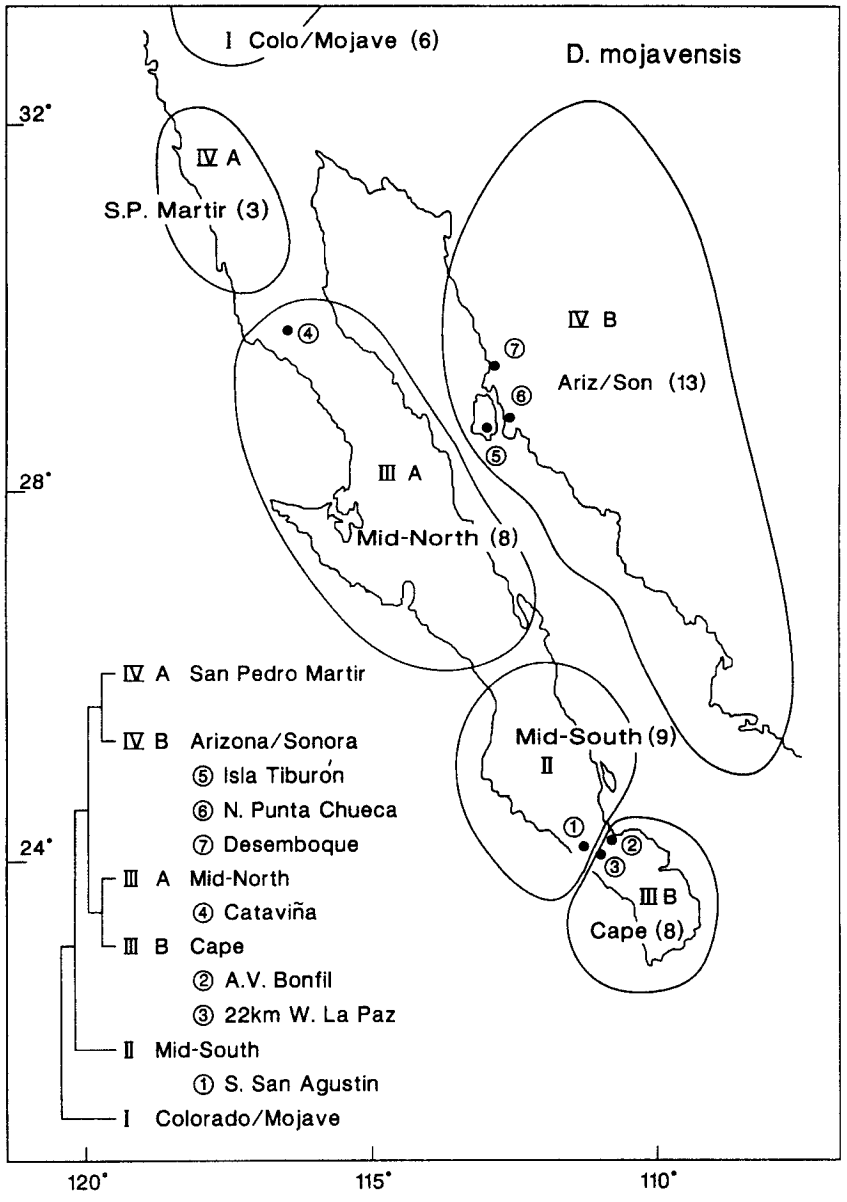

Figure 6.8 *(opposite page)* A summary of the genetic distance diagram in figure 6.7 is presented and the chief clusters are mapped on to the Sonoran Desert and adjacent regions. Four main clusters are considered (two of them are subdivided [A and B]). Several geographic disjunctions in relatedness are noticeable among the clusters and among several localities within them. The Colorado/Mojave cluster (Cluster I with 6 populations) is 900 km removed from the Mid-South portion of the Baja California penninsula (Cluster II with 9 populations). Cluster III is divided by Cluster II into a Mid-North region (8 populations) and the Cape region (8 populations). Cluster IV is centered in the Arizona/Sonora region (13 populations) with an element in the San Pedro Martir region (3 populations).

The samples from localities 1 to 7 have inversion frequencies most similar to other regions or are nebulously placed in a pre-cluster position. This is probably due to their ecotonal nature (situated between vegetational subdivisions). For instance, the S. San Agustin population is in the midst of a cline in inversion frequencies from the Magdalena plain into the Cape region and by chance is more similar to the Isla Tiburón population than those of the Mid-South cluster (see fig. 6.7). Similar reasoning may be applied to populations from localities 2, 3, and 4. Populations represented by localities 5, 6, and 7 are remnants of an earlier west-to-east dispersal across the midriff islands similar to the probable dispersal of their most favored host cactus, the pitahaya agria.

Conclusions

The present distribution of inversion polymorphisms in both *Drosophila mojavensis* and *D. pachea* has been influenced by the same climatic factors that have shaped the vegetational subdivisions in and around the Sonoran Desert. The same forces that have produced the vegetational subdivisions and influenced the distribution of the host cacti found within them have secondarily molded the karyotypic variation in both species. These results imply that the ecological mosaic of the vegetational subdivisions of the Sonoran Desert surely influence genetic variation in many other insect species that use desert plants to carry out their life cycles. Surprisingly, within the relatively small range of the Sonoran Desert and adjacent provinces, the extent of genetic variation among regions (F_{rt}) for both species was comparable to the whole of western North America for *D. pseudoobscura* and of Europe and North Africa for *D. subobscura*. In this light, the vegetational subdivisions are considered a potent source of ecological variability that have structured the organization of karyotypic diversity in populations of *D. mojavensis* and *D. pachea*.

The AMOVA analyses have shown host plant effects to be equally pronounced in *Drosophila mojavensis* and even more so in *D. pachea* than the effects of the vegetational subdivisions on chromosomal polymorphisms. This is not surprising in light of the monophagy exhibited by *D. pachea* on senita cacti and the distinct polytypic monophagy exhibited by *D. mojavensis* on pitahaya agria, organ pipe, sina, and barrel cacti in their respective geographic areas.

The major part of the polymorphism for *Drosophila pachea* resides in the transition zones between *Lophocereus schottii schottii* and *L. s. tenuis* on the mainland in the Guaymas area, and between its nominate race and *L. s. australis* in the peninsular La Paz area. Changes in gene arrangement frequency across these zones account for the localization of 45% and 50% heterozygosities in each area, respectively.

In *Drosophila mojavensis,* all polymorphism on the second chromosome is restricted to pitahaya agria–using populations. The mean heterozygosity for the entire peninsula for this chromosome is 27% (range, 0% to 63%). The peninsular frequencies drop rapidly as one progresses from west to east across the midriff islands to the Desemboque area on the mainland and then reach zero in the remainder of the species distribution. The density of breeding sites is significantly greater in Baja California than the other two major areas, and this may have influenced the formation and retention of second chromosome polymorphism.

There is also a concomitant change in stem volume of the host plants of *Drosophila pachea* and *D. mojavensis* in relation to their degree of chromosomal heterozygosity. It appears that stem volume differences have influenced genetic differences in larval longevity by natural selection, which in turn has caused evolution in other components of the life history of these insects. Extensive studies by Etges have shown that major changes between agria- and organ pipe–using populations of *D. mojavensis* have resulted in the evolution of host races.

In regard to climate, tests for the effects (correlations) of mean ranges of temperatures, longitude, latitude, and elevation on chromosomal heterozygosity were not in accord across the entire geographic distributions of either *Drosophila pachea* or *D. mojavensis* in the Sonoran Desert and adjacent regions. Thus responses to climatic effects are difficult to detect directly by the use of the degree of heterozygosity as a variable.

With respect to evolutionary history, it may be seen that the ancestral

karyotype for *Drosophila pachea* is found in southern Sonora, while the ancestral karyotype for *D. mojavensis* is found in southern California, northern Arizona, and Santa Catalina Island. Thus the history of the two species must be quite different. We have attempted to reconstruct the history of *D. mojavensis* by use of distance trees based on karyotype frequencies. The results suggest that a number of extinctions and recolonizations must have taken place along the length of Baja California, which suggests a dynamic sequence of events leading up to the present geographic pattern of the various gene arrangements. This highlights that the commonality in karyotypic response in the two species analyzed in the present study is much more than a chance phenomenon.

The interaction between hosts and karyotypes in these species within the context of the biogeography, history, and present-day vegetational subdivisions of the Sonoran Desert has indeed provided a wellspring of understanding into the maintenance of inversion polymorphisms in natural populations of *Drosophila* not heretofore possible to obtain in other species. The study of insect-host plant interactions in these arid lands has provided a unique insight into the history of insect diversification and the maintenance of genetic polymorphism.

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Notes

1. It is significant that each of the four species of *Drosophila* endemic to the Sonoran Desert and adjacent areas traces its lineage independently to central and southern Mexico (Heed 1982). The endemics *D. nigrospiracula* and *D. mettleri* are not discussed in the present text because the former species has not been found to have any inversion polymorphism (Cooper 1964) and the latter species has not been analyzed. The host plant for *D. nigrospiracula* is the saguaro (*Carnegiea gigantea*) in Arizona and Sonora, and the cardón (*Pachycereus pringlei*) in coastal Sonora and Baja California. Whether or not these cacti have an immediate or even indirect effect on blocking incipient inversion polymorphism can only be conjectured at the present time.

2. Manuel del Barco, a Jesuit priest who lived in Lower California from 1738 to 1768, gives a wonderful description of organ pipe, pitahaya agria, and senita cacti in *The Natural History of Baja California,* Dawson's Book Shop, Los Angeles, 1980.

3. Adult female *Drosophila mojavensis* collected in the field were isolated into separate vials in the laboratory containing 15 to 20 ml of banana-agar-yeast-malt food supplemented with dried agria powder. Adults reared from cactus rots were randomly pair-mated and their progeny were reared under the same conditions. One third-instar larva was chosen at random from each vial and the salivary glands were dissected out, fixed, and stained in 1% natural orcein in lactoacetic acid solution for 5 to 10 minutes and squashed directly on a slide. Karyotypes of *D. pachea* larvae were obtained in five different ways: 1) offspring of wild caught females; 2) F1s of wild caught males mated to females of a laboratory homokaryotypic stock; 3) pair matings between rot-reared adults; 4) matings between rot-reared virgin adults and adults of a laboratory homokaryotypic stock; 5) rot larvae. All polytene chromosomes were viewed with a standard light microscope with oil immersion.

4. The AMOVA analyses produce variance components and associated statistics, as well as F statistics for estimating hierarchical population structure. Significance values of the variance components were calculated by obtaining null distributions of individuals in populations and populations in regions and testing for significance after 50 random permutations. Unlike F statistics, the AMOVA requires an input matrix of all pairwise, inter-karyotype distances for use in calculating statistics. This matrix was formed by calculating the inter-karyotype distance between all possible karyotypes weighted by global inversion frequencies for those gene arrangements (see Excoffier et al. 1992). For *Drosophila pachea,* there were three observed karyotypes, and therefore a 3 × 3 distance matrix was used. For *D. mojavensis* with four second-chromosome gene arrangements and two third-chromosome gene arrangements, there were 30 possible karyotypes, and therefore a 30 X 30 distance matrix was formed. Frequency data for each population were pooled if sampled more than once. Temporal variation was small relative to the overall pattern of geographic variation in each species (appendix 6.1; appendix 6.2).

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Appendix 6.1 Collection Data and Chromosome Frequencies of *Drosophila mojavensis*.

Locality		Collection			Second Chromosome				Third Chromosome					
Name[a]	Region[b]	No.[c]	Date	N^d	LP	ST	BA	SL	ST	MU	h_2	h_3	H	TMR[e]
Baja California Norte														
1. Ensenada	SPM	A756	12-79	14	0.86	0.00	0.14	0.00	0.93	0.07	0.24	0.13	0.19	8.6
2. San Telmo	SPM	A758	12-79	106	0.70	0.00	0.30	0.00	0.86	0.14	0.42	0.24	0.33	10.8
3. El Socorro	SPM	A519	7-74	132	0.93	0.00	0.07	0.00	0.89	0.11	0.13	0.20	0.17	5.9
4. Cataviña	VIZ	A761	12-79	100	0.77	0.02	0.21	0.00	0.30	0.70	0.36	0.42	0.39	13.5
5. Punta Prieta a	VIZ	A420	2-74	106	0.44	0.18	0.38	0.00	0.04	0.96	0.63	0.08	0.36	11.4
Punta Prieta b	VIZ	A896	5-85	230	0.43	0.31	0.25	0.01	0.06	0.94				
6. San Borja	VIZ	A350*	11-71	56	0.52	0.46	0.02	0.00	0.30	0.70	0.52	0.42	0.47	11.1
7. El Barril	CGC	A570	3-75	54	0.52	0.46	0.00	0.02	0.02	0.98	0.52	0.04	0.28	14.3
Baja California Sur														
8. Tres Virgenes	CGC	A567*	11-74	100	0.61	0.29	0.08	0.02	0.42	0.58	0.54	0.49	0.51	15.3
9. San Lucas	CGC	A422+	2-74	132	0.35	0.49	0.07	0.09	0.20	0.80	0.62	0.32	0.47	16.3
10. Punta Concepción	CGC	A352*	11-71	94	0.39	0.60	0.01	0.00	0.38	0.62	0.49	0.47	0.48	16.2
11. Bahía Coyote	CGC	A427	4-74	64	0.58	0.38	0.00	0.04	0.37	0.63	0.52	0.47	0.50	16.2
12. Loreto	CGC	A385*	3-72	106	0.24	0.76	0.00	0.00	0.95	0.05	0.36	0.09	0.22	14.1
13. Puerto Escondido	CGC	A428	4-74	68	0.40	0.57	0.00	0.03	0.78	0.22	0.51	0.34	0.42	14.1
14. Isla San Jose	CGC	A593*	3-76	54	0.09	0.83	0.07	0.00	0.96	0.04	0.30	0.08	0.19	12.1
15. Sierra Giganta	GIG	A429*	4-74	70	0.11	0.88	0.00	0.01	0.96	0.04	0.21	0.08	0.14	14.9
16. La Presa	GIG	A376*	3-72	104	0.00	1.00	0.00	0.00	0.98	0.02	0.00	0.04	0.02	14.9
17. San Ignacio a	MAG	A367*	4-72	54	0.24	0.67	0.09	0.00	0.02	0.98	0.42	0.12	0.27	12.4
San Ignacio b	MAG	A421	2-74	126	0.08	0.74	0.16	0.02	0.10	0.90				
San Ignacio c	MAG	A566+	11-74	82	0.12	0.73	0.14	0.00	0.70	0.30				
18. V. Insurgentes	MAG	A430	4-74	60	0.00	1.00	0.00	0.00	0.70	0.30	0.00	0.42	0.21	12.4
19. Santa Rita	MAG	A564	11-74	64	0.03	0.94	0.03	0.00	0.96	0.04	0.11	0.08	0.10	11.6

Appendix 6.1 continued

Locality		Collection			Second Chromosome				Third Chromosome					
Name[a]	Region[b]	No.[c]	Date	N[d]	LP	ST	BA	SL	ST	MU	h_2	h_3	H	TMR[e]
20. 50 km S. S. Rita	MAG	A431	4-74	80	0.05	0.95	0.00	0.00	0.91	0.09	0.09	0.16	0.13	12.0
21. San Agustin	MAG	A563	11-74	82	0.61	0.33	0.06	0.00	0.88	0.12	0.52	0.21	0.37	7.8
22. 10 km S. San Ag.	MAG	A587	3-76	70	0.89	0.11	0.00	0.00	0.76	0.24	0.20	0.36	0.28	7.8
23. 22 km W. La Paz	CAPE	A560	11-74	86	0.92	0.03	0.03	0.02	0.40	0.60	0.15	0.48	0.32	11.8
24. AV Bonfil	CAPE	A768	3-80	100	0.84	0.14	0.02	0.00	0.69	0.31	0.27	0.43	0.35	11.8
25. Virgin Maria	MAG	A770	3-80	100	0.94	0.05	0.00	0.01	0.30	0.70	0.11	0.42	0.27	12.7
26. San Bartolo	CAPE	A561	11-74	56	0.96	0.04	0.00	0.00	0.16	0.84	0.08	0.27	0.18	11.9
27. 10 km S. San Bart.	CAPE	A433	4-74	80	0.95	0.05	0.00	0.00	0.00	1.00	0.09	0.00	0.05	11.9
28. Punta Pescadero	CGC	A374*	3-72	78	1.00	0.00	0.00	0.00	0.11	0.89	0.00	0.20	0.10	12.3
29. Santiago	CAPE	A597	3-76	82	0.98	0.00	0.00	0.02	0.06	0.94	0.04	0.11	0.08	13.5
30. La Huerta	CGC	A772	3-80	40	0.95	0.05	0.00	0.00	0.20	0.80	0.10	0.32	0.21	13.0
31. San Pedro	CAPE	A767	3-80	74	0.97	0.03	0.00	0.00	0.08	0.92	0.06	0.15	0.10	11.0
32. El Caimancito	CGC	A769	3-80	80	0.96	0.04	0.00	0.00	0.11	0.89	0.08	0.20	0.14	11.8
33. Todos Santos	CAPE	A771	3-80	76	0.82	0.08	0.10	0.00	0.23	0.77	0.31	0.35	0.33	9.3
Arizona														
34. S. Rosa Mtns.[f] a	ARIZ	A572	2-75	72	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	23.1
S. Rosa Mtns. b	ARIZ	A900	3-85	214	1.00	0.00	0.00	0.00	0.99	0.01				
35. Organ Pipe NM[f]	ARIZ	A345*	9-71	30	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	20.8
Sonora														
36. Altar Valley[f]	ARIZ	A319	4-71	58	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	18.9
37. Caborca[f]	LC	A316	4-71	44	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	20.8
38. Punta Libertad[f]	CGC	A514*	4-74	56	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	17.3
39. Desemboque[g] a	CGC	A361*	12-71	56	0.96	0.04	0.00	0.00	0.88	0.12	0.08	0.21	0.15	17.9
Desemboque b	CGC	A366*	3-72	102	0.99	0.01	0.00	0.00	0.95	0.00				
Desemboque c	CGC	A388	3-72	100	0.98	0.02	0.00	0.00	0.98	0.02				
Desemboque d	CGC	A509	3-74	100	0.78	0.18	0.04	0.00	0.94	0.06				
Desemboque e	CGC	A856	2-84	40	0.98	0.02	0.00	0.00	0.95	0.05				
40. Campo Vibora[g]	CGC	A510	3-74	100	1.00	0.00	0.00	0.00	0.91	0.09	0.00	0.16	0.08	17.8
41. Ran. del Puerto[g]	CGC	A580	7-75	84	1.00	0.00	0.00	0.00	0.97	0.03	0.00	0.06	0.03	17.8
42. 25 km N. Chueca[g]	CGC	A581	7-75	42	0.93	0.07	0.00	0.00	0.95	0.05	0.13	0.10	0.12	17.8
43. Bahía Kino[f]	CGC	A511	3-74	46	1.00	0.00	0.00	0.00	0.87	0.13	0.00	0.23	0.12	17.7
44. San Carlos[f]	CGC	A512	3-74	100	1.00	0.00	0.00	0.00	0.82	0.18	0.00	0.30	0.15	13.1
45. I. S. Ped. Nolas.[f]	CGC	A513	3-74	100	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	—
46. Isla Tiburón[g] a	CGC	A506*	11-74	80	0.87	0.12	0.00	0.01	0.93	0.07	0.23	0.13	0.18	17.8
Isla Tiburón b	CGC	A732	5-78	100	0.97	0.03	0.00	0.00	1.00	0.00				
47. Isla San Esteban	CGC	A731	5-78	100	0.99	0.01	0.00	0.00	1.00	0.00	0.02	0.00	0.01	—
Sinaloa														
48. Los Mochis[f]	STS	A337	11-71	110	1.00	0.00	0.00	0.00	0.96	0.04	0.00	0.08	0.04	13.4
49. Topolobampo[f]	STS	A559	11-74	4	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	11.2
California														
50. S. Catalina Is.[h]		A826	10-81	60	0.00	1.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	—
51. Vallecito[i]	LC	A753	12-79	100	0.00	1.00	0.00	0.00	0.99	0.01	0.00	0.00	0.00	—

Note: Inversion heterozygosity estimates of second (h_2) and third (h_3) chromosomes and their mean (H) for *D. mojavensis* are presented where $h_x = 1 - \Sigma x_i^2$, with x_i being the frequency of the i^{th} inversion. For populations that were sampled more than once, heterozygosities were calculated for pooled data. Temperature data were taken from Hastings and Humphrey (1969a, 1969b).

[a] Site numbers refer to the collecting sites as numbered in figure 6.5.

[b] Vegetational subdivisions: ARIZ = Arizona Upland; CAPE = Cape region in Baja California Sur; CGC = Central Gulf Coast; GIG = Sierra Giganta; LC = Lower Colorado Valley; MAG = Magdalena; SPM = San Pedro Martir; STS = Sinaloan thornscrub forest; VIZ = Vizcaíno.

[c] Cultures and chromosome analyses were derived from field-captured isofemales, except those indicated by *, which were derived from flies reared from cactus rots. + SI gene arrangement in the second chromosome is also present.

[d] N = number of chromosomes observed per collection.

[e] TMR is the difference between the highest average monthly temperature and the lowest average monthly temperature at the closest weather station.

[f] Mainland and island localities where organ pipe is present and pitahaya agria is not.

[g] Mainland and island localities where pitahaya agria is present.

[h] Locality where *Opuntia* is present and other hosts are not.

[i] Locality where the California barrel cactus, *Ferocactus cylindraceous*, is present and other hosts are not.

Appendix 6.2 Collection Records and Karyotypes of *Drosophila pachea* from Arizona, Baja California, and Sonora, Mexico.

Locality		Collection			Type of	No. Observed Karyotypes[a]					
Name[b]	Region[c]	Cactus	No.	Date	Collection[d]	+/+	+/A	A/A	Frequency (+)	h_7	TMR
Baja California Norte											
1. Bahia de Los Angeles[e]	CGC	*	A191	3-68		0	0	17	0.00	0.00	15.4
2. Bahia de Los Angeles	CGC	*	A606	3-76	PM7	0	0	13	0.00		
3. San Borja	VIZ	*	A605	3-76	PM7	0	0	16	0.00	0.00	11.1
Baja California Sur											
4. Bahía Tortugas	VIZ	*	A608	3-76	RL	0	0	35	0.00	0.00	8.3
5. Mulege	CGC	*	A603	3-76	PM7	0	1	31	0.02	0.23	16.2
6. Mulege	CGC	*	A607	3-76	PM1	1	19	33	0.20		
7. Comondu	MAG	*	A622	3-62		1	6	16	0.17	0.28	11.7
8. San Agustin	MAG	†	A720	1-78	FCF7, PM1	9	7	1	0.74	0.49	7.8
9. San Agustin	MAG	†	A719	1-78	PM1	3	6	2	0.55		
10. La Paz	CAPE	†	A596	3-76	PM7	7	12	5	0.54	0.50	11.8
11. La Paz	CAPE	†	A679	3-77	PM1, PM7	2	5	2	0.50		
12. La Paz	CAPE	†	A677	3-77	PM1, PM7, MF, FCF1	4	13	8	0.42		
13. E. La Paz	CGC	†	A595	3-76	PM7	13	26	7	0.56	0.51	12.5
14. La Aguja	MAG	†	A674	3-77	PM1, PM7, MM	3	4	5	0.42	0.54	9.8
15. La Aguja	MAG	†	A672	3-77	PM1, PM7, MM, MF	2	7	4	0.42		
16. La Aguja[e]	MAG	†	A202	4-68		3	9	13	0.30		
17. San Pedro	CAPE	†	A721	1-78	FCF7, PM1	5	24	43	0.27	0.32	12.0
18. San Pedro	CAPE	†	A686	3-77	FCF1, PM1, MM	0	14	32	0.15		
19. El Carrizal	CAPE	†	A691	3-77	MF, MM	0	4	8	0.17	0.28	12.0
20. Todos Santos	CAPE	†	A684	3-77	FCF1, MM, MF	0	2	9	0.09	0.46	9.3
21. Todos Santos	CAPE	†	A693	3-77	MF, MM	1	2	7	0.20	0.46	9.3
22. Todos Santos	CAPE	†	A725	1-78	PM7	0	6	6	0.25		
23. San Bartolo	CAPE	†	A688	3-77	FCF1, PM1	0	4	41	0.04	0.09	11.9
24. La Ribera	CAPE	†	A689	3-77	FCF1, PM1	0	4	48	0.04	0.08	12.7
25. Santiago	CAPE	†	A694	3-77	FCF1, FCM	0	0	12	0.00	0.00	12.7
26. Caduaño	CAPE	†	A696	3-77	PM1, MM	1	3	17	0.12	0.21	13.0
27. S. Jose d. Cabo	CAPE	†	A723	1-78	FCF1, PM1	1	10	32	0.14	0.24	13.0
28. Cabo San Lucas	CAPE	†	A724	1-78	FCF7, PM1	1	2	9	0.17	0.28	9.9
Sonora											
29. Sasabe[f]	ARIZ	*	A650	11-76	PM	0	1	22	0.02	0.04	16.3
Sonoita[g]	ARIZ	*			RL	0	4	68	0.03	0.05	20.8
Magdalena[g]	ARIZ	*			FCF1	0	1	49	0.01	0.02	17.2
Santa Ana[g]	ARIZ	*			FCF1, RL	0	1	64	0.01	0.02	17.4
Altar Valley[g]	LC	*			RL	0	2	118	0.01	0.02	18.9
P. Peñasco[g]	LC	*			RRF3	0	0	21	0.00	0.00	18.9
Desemboque[g]	CGC	*			RL	1	29	111	0.10	0.20	17.9
Kino[g]	CGC	*			RRF2	3	21	23	0.29	0.41	17.7
Empalme[g]	CGC	•			RRF1	45	41	5	0.72	0.40	12.2
Guaymas[g]	CGC	•			RRF2	73	87	24	0.63	0.46	13.1
30. Cerro Colorado	LC	*	A652	11-76	PM1	0	0	25	0.00	0.00	19.5
31. Caborca[f]	LC	*	A651	11-76	RL, PM1	0	0	47	0.00	0.07	20.8
32. Isla Tiburón	CGC	*	A663	11-76	PM7	1	18	23	0.27	0.39	17.8
33. N. Guaymas	CGC	•	A660	11-76	FCFF2	23	21	0	0.76	0.42	—
34. N. Guaymas	CGC	•	A665	1-77	FCF1	63	54	18	0.67		
35. Navojoa[f]	STS	•	A658	11-76	FCFF2	29	0	0	1.00	0.00	14.6
Vicam[g]	STS	•			RRF1	16	0	0	1.00	0.00	17.4
Cd. Obregón[g]	STS	•			RL	110	3	0	0.99	0.03	15.1
Zaragosa[g] (Sinaloa)	STS	•			RL	90	0	0	1.00	0.00	14.6
Hermosillo[g]	PLS	•			RRF1	4	11	3	0.53	0.50	15.2

Appendix 6.2 continued

Note: Localities are usually the closest weather station. Inversion heterozygosity estimates of the seventh chromosome (h_7) are presented along with TMR data. Chromosome data from populations sampled more than once were pooled. The subspecific status of senita cactus for each collection is designated as follows: *Lophocereus schottii schottii* (*), *L. s. australis* (†), and *L. s. tenuis* (•). The temperature data were taken from Hastings and Humphrey (1969a, 1969b). For collection records for populations from Sonora and Sinaloa, see Ward et al. (1975).

[a] All collections were found to be in Hardy-Weinberg equilibrium (X^2 analyses, all p values $> .05$).

[b] Site numbers refer to the collecting sites as numbered in figure 6.4.

[c] Vegetational subdivisions: ARIZ = Arizona Upland; CAPE = Cape region in Baja California Sur; CGC = Central Gulf Coast; LC = Lower Colorado Valley; MAG = Magdalena Plain; PLS = Plains of Sonora; SPM = San Pedro Martir; STS = Sinaloan thornscrub forest; VIZ = Vizcaíno.

[d] FCF1 = field-caught isofemales, 1 larva squashed per female; FCF7 = field-caught isofemales, 7 larvae squashed per female; FCM = field-caught males mated to Zaragosa females, 7 progeny squashed per male to determine his karyotype; PM1 = pair matings between rot-reared adults, 1 larva squashed per pair; PM7 = pair matings between rot-reared adults, 7 larvae squashed per pair to determine karyotypes of the parents; MM = matings between rot-reared males and Zaragosa females, 7 progeny squashed per female; MF = matings between rot-reared females and Zaragosa males, 7 larvae squashed per female; RL = rot larvae squashed and scored; FCFF2 = F_2 progeny of field-caught isofemales; RRF1 = F_1 larvae of rot-reared flies; RRF2 = F_2 larvae of rot-reared flies; RRF3 = F_3 larvae of rot-reared flies.

[e] From the unpublished records of W. B. Heed.

[f] Inversion data were combined with those from Ward et al. (1975) for heterozygosity estimates.

[g] Inversion data from Ward et al. (1975). For multiple samples from a single location, data were pooled.

7 Ecological Consequences of Agricultural Development in a Sonoran Desert Valley

Laura L. Jackson and Patricia W. Comus

If one were to construct a generalized land-use map of the Sonoran Desert, showing cropland in black and other uses in white, and place it next to a similar map of the midwestern prairie/corn belt, the two would look like photographic negatives of one another. While agriculture in the Midwest occupies virtually every square meter of upland, Sonoran Desert agriculture is found nowhere but on the valley floors. The availability of water for irrigation, and fine-textured lowland soils capable of retaining that water, are prerequisites for desert agriculture. Both of these requirements are found only on valley floors.

This landscape pattern, while excusing a great deal of desert habitat from intensive use, nevertheless singles out lowland vegetation types, moisture regimes, and soils, and the lowland landscape element itself for extensive disturbance. The effects go beyond fields: reduced stream flow caused by surface and groundwater pumping, increased silt load and dissolved salts in the streams due to return of used irrigation water, and changes in river hydroperiod caused by dams all damage downstream reaches as effectively as does cultivation.

The changes wrought by agriculture on lowland deserts have ranged from slight to profound, depending on the type of agriculture. Floodwater farming by the Tohono O'odham Indians involved the careful selection of land at the mouth of an ephemeral wash, where floodwaters after winter and summer rains would collect and then spread overland. Farmers used low earthen berms, brush dams, and rock alignments to slow the water down and train it into their fields, where it dropped its load of nutrient-rich