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EVOLUTIONARY HISTORY OF *DROSOPHILA BUZZATII*. I. NATURAL CHROMOSOMAL POLYMORPHISM IN COLONIZED POPULATIONS OF THE OLD WORLD

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Most species arise in a center of origin from where they disperse to larger areas. The ability to colonize varies from species to species and must be related to its genetic endowment. Yet, the relationship between genotype and colonizing ability is not well defined. Chromosomal polymorphism has been related to ecogeographical distribution by several authors and there is ample evidence (Carson, 1958; Da Cunha et al., 1959; Carson and Heed, 1964; Sperlich, 1964) that in many widespread species of *Drosophila* central populations are more polymorphic for inversions than marginal populations. The adaptive significance of this chromosomal differentiation is still subject to debate and it is often related to environmental heterogeneity (Dobzhansky, 1951) and/or to selective pressure for new genic recombinants (Carson, 1959).

Carson (1965) has advanced the idea that much original chromosomal polymorphism is lost when endemic species become widespread. Genetic drift and selection of homozygotes (homoselection) may be contributing factors for this phenomenon. However, there are several widespread species which have maintained polymorphism for certain inversions throughout their entire distribution. This polymorphism is generally termed as rigid in opposition to flexible polymorphism, which is typical of endemic species (Dobzhansky, 1962).

One way to become a widespread species is to fix a genetic novelty highly adapted to a narrow niche, such as a host plant, which exists in many parts of the world. This may be the case of *Drosophila buzzatii*, which is closely associated with several species of *Opuntia* (prickly pear). These plants originated in the New World but have been disseminated by human activities. Most probably *D. buzzatii* has followed its host plant and spread all over the world. We have studied several populations and laboratory strains of the Mediterranean area, Macaronesian Islands and Western Africa in an attempt to compare their chromosomal polymorphism with that found in other colonized regions and also in South America, their presumed ancestral home. In the present paper we will show that (a) high chromosomal polymorphism characterizes the populations studied and (b) that there are significant differences between populations. The level of polymorphism found in colonized areas is comparable to that described in the ancestral areas. Moreover, some new inversions are reported which were not detected in previous work with this species. The new information reported here suggests that chromosomal polymorphism in colonizing populations of *D. buzzatii* is highly dependent on founding events, but some possibly adaptive factors are also discussed.

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Phylogeny, Ecology and Colonization of D. buzzatii *in the Old World*

Drosophila buzzatii belongs to the *mulleri* subgroup of the *repleta* group of the genus *Drosophila*. According to Wasserman (1962) the chromosomes of the species are derived from the most primitive chromosomal sequence of the group by fixing three inversions in the second chromosome ($2x^3$, 2k, $2w^3$) and one inversion in the fifth chromosome (5g). In addition, *D. buzzatii* has been reported heterozygous for several inversions in the second chromosome (Wasserman, 1962; Carson and Wasserman, 1965). The species is closely associated with different species of *Opuntia*, where it utilizes the decaying fruits and pads as feeding and breeding sites. *Drosophila buzzatii* has been found to coexist with other *Drosophila* species in the *Opuntia* fruits. It is by far the most prevalent species of *Drosophila* in the rotting pads of *Opuntia ficus-indica* in the Iberian Peninsula (unpubl. data).

TABLE 1. *Worldwide geographical distribution of inversions of second chromosome of* Drosophila buzzatii.

Locality	Number of chromosomes examined	Chromosome arrangement st	p	jq[7]	je[3]	y[3]
Argentina						
Córdoba[a]	?	+	+	−	−	−
San Luis[a]	?	+	−	−	+	+
Bolivia						
Cochabamba[a]	?	+	+	−	−	−
Brazil						
Carumba[b]	?	+	−	−	−	−
Australia						
Mogill[d]	?	+	+	−	−	−
Deer Park (Victoria)[c]	52	0.405	0.595	−	−	−
Wildwood (Victoria)[c]	28	0.143	0.857	−	−	−
Ethiopia						
Erter Valley (near Harar)[c]	32	0.657	0.343			
Israel						
Quiryat Anavim[c]	47	0.851	0.149		−	−
Lebanon						
Ain Anub[a]	?	+		−	−	−
Byblos[b]	?	+	−	−	−	−
Beirut[b]	?	+	t			−
Ksara[b]		+	+			−
Italy						
Trapani[c]	?	+	+	−		−
Carpenteria[b]	?	+	−		−	

Only when a sample of a natural population has been analyzed are the inversion frequencies given. Otherwise, when the analysis has been done with laboratory strains, only the occurrence or absence of inversion types are reported (+ indicates occurrence, and − absence).
These data have been reported by different authors as follows: [a] Wasserman, 1962, [b] Wasserman, 1954, [c] Carson and Wasserman, 1965, [d] Mather, 1957.

Opuntia probably originated in Mexico (Gibson, pers. comm.) and has spread throughout the American continent. It was brought by man to the Old World. *Drosophila buzzatii* probably has spread with *Opuntia* and now we have records of this species in many parts of the world (Table 1). *Drosophila buzzatii* has not reached some geographical areas where *Opuntia* is present, like the Hawaiian archipelago (Carson, pers. comm.) and Indonesia (Barker and Bock, 1977). Most surprising is that this species has not been collected in Mexico and Central America where *Opuntia* originated and is very abundant. Although the present biogeographical data support the idea that *D. buzzatii* originated in South America, the site of origin is still obscure. Wasserman (1962) and Carson and Wasserman (1965) suggested from chromosomal data that Argentina may be its center of origin.

Opuntia was probably brought to Europe soon after the discovery of America in 1492. Gonzalo Fernández de Oviedo, a Spanish naturalist and the author of "La Historia Natural de las Indias," published in 1525, described these plants in great detail. We believe that *Opuntia* plants were introduced through Spanish ports

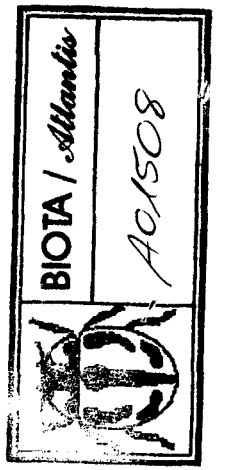

TABLE 2. *Arrangement polymorphism on the second and fourth chromosomes of* Drosophila buzzatii *populations of Mediterranean and Atlantic localities in the Old World.*

Locality	Number of chromosomes examined	Second chromosome arrangement				Fourth chromosome arrangement	
		st	j	jo[1]	jz[1]	t	
Iberian Peninsula							
1 Carboneras	173	0.457	0.422	0.052	**0.069**	0.717	0.283
2 Plasencia	160	0.362	0.556	–	**0.041**	0.725	0.275
3 Sitges	192	0.219	0.479	0.083	0.218	0.802	0.197
4 Puebla del Rio	187	0.342	0.545	0.091	0.021	0.759	0.241
5 Portosin	180	+	+	–	–	+	–
11 Evora	156	+	+	–		+	t
Balearic Islands							
6 S. Jordi	216	0.259	0.643		0.097	0.759	0.241
Canary Islands							
7 Adeje	310*	0.377	0.410	**0.126**	**0.040**	0.429	0.170
8 Pingado	216	0.454	0.329	0.037	0.180	**0.815**	0.185
9 Los Cristianos	56	0.411	0.500	0.036	0.053	*0.750*	0.250
10 Mogán	82	0.536	0.305	0.073	0.085	0.732	0.268
Madeira Island							
12 Cancela	126	0.468	0.532	–	–	*0.682*	0.317
Dahomey							
13 Cotonou	24	0.292	0.708	–	–	0.917	0.083
Egypt							
14 El Khánka	284	0.655	0.345	–	–	1.000	0.000

* Only 305 genomes have been examined for the fourth chromosome.

and disseminated very rapidly along the Northern Mediterranean coast. Thus, Andrés de Laguna observes *Opuntia* in Italy as early as in 1570 (Font Quer, 1973).

The time of arrival of *D. buzzatii* in Europe is more controversial. The original *Opuntia* plants were certainly brought to Europe from Mexico and tropical America, where *D. buzzatii* is not present. During the sixteenth and the seventeenth centuries commerce between America and Spain was monopolized between ports in the Caribbean and Seville in Spain. In the middle of the eighteenth century several ports of Argentina were open to exports. This restricted situation would have prevented the colonization of *D. buzzatii* during the early colonial times. The most important plant associated with *D. buzzatii* in the Old World is *O. ficus-indica* of Mexican origin (Bravo, pers. comm.), although other *Opuntia* species exist in the area surveyed by us (*O. maxima*, *O. dillenii*, *O. robusta*, *O. tomentosa*). These historical data suggest that *D. buzzatii* might have been introduced not earlier than the middle of the eighteenth century, when *Opuntia* was already abundant and well established.

Materials and Methods

Description of Collections

The names of localities are given in Table 2 and their geographical locations, except for population 14, are shown in Figure 1.

We studied chromosomal polymorphism of four populations (1–4) and two strains (5, 11) of the Iberian Peninsula, four populations of the Canary Islands (7–10), one population of the Balearic Islands (6), one population of the Madeira Island (12), one population in Dahomey (13) and one population of Egypt (14).

Biogeographical differences between localities are large. They include climates as diverse as mediterranean (1, 3, 4, 6), continental (2), atlantic (5, 11), subtropical (7, 8, 9, 10, 12), tropical (13) and desertic (14). Also, trophic niches are distinct from one locality to the other.

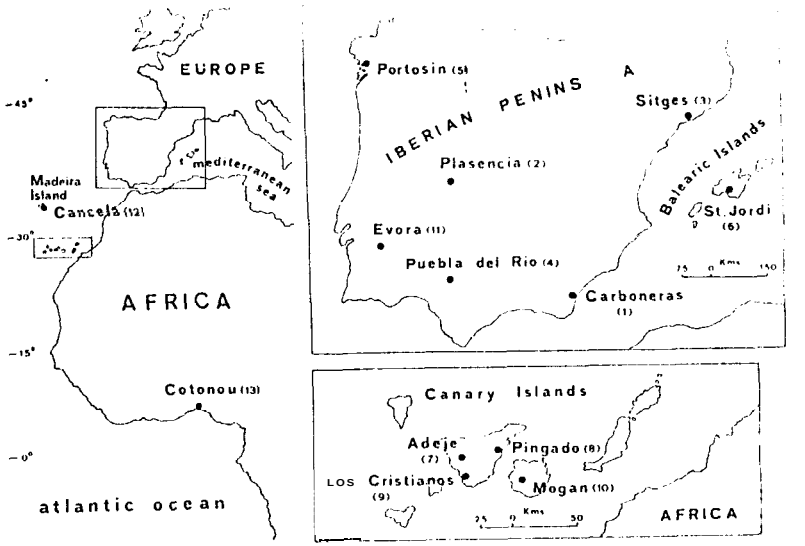

FIG. 1. Geographical localities from which *D. buzzatii* populations were sampled.

In most localities (1, 2, 3, 5, 6, 8, 10, 11, 12, 14) only *O. ficus-indica* is present. Locality 7 had *O. dillenii* as the most abundant *Opuntia* species and also some scattered plants of *O. ficus-indica*. *Opuntia dillenii* is the only host cactus present in locality 9. On the other hand, very few stands of *O. dillenii* and *O. ficus-indica* exist at locality 4, where *O. maxima* and *O. robusta* are the first and second most abundant host plants, respectively.

Collections were made by aspiration of adults from decaying fruits and pads in most of the localities (1, 2, 4, 6, 7, 8, 9, 10). Fermenting banana traps were used at localities 13 and 14. When adult population size was not large (13, 5, 11) we took rots to the laboratory and either picked up larvae or reared adults from them. Dates of collection are diverse and range from July 1977 to March 1979.

Chromosomal Study

Adult males and females have been used according to circumstances. Thus, when enough females were collected and there was no need to know wild genotype frequencies, females were put individually in vials and one progeny larva of each female was checked for inversions. This method gives two genomes sampled per female.

When the female sample was not sufficient, or when we computed genotype frequencies, males were crossed individually to females of a laboratory stock homozygous both for the j inversion in the second chromosome and for the st inversion in the fourth chromosome (see below). The analysis of one larva of each male progeny allows identification of one population genome per male. On the other hand, the analysis of eight larvae per male progeny enables determination of inversion frequencies and male genotypes with a probability greater than 0.95 and con-

sequently gives also two genomes per male.

Salivary glands were dissected into acetic alcohol (1 part glacial acetic acid to 3 parts absolute ethyl alcohol), then transferred to an aceto-lactic orcein mixture for 30 min. Slides are then squashed, stored at 4 C and read 8 days later.

Data Analysis

Chromosomal polymorphism of *D. buzzatii* (Table 2) shows geographical heterogeneity. In order to determine whether similarity among populations may be related to any biogeographical component, we performed a factorial analysis of correspondences using the absolute frequencies of chromosomal arrangements (Hill, 1974; Benzécri, 1976). This analysis was carried out for each chromosome independently and also for the joint distribution of arrangements at both chromosomes. This technique allows depiction of the different populations and also each of the arrangements on the same plane. The distance between two population points is a measure of their similarity and, in the same way, the arrangement distances are representative of the degree of common incidence of several arrangements on the whole set of populations. Thus, closeness of certain arrangements to a group of populations indicates that these arrangements are the most influential to locate those populations.

As most, if not all, of the ordination methods, the factorial analysis of correspondences suffers from several shortcomings. It is dependent on the number of analyzed populations, and gives better resolution for peripheral than for central groups. In order to check the results of this analysis we also have computed genetic distances between populations, using the formula developed by Prevosti (1974, 1975):

$$D = \frac{1}{2r} \sum_{i=1}^{r} \sum_{j=1}^{s_i} |p_{1ij} - p_{2ij}|$$

where r is the number of chromosomes; s_i the number of different arrangements in the i chromosome; p_{1ij} and p_{2ij} the frequencies of arrangement **j** of the i chromosome in the populations **1** and **2**, respectively. This is a coarse measure of population differences, but it has the advantage of being independent from arrangement frequencies, number of arrangements per chromosome and most important, from the evolutionary process which generated the observed divergence.

The most important shortcoming of Prevosti's distance is that there is no appropriate statistical treatment for it. We have performed χ^2 tests with absolute arrangement frequencies to compare populations in pairs when necessary. This is an indirect method to test significance between arrangement distributions. However, this test is said to be inefficient when one or more arrangements are not present in one population. In this case, pooling of data from different arrangements allows the test to be made, but it has a misleading effect on true biological comparisons. For this reason, when an arrangement is missing in a population, we have computed the χ^2 heterogeneity test without pooling. Since in all cases our expected values are much greater than one, the reliability of the tests is not much impaired (see Everitt, 1977). We feel that pooling has no biological meaning and, therefore, introduces still more uncertainty to the test.

Results

Second Chromosome

Table 2 shows the second chromosome arrangement distribution of 12 populations and two strains analyzed by us. Arrangements st (standard) and j have been found in all the localities, though their frequencies are not homogeneous. The frequency of st ranges from 0.219 (3) to 0.655 (14) and a similar range is shown by the j arrangement (0.305 to 0.708). The constant presence of st is in accordance with previous data (Table 1), which also show a high incidence of j.

Most interesting is the presence of arrangement jz^3 in the majority of the localities of the Iberian Peninsula, the Balearic Islands and the Canary Islands. This indicates that a large proportion of populations are polymorphic for this inversion. On the other hand, the inversion is absent in two western localities of the Iberian Peninsula (5, 11), on the island of Madeira (12), in Egypt (14) and in Western Africa (13). This inversion was discovered in an Argentinian strain (San Luis) by Wasserman (1962) and had not been found elsewhere (Table 1). However, Barker (pers. comm.) recently has found this inversion in one population of Australia. The jz^3 frequencies in the populations studied by us (Table 2) range from 0.021 (4) to 0.219 (3).

The Carboneras population has a new inversion in the second chromosome. This inversion is always associated and overlaps with 2j and has been named tentatively as jq^7 (Ruiz and Fontdevila, unpubl.). The jq^7 arrangement shows a reduced distribution in the surveyed area; it is absent in the following localities: 2, 5, 11, 6, 12, 14 and 13. Some of these localities represent geographical isolates and/or places with high seasonality. However, jq^7 arrangement is present in about half of the sampled localities at frequencies ranging from 0.03 to 0.13. The populations of the Canary Islands show a large range of frequency variation (Table 2). This contrasts with the absence of jq^7 in other island or geographically isolated localities.

Finally, inversion y^3 has not been found in our survey. This is in accordance with previous work (Table 1), which suggests that this arrangement is rare and restricted to Argentina (Wasserman, 1962).

Fourth Chromosome

All the populations and strains studied by us, except population 14 and strain 5, have been found to be polymorphic for the fourth chromosome. This chromosome shows two arrangements: the standard (st) which is the primitive fourth chromosome of the *repleta* group (Wasserman, 1962), and another arrangement which bears a new inversion. This inversion has been described elsewhere (Ruiz and Fontdevila, unpubl.) and named tentatively as s.

The new polymorphism of the fourth chromosome is high in the majority of the surveyed natural populations (Table 2). Variability among populations is low, the maximum deviation corresponding to populations 13 and 14, whereas the st frequency is very high in the former and equals one in the latter. The s arrangement shows frequencies ranging from 0.170 to 0.300 in most of the area surveyed by us and it has never been found outside this area (Table 1).

Joint Analysis of Chromosomal Polymorphism

The upper half of Table 3 (above diagonal) shows a series of comparisons between populations which belong to the Mediterranean area. Populations 1, 3 and 6 exhibit low similarity (high values of distance), although they are geographically close. Population 3 is very distinct which is reflected by its great distance from the other Mediterranean populations. These differences are highly significant by the χ^2 paired-test between arrangement distributions of population (below diagonal).

Populations 2 and 6 are similar to each other and are qualitatively different from the other populations because they lack the jq^7 arrangement. However, when looking at genetic distances, population 6 has a polymorphism slightly more similar to southern populations of the Iberian Peninsula (1, 4) than population 6. This is supported by the nonsignificance of the χ^2 paired-test between populations 2 and 6, and the significance of χ^2 tests when both populations are compared with southern populations (1, 4).

The lower half of Table 3 shows some relevant distances and comparisons between southern Iberian populations and Canarian populations, and also among populations of the Canary Islands. There is certain degree of heterogeneity among Canarian populations, but most of the paired comparisons are not significantly different. When comparing the two Southern Iberian populations (1, 4) with those of the Canary Islands, it is appar

TABLE 3. *Values of genetic distances (above diagonal) and heterogeneity χ^2 (below diagonal) for paired comparisons of the second chromosome polymorphism among several Mediterranean populations (upper half) and among Southern Iberian and Canarian populations (lower half). Comparisons among Canarian populations are framed.*

Locality	Locality 1	4	2	3	6
1		0.1624	0.1462	0.2379	0.2494
4	12.31**		0.0909	0.1974	0.1739
2	13.36**	20.97***		0.2208	0.1032
3	31.22***	36.44***	31.24**		0.2049
6	31.56***	32.84***	4.64 n.s.	33.26***	

	1	4	8	10	7	9
1			0.1112	0.1171	0.0851	0.0780
4			0.2706	0.2583	0.1293	0.1006
8	11.81**	42.54***		0.1190	0.1762	0.1713
10	5.33 n.s.	18.27***	6.11 n.s.		0.1639	0.1951
7	7.99*	12.86**	26.04***	7.62 n.s.		0.1172
9	1.17 n.s.	0.61 n.s.	8.42*	1.64 n.s.	4.52 n.s.	

***$P < .001$, **$P < .01$, *$P < .05$, n.s. means statistically nonsignificant ($P > .05$).

that each of the two peninsular populations behaves somewhat differently. Overall, population 2 looks more like Canarian populations ($\bar{d} = 0.0970$) than does population 4 ($\bar{d} = 0.1897$).

The polymorphism of population 12 is qualitatively very different from that of the rest of populations because it lacks two of the arrangements (genetic mean distance between 12 and each of the other populations equals 0.1789). The same situation applies to populations 13 and 14, but in these cases the differentiation is even greater. This is reflected by genetic mean distances of 0.2802 and 0.2563, respectively.

Comparisons among populations for the fourth chromosome are less clearcut, due mostly to their uniformity and the low values of their distances, which, generally, are smaller than 0.100. Only populations 13 and 14 show a clear differentiation, reflected by their genetic mean distances of 0.1526 and 0.2284, respectively.

Figure 2 shows the graphical representation of populations and arrangements in the two principal component axes of a factorial analysis of correspondences. Part a of the figure deals only with chromosome 2 polymorphism and part b has been drawn for the whole chromosomal polymorphism (chromosomes 2 and 4). These graphs confirm most of the points revealed by direct paired comparison but they add a new picture of global understanding of similarities and differences.

Some of the peripheral populations (3, 12, 13, 14) appear quite distinct. Three Iberian populations (1, 2, 4) lie on the center of the distribution and may not be significantly different from most of the Canarian populations. The high frequency of *j arrangement in population 6* (0.643) accounts for its position in the graph and, in a similar way, the peculiar combination of arrangements jz^3 and jq^7 are most responsible for the differentiation of the population 3. Fourth chromosome arrangements (st, s) produce a centripetal pull of the populations and diminish their reciprocal distances (Fig. 2b), due mostly to their common incidence in many of the populations. The general conclusion of data analysis might be summarized as follows. First, genetic distances between populations are in general small, but there

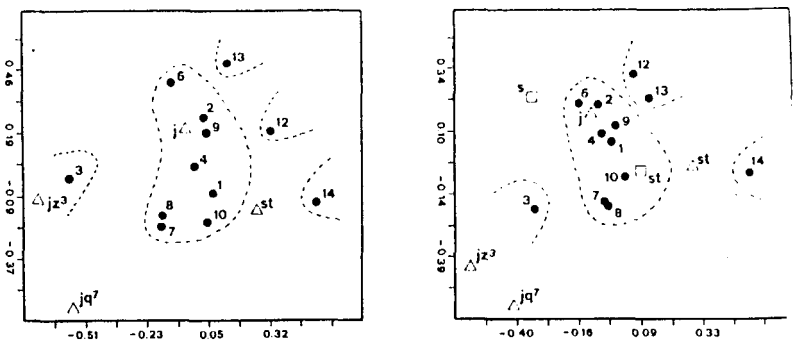

FIG. 2. Factorial analyses of correspondences for the geographical distributions of chromosome 2 arrangements (a, left) and of the whole chromosomal polymorphism (b, right) of *D. buzzatii*. Populations (●) are indicated by their numbers in the map and text (see Fig. 1 and Material and Methods). Second (△) and fourth (□) chromosome arrangements are labelled with their own symbols. Dashed lines separate primary from secondary colonization areas, except for population 3 which is also shown apart.

are significant differences. Second, the second chromosome polymorphism more effectively differentiates populations than that of the fourth, which shows a more uniform distribution between localities. Third, no clear-cut geographical clustering is observed, but some population groups and individual populations are differentiated.

DISCUSSION

The emerging picture from the sampled populations of *D. buzzatii* regarding geographical chromosomal polymorphism is that one finds marked differences in the degree of variability from one site to another. There are regions, like the Iberian Peninsula and the Canary Islands, where the polymorphism is high; however, other geographical areas of the Old World show a much lower polymorphism.

There are historical reasons for this. In the *primary colonization*, the species may have been brought in great numbers to the Canarian and Iberian regions and/or the founders may have found a host plant already established in most of these areas. Both circumstances would greatly contribute to maintain the original chromosomal variability. Later, the species further disseminated towards other areas of *secondary colonization* in successive founding events where either one or both of those initial circumstances did not necessarily hold. This would promote the observed loss of polymorphism in these areas through drift. The effect of drift can already be observed in populations geographically close to the region of primary colonization. Some of these populations (6, 12) are small sea islands and others (5, 11) are actual isolates with low number of *Opuntia* plants and adverse conditions in winter. However, the farther we move from the region of primary colonization the lower the polymorphism. This is especially obvious in the fourth chromosome polymorphism, where the 4s arrangement has been lost in all of the Mediterranean areas of secondary colonization.

Data show that second chromosome polymorphism is very widespread. In spite of drift events, selective forces may be at work. Carson (1965) suggested that widespread species rigid polymorphisms acquired after the essential evolutionary steps for colonizing ability have occurred. In the *repleta* group species, the second chromosome shows a much higher polymorphism than any other chromosome

Since one of the main features of *repleta* group evolution is adaptation to new hosts, there is the possibility that second chromosome polymorphism may play a role in this adaptation.

The maintenance of chromosomal polymorphism in colonizing populations of *D. buzzatii* may be explained in terms of niche components, which may not be much correlated with macroclimatic factors. An important factor which may be decisive for adaptation is the species of *Opuntia*. Canarian populations in the same island and with similar biogeographical conditions (7 and 8 in Tenerife) are equally distinct as populations from different islands (7 and 10, for instance). Those localities which share the same host plant (7 and 9 share *O. dillenii*; 8 and 10 share *O. ficus-indica*), show a similar polymorphism, independently of other biogeographical conditions. A similar explanation could be given for the higher differentiation of population 4 where *O. maxima* is the host plant instead of *O. ficus-indica*. Among the factors which may be relevant to niche adaptation, are the essential compounds manufactured by yeasts, such as sterols or alcohols. We have studied yeast diversity and found important differences between localities. Both geographical and seasonal differences in *Opuntia* yeast species have been observed also by Barker (1977).

The degree of flexibility of *D. buzzatii* chromosomal polymorphism has to be tested in experimental conditions. Some preliminary observations (unpubl. data) by the authors indicate that alcohol concentration in larval substrate causes significant changes in arrangement frequencies. The presence of new inversions and their maintenance, sometimes in high frequencies, in these areas of primary colonization is still a dilemma, but seems to be dependent on founding events followed by microenvironmental adaptation. It is very probable that *D. buzzatii* changed host plants upon its primary colonization, since the species of *Opuntia* of the Old World do not occur naturally in Argentina. The abundance of *Opuntia* plants coupled with the absence of competitors in the areas of primary colonization may have provided an opportunity for chromosomal adaptation through changes in arrangement frequencies. However, the original polymorphism would have been preserved in these areas and only the effect of successive stepping-stone events of colonization would have reduced the polymorphism in areas of secondary colonization. This suggests that in widespread colonizing populations of species with a narrow niche, the loss of chromosomal polymorphism is highly dependent on founding events and the adaptation to new hosts may be achieved by quantitative changes in the original chromosomal polymorphism.

Summary

Twelve natural populations and two strains of *Drosophila buzzatii* in colonized Old World regions, have been found to be polymorphic for arrangements in the second and fourth chromosomes. In most cases, this polymorphism is higher than that found in previous studies of colonized and endemic populations of this species. Two new inversions (2jq^7 and 4s) have been found in significant frequencies. The evolutionary significance of this polymorphism is difficult to interpret until the original area of this species in South America can be thoroughly sampled. However, the colonizing history of *D. buzzatii* and its host plant *Opuntia* together with its present distribution in the Old World suggest that founding events are important in the study of this evolutionary history.

The computed genetic distances between populations and the factorial analysis of correspondences show that populations of primary colonization are, in general, the most polymorphic and that geographical differentiation among them is low. On the other hand most of the populations which are presumably the result of secondary colonizations exhibit low polymorphism and high differentiation from the rest. These results may be interpreted by the steady increase of overall genetic variance due to successive founding events. However, the pervasive presence of several arrangements in high frequencies all over the species distribution suggests the operation of some kind of selection. At the present stage, it is not possible to define the degree of rigidity of this polymorphism, but the lack of correlation between biogeographical conditions and polymorphism suggests that macroenvironmental factors must be of low importance in this case. The close association of *D. buzzatii* to different *Opuntia* species exposes this species to several microenvironmental components which may be relevant for adaptation in colonizing populations.

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