GENETICS OF NATURAL POPULATIONS. XX. CHANGES INDUCED BY DROUGHT IN *DROSOPHILA PSEUDO-OBSCURA* AND *DROSOPHILA PERSIMILIS* [1]

Theodosius Dobzhansky

Columbia University, New York

Introduction

Although evolutionary changes are mostly too slow to be observed within a human lifetime, cases of genetic alterations in populations of various organisms have been reported in recent years. Naturally enough, most of these changes have been observed either in microorganisms, or in species directly influenced by human activities. Changes in higher organisms in which man is not a causative agent are of two kinds. Cyclic seasonal changes are known in several species of *Drosophila,* in the beetle, *Adalia bipunctata,* in the hamster, *Cricetus cricetus,* and in some others (Timofeeff-Ressovsky, 1940; Gershenson, 1945; Dobzhansky, 1948; and others). Trends of change which persist for several years are also recorded. The most widely known trend of this sort involves the development of melanism in industrial regions in several species of moths. Ford (1937, 1945) interprets the spread of industrial melanism as a result of release of the selection pressure which discriminates against the melanic mutants in non-industrial territories. Dobzhansky (1947) has reported a change in the incidence of chromosomal variants in a population of *Drosophila pseudoobscura* in the population of Keen Camp, in California, between 1939 and 1946. Finally, Fisher and Ford (1947) have described a change in the population of the moth, *Panaxia dominula,* in a locality in England, which involves an increase of the incidence of a certain genotype between 1929 and 1939, and a decrease of the same genotype thereafter.

Neither Dobzhansky nor Fisher and Ford were able to discern the causes which brought about the changes which they recorded.

The present article describes observations on the populations of *Drosophila pseudoobscura* and *Drosophila persimilis* at Mather, in the Sierra Nevada of California (some 350 miles from Keen Camp). Changes in these populations have been observed between 1945 and 1951. It is probable, although not fully established, that these changes were induced by the cumulative effects of a succession of dry years during this period.

Material

The flies which served as material for this study were collected at Mather and in adjacent localities in the summers of 1945, 1946, 1947, 1950, and 1951. Cups with fermenting banana were used to attract the flies, except in a few cases where larger containers were used (see below). The cytological examinations were made mostly in the field laboratory at Mather, but some flies were sent to the laboratory in New York. Wild females were placed singly in bottles with the cornmeal-molasses, or with the cream of wheat-molasses, medium. Chromosomes were studied in a single larva from the progeny of each female. All the determinations of the gene arrangements were made by the writer.

Gene Arrangements in the Mather Population of *Drosophila Pseudoobscura*

Seven gene arrangements occur in the third chromosomes of the Mather population of *D. pseudoobscura*. Two of them,

TABLE 1. *Frequencies (in per cent) of the gene arrangements in the Mather population of* Drosophila pseudoobscura. ST—Standard; AR—Arrowhead: CH—Chiricahua; TL—Tree Line; PP—Pikes Peak; SC—Santa Cruz; OL—Olympic; n—Number of chromosomes studied

Month	Year	ST	AR	CH	TL	PP	SC	OL	n
May	1947	25.7	47.1	18.6	4.3	—	—	4.3	140
June	1946	21.9	42.7	20.2	11.2	0.6	1.7	1.7	178
	1947	29.5	42.6	19.7	5.7	—	1.6	0.8	122
	1950	16.1	57.8	15.0	8.9	1.1	0.6	0.6	180
	1951	27.0	47.0	12.0	7.0	2.0	2.0	3.0	100
	Total	22.6	48.1	17.1	8.6	0.9	1.4	1.4	580
July	1945	35.7	35.7	17.2	10.4	—	0.6	0.3	380
	1947	30.3	38.2	20.4	8.2	1.0	1.6	0.3	304
	1950	19.8	55.7	16.0	4.7	3.8	—	—	106
	1951	29.3	46.2	10.8	8.2	3.8	1.0	0.7	416
	Total	30.4	42.1	15.6	8.5	2.0	1.0	0.4	1,134
August	1946	39.9	30.4	13.9	10.1	—	3.2	2.5	158
	1950	21.9	45.8	18.4	9.5	3.2	1.0	0.2	526
	1951	29.7	38.5	11.5	12.1	6.2	1.2	0.9	340
	Total	27.2	41.0	15.4	10.4	3.7	1.4	0.8	1,024
Sept.	1947	35.8	31.2	20.8	7.5	0.8	3.3	0.4	240
Grand Total									3,118

namely, Arrowhead (AR) and Standard (ST) are very common; two others, Chiricahua (CH) and Tree Line (TL), are moderately frequent; and three, Pikes Peak (PP), Santa Cruz (SC), and Olympic (OL), are rare. Of course, some of the wild flies carry two chromosomes with the same gene arrangement (structural homozygotes), and others have two chromosomes with different gene arrangements (structural heterozygotes).

A summary of the data on the relative frequencies of the gene arrangements is presented in table 1. The data for 1945–1947 have been published in Dobzhansky, 1948. It is clear at a glance that the frequencies of some of the gene arrangements undergo cyclic seasonal changes and are often different in successive months. Thus, ST chromosomes are relatively rare in May and June and more frequent in the latter part of the summer. To test the statistical validity of these changes, the chromosomes are divided into two classes, those with ST and those with gene arrangements other than ST.

The chi-square for the monthly totals turns out to be 19.12, which, for 4 degrees of freedom, has a probability of chance occurrence of about 0.001. The changes in AR chromosomes are the converse of those in ST: the frequencies of AR decrease from 47–48 per cent in May and June to about 40 per cent in late summer. The chi-square for AR chromosomes is 21.74, which may occur by chance less than once in one thousand trials. No significant changes in frequencies in different months are found for CH and TL chromosomes (chi-squares 5.38 and 7.16, probabilities of chance occurrence about 0.25 and 0.13, respectively). Among the rare gene arrangements, only PP appears to undergo changes in frequency with season, but this arrangement was too infrequent before 1950 to enable us to judge the cyclic nature of the changes recorded. If the chromosomes listed in table 1 are divided into three classes, namely, ST, AR, and "others," the joint chi-square for homogeneity on different months becomes 30.64. For 8 degrees

of freedom, this has a probability of chance occurrence less than 0.001.

The changes so far analyzed are cyclic, and they have apparently recurred in every year for which at least two observations are available (1946, 1947, 1950, and 1951). Further consideration of the data in Table 1 discloses that the composition of the Mather population was significantly different during the same season in different years. Starting with 1945, the frequencies of ST chromosomes were decreasing, and those of AR were increasing, until the former reached minimal and the latter maximal frequencies in 1950 (unfortunately, no data are available for 1948 and 1949). In 1951, ST chromosomes were again more common, and AR were less frequent, than they were on corresponding months in 1950. No definite trends are apparent for CH and TL chromosomes; if anything, the CH chromosomes were becoming less frequent during the period of observation. A very clear gain has, however, been observed in PP chromosomes. The PP gene arrangement was not encountered at all at Mather in 1945; in 1946 a single chromosome was recorded; in 1947 several chromosomes were found; in 1950, and especially in 1951, PP chromosomes were found regularly in all samples, and their frequency reached 6.2 per cent in August of 1951.

To test the statistical validity of the changes from year to year, the chromosomes are again divided into three classes: ST, AR, and "others." Since seasonal changes are known to occur, the analysis for the changes from year to year must be made separately for each month. The chi-squares obtained are as follows:

Month	Chi-Square	Degrees of freedom	Probability
June	16.02	6	0.01
July	20.31	6	0.003
August	23.50	4	<0.001

THE GENE ARRANGEMENTS IN THE *Drosophila Pseudoobscura* POPULATIONS OF THE SIERRAN TRANSECT

The Mather locality lies at an elevation of 4,600–4,700 feet on the western slope of the Sierra Nevada of California. Dobzhansky (1948) has taken samples of the populations of several other localities in the same region, ranging in elevation from 850 to 10,500 feet and forming a rough west-east transect across the Sierra Nevada mountain system. Examination of the frequencies of the gene arrangements in the third chromosomes in these populations showed that ST chromosomes become progressively less frequent, and AR chromosomes more frequent, with increasing elevation. Seasonal changes in the frequencies of ST and AR chromosomes were observed in 1947 at Lost Claim Camp (elevation about 3,000 feet) and at Aspen Ranger Station (elevation 6,200 feet). These changes have the same character as described for Mather, i.e., the frequencies of ST increase and those of AR dwindle with season.

On July 13–17, 1951, a sample of 152 third chromosomes was taken at the Aspen Ranger Station, and on August 18–19, 1951, a sample of 28 third chromosomes was obtained on Porcupine Flat (elevation 8,000 feet). The observed frequencies of the gene arrangement are shown in Table 2:

TABLE 2. *Frequencies (in per cent) of the gene arrangements in the Aspen and Porcupine populations of* Drosophila pseudoobscura
The abbreviations are the same as in Table 1

Locality	ST	AR	CH	TL	PP	OL	n
Aspen	21.1	52.6	13.2	5.9	6.6	0.7	152
Porcupine	7.1	60.7	21.5	3.6	7.1	—	28

Comparison of the data in tables 1 and 2 shows that, in July and August of 1951, ST chromosomes were most frequent at Mather, less so at Aspen, and least at

Porcupine. Conversely, AR chromosomes were most frequent at Porcupine, less so at Aspen, and least at Mather. This confirms the existence of the altitudinal gradients in the frequencies of ST and AR chromosomes recorded by Dobzhansky (1948). Whether the genetic changes which took place in the composition of the Mather population between the years 1945 and 1951 occurred also at Aspen and at Porcupine is uncertain. The data are suggestive only with respect to the PP gene arrangement, which, as shown above, increased in frequency at Mather during the above period. Only a single PP chromosome was found among the 478 third chromosomes examined from Aspen in 1946 and 1947. None were found among the 38 chromosomes from Porcupine taken on the same year. Yet, in 1951 the PP chromosomes constituted 6–7 per cent of the samples from these localities. It appears that the PP gene arrangement was gaining ground in the Sierran populations.

THE GENE ARRANGEMENTS IN THE MATHER POPULATIONS OF *Drosophila Persimilis*

Drosophila persimilis is a species closely related to *D. pseudoobscura* and yet maintaining its identity in mixed populations with the latter (cf. Dobzhansky, 1951, and other work). Five gene arrangements occur in the third chromosomes of the Mather population (not counting a sixth which has been seen only once and may conceivably represent a recently arisen mutant). These are Whitney (WH), Standard (ST), identical with the ST of *D. pseudoobscura*, Klamath (KL), Mendocino (MD), and Sequoia (SE). In contrast to *D. pseudoobscura*, no significant seasonal changes in the incidence of the gene arrangements have been observed in *D. persimilis* (Dobzhansky, 1948, and more recent data). It is, therefore, legitimate to group the data by the year (or, rather, summer) of collecting. Table 3 presents the data in this form.

It can be seen that the incidence of WH chromosomes in the population rose from a minimum in 1945 to a maximum in 1950, but fell again in 1951 to almost the 1945 level. The converse happened with the ST and KL chromosomes, the frequency of which decreased between 1945 and 1950, and rose again in 1951. MD and SE remained rare throughout and showed no consistent changes. To test the statistical significance of the observed changes, the chromosomes were divided into four classes: WH, ST, KL, and "others." The chi-square computed from the data is 42.36. For 12 degrees of freedom the probability of such or greater value is much less than 0.001. One may also divide the chromosomes in two groups: those with the WH gene arrangements and "others." The chi-square then turns out 23.96, which for 4 degrees of freedom has a probability less than 0.001. The changes observed from year to year are quite significant.

TABLE 3. *Frequencies (in per cent) of the gene arrangements in the Mather populations of* Drosophila persimilis. WH—Whitney; KL—Klamath; MD—Mendocino; SE—Sequoia; n—Number of chromosomes studied

Year	WH	ST	KL	MD	SE	Others	n
1945	69.7	8.6	15.2	6.1	0.5	—	198
1946	76.6	10.9	10.2	1.6	0.8	—	128
1947	79.5	8.3	6.9	4.8	0.2	0.2	434
1950	87.1	4.9	5.4	2.2	0.4	—	224
1951	72.1	10.3	15.4	1.8	0.4	—	272
Total	77.4	8.4	10.1	3.6	0.4	0.1	1,256

TABLE 4.   *Frequencies (in per cent) of the gene arrangements in the Aspen and Porcupine populations of Drosophila persimilis*
The abbreviations are the same as in table 3

Locality and year	WH	ST	KL	MD	SE	n
Aspen, 1946	68.5	11.1	14.8	5.6	—	108
Aspen, 1947	81.3	9.2	5.3	4.2	—	262
Aspen, 1951	87.5	2.5	7.5	2.5	—	40
Aspen, Total	78.5	9.0	8.0	4.4	—	410
Porcupine, 1946	76.8	11.0	7.3	4.9	—	82
Porcupine, 1947	85.1	9.1	2.5	2.5	0.8	121
Porcupine, 1951	96.7	—	2.2	1.1	—	92
Porcupine, Total	86.4	6.8	3.7	2.7	0.3	295

THE GENE ARRANGEMENTS IN THE *Drosophila persimilis* POPULATIONS OF THE SIERRAN TRANSECT

Like those of *Drosophila pseudoobscura,* the populations of *D. persimilis* show altitudinal gradients in the frequencies of the gene arrangements at different elevations. Namely, the WH chromosomes become progressively more frequent as one ascends the slope of the Sierra, while ST, KL, and MD are appreciably more common at low than they are at high elevations (Dobzhansky, 1948). The results of the samplings of the populations of Aspen Ranger Station and of Porcupine Flat are summarized in table 4.

It can be seen that the Aspen and Porcupine Flat populations suffered the same changes which occurred in the Mather population between 1945 and 1951. The frequencies of WH chromosomes have risen and those of the other gene arrangements have fallen with time. Unfortunately, no samples have been taken between 1948 and 1950, and it is consequently unknown whether the 1951 frequency of WH chromosomes is or is not lower than it was in 1950, as observed at Mather. Statistically, the reality of the changes is assured. Dividing the chromosomes into two classes, those with WH and with "other" gene arrangements, the chi-squares for the Aspen and Porcupine populations are 10.10 and
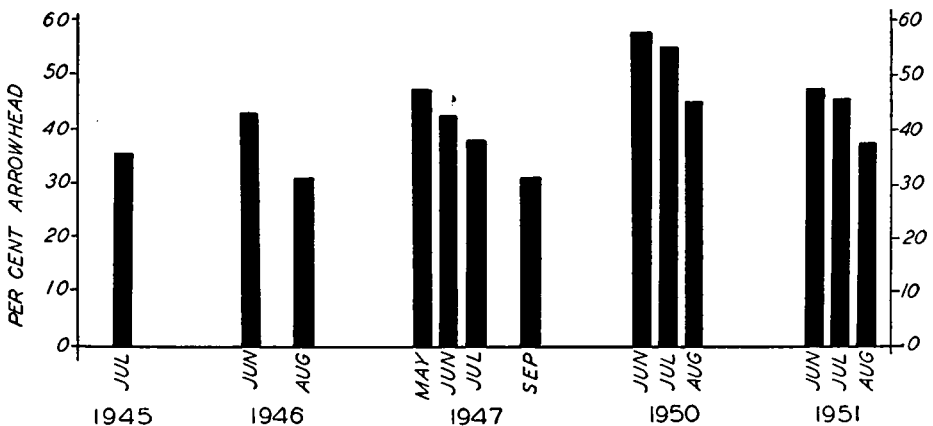

FIG. 1. The frequencies of the Arrowhead gene arrangement in *Drosophila pseudoobscura* at Mather, California.
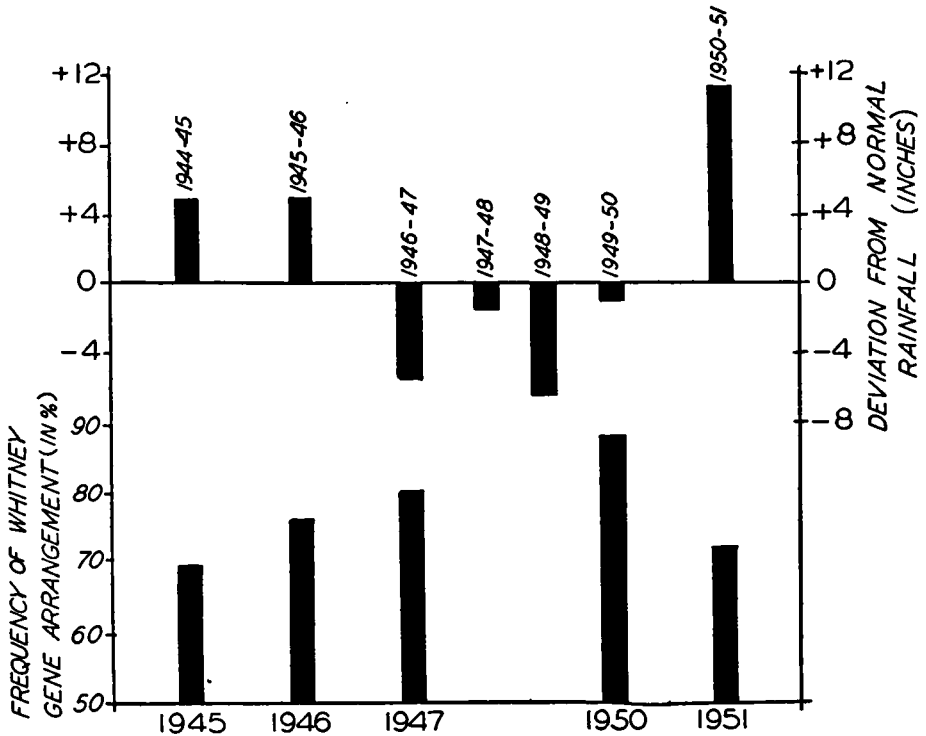
FIG. 2. The frequencies of the Whitney gene arrangement in *Drosophila persimilis* at Mather, and the deviations from the normal amounts of precipitation observed at Yosemite Park Headquarters, in California.

31.92, respectively. For 2 degrees of freedom the probability of chance occurrence of such values is less than 0.01.

POSSIBLE CORRELATIONS WITH THE CLIMATE CHANGES

It has been shown that the two species, *Drosophila pseudoobscura* and *D. persimilis,* were undergoing parallel changes in the genetic composition of their populations in the Yosemite Park region of the Sierra Nevada of California. At Mather, the ST chromosomes in *D. pseudoobscura* fell in frequency between 1945 and 1950 and recovered some of the lost ground in 1951. AR chromosomes changed in the direction opposite to ST. PP chromosomes reached their maximum frequency in 1951. In *D. persimilis* the incidence of WH chromosomes rose and of ST and KL chromosomes fell in the Mather population between 1945 and

1950, a partial reversal of the change taking place in 1951. The *D. persimilis* populations of the neighboring localities, Aspen and Porcupine, suffered apparently the same changes as did the population of Mather. Whether the changes in *D. pseudoobscura* were also parallel in the three localities is not clear but it seems probable.

The situation is clearly one which suggests that most of the changes observed had a common cause, and the experience gained in studying the Sierran populations during five summers points to the increasing aridity as a possible factor. The Transition Life Zone of the Sierra Nevada is characterized by almost rainless summers, and by relatively abundant precipitation, both in the form of rain and snow, from November to April. The amount of precipitation received during winter determines the ground water level

TABLE 5. *The deviation (in inches) from the normal amounts of precipitation observed in various years at the Hetch-Hetchy and the Yosemite Park Meteorological Stations*

Year	Hetch-Hetchy	Yosemite Park
1945–1946	+2.57	+4.93
1946–1947	−6.38	−5.36
1947–1948	−1.47	−1.14
1948–1949	−8.69	−6.19
1949–1950	−4.56	−0.72
1950–1951	+15.11	+11.25

and the welfare of the vegetation, as well as of much of the animal life, during the summer months. Dr. W. M. Hiesey has very generously furnished the data on the mean precipitation and mean temperature recorded at Hetch-Hetchy (about 5 miles north of Mather) and at the Yosemite National Park headquarters (about 17 miles southeast of Mather) as copied by him in the office of the U. S. Weather Bureau in San Francisco. Table 5 shows the deviations from the normal (average) precipitation records observed between July of the preceding and June of the succeeding year.

The precipitation was deficient in the Yosemite Park region between 1946 and 1950, which is the period during which the *Drosophila* populations suffered the changes reported above. The winter of 1950 was, however, very wet, and, although the spring months of 1951 were again drier and warmer than normal, the early summer of 1951 at Mather showed every indication of abundant water supply in the soil. The *Drosophila* populations have in the summer of 1951 largely restored the genetic composition which they had in 1945–1946.

RELATIVE FREQUENCIES OF SPECIES IN THE MATHER POPULATION

The changing environmental pressures on populations of ecologically similar species may manifest themselves in variations of the relative abundance of these species in a locality. This is the consequence of the fact that sympatric species,

even ecologically parallel ones, exploit the environment in somewhat different ways. Three species of the *obscura* group, namely, *Drosophila pseudoobscura, D. persimilis,* and *D. azteca,* occur at Mather. Their females are difficult to distinguish in making mass classifications; males of *azteca* can, however, be easily separated from the other two species. Table 6 summarizes the data for the Mather samples.

Table 6 shows that *D. azteca* increases in relative frequency in the population as the season progresses. The changes are surprisingly regular; except for a very high frequency in September of 1947, no appreciable variations from year to year are recorded. At elevations higher than that of Mather (4,700 feet), *D. azteca* becomes rare or absent. At Porcupine Flat (8,000 feet), a single male of this species was identified in August of 1951 among several hundred males of *D. pseudoobscura* and *D. persimilis*. At Aspen (6,200 feet), *D. azteca* is less

TABLE 6. *Frequency of* Drosophila azteca, *in per cent of the males belonging to this species in samples containing* D. azteca, D. pseudoobscura, *and* D. persimilis, *at Mather, California*

Time of collecting	Males classified	Per cent *azteca*
June 8–15, 1945	547	36
August 10, 1945	167	39
August 22–September 5, 1945	1,134	50
June 4–15, 1946	718	18
June 26–30, 1946	201	30
August 9–10, 1946	227	45
June 22–26, 1947	188	12
July 26, 1947	584	34
September 1–4, 1947	1,139	77
September 12, 1947	393	68
June 29, 1950	314	32
July 25–28, 1950	285	35
August 18–27, 1950	890	42
June 25, 1951	87	33
July 6–19, 1951	481	25
August 10–26, 1951	407	43

TABLE 7. *Percentages of* Drosophila persimilis *in samples from Mather containing the species named and* D. pseudoobscura

Time of collecting	Strains examined	Per cent *persimilis*
July 8–15, 1945	155	37
August 22–September 5, 1945	543	40
June 4–15, 1946	2,065	34
August 9–10, 1946	79	29
May 15, 1947	59	41
June 22–26, 1947	100	39
July 5, 1947	66	21
July 26, 1947	116	14
September 1–12, 1947	110	45
June 29, 1950	68	30
July 25–28, 1950	57	30
August 18–27, 1950	141	51
June 26–30, 1951	56	11
July 1–15, 1951	132	11
July 16–30, 1951	57	5
August 7–16, 1951	· 38	3

common than at Mather, but it shows the same increase in relative abundance towards the end of the season.

D. persimilis can be distinguished from *D. pseudoobscura* either by outcrossing wild flies or their offspring to known representatives of the sibling species (genetic method), or by examination of the chromosomes in salivary gland preparations (cytological method), or by examination of the male genitalia as indicated by Rizki (1951). The first two methods have been used for classification of the samples from Mather. The results are summarized in table 7.

The relative frequencies of *D. pseudoobscura* and *D. persimilis* oscillate rather irregularly. In 1947, but apparently not in 1950, frequency of *D. persimilis* declined with the season. Most remarkable, however, is the almost catastrophic drop which *D. persimilis* has suffered in 1951, after having maintained a rather constant incidence from 1945 till 1950. This behavior parallels neither the known climatic changes nor the changes in the relative frequencies of the gene arrange-

ments through which both species have passed between 1945 and 1951 (see above).

A word of warning must be added at this point. The relative frequencies of the species in collections depends not only upon their incidence in the locality but also on collecting techniques. Thus, *D. persimilis* is more common among the flies collected in the morning than in the evening (Dobzhansky, 1951), *D. azteca* is less frequent when cups with rather fresh fermenting banana bait are used for traps than when large cans with old bait are used (the "Texas method"). Furthermore, there occur local concentrations of these species in various microenvironments. Tables 6 and 7 include, therefore, only the samples collected with the aid of the same technique (banana cups, evening collecting), and in exactly the same neighborhoods.

DISCUSSION

The concept of "type" is inherited from the pre-evolutionary age. Nevertheless, it still colors the thinking of many biologists. It is frequently assumed that natural populations consist of "normal," or "typical," representatives of their species and races, with a scattering of rare "aberrant," or "mutant," individuals. Only where a species is obviously composed of two or more clearly distinct categories of individuals, the existence of polymorphism is recognized as a more or less exceptional situation. Now, in biology the idea of "type" is an oversimplification which is often quite misleading. Careful study discloses that polymorphism is a rule rather than an exception. Mendelian populations, i.e., communities of sexually reproducing and cross-fertilizing organisms integrated by bonds of mating and parentage, are always genetically polymorphic. Of course, the polymorphism is more abundant in some and more limited in other populations. This is because polymorphism is usually, although not necessarily, adaptive. Mendelian populations are poly-

morphic, because every species lives not in a single absolutely constant environment, but in a variety of environments which undergo frequent changes. The greater the diversity of environments to which a population is exposed, the greater, in general, will be the polymorphism. This is because no single genetic constitution is likely to prove superior in adaptive value to all others in all environments. It is manifestly advantageous to a species to include a variety of genetic constitutions which engender optimal phenotypes in different environments that the species is likely to encounter. By and large, the more polymorphic a species is, the greater variety of habitats it can settle and exploit (da Cunha, Burla, Dobzhansky, 1950).

When a species, or any constituent Mendelian population, is exposed to a succession of different environments, it may react to them by genetic reconstructions. The speed of the reaction will depend, among other things, upon the speed of reproduction. Species which give a single generation per year, or in which a generation takes several years, are likely to react to climatic changes which continue for several or for many years. Only exceptionally will such species evince genetic changes in response to seasonal alternations in the environment (as found by Gershenson, 1945, in the hamster). More rapidly breeding organisms may undergo cyclic genetic changes induced by the succession of the seasons, as well as by climatic and biotic variations on successive years. This is the case in *Adalia* (Timofeeff-Rossovsky, 1940) and in *Drosophila*.

Fisher and Ford (1947) discovered changes from year to year in the composition of a certain population of *Panaxia dominula* in England. These changes are presumably due to natural selection. Fisher and Ford allege that this fact invalidates Sewall Wright's theory · of genetic drift. What this and similar facts invalidate is the notion that genetic drift is the *sole* cause of evolutionary changes, which Fisher and Ford see fit to impute to Wright. But Wright (1948 and earlier work) has stated quite explicitly that the importance of genetic drift in evolution lies precisely in its interaction with natural selection. The incidence of a genetic variant in a population may vary at times chiefly owing to selection and at other times due chiefly to drift. Genetic variants which differ in adaptive values as much as do the chromosomal forms in *Drosophila* will seldom or never be influenced by drift. Other genetic variants in the same species, such as the heterozygotes for concealed recessive mutant genes, may well be influenced by the drift more than by selection (Dobzhansky and Wright, 1947). Evolution is not caused by any single factor; it is brought about by interaction of many factors, frequently opposed to each other. It is the balance of all the factors which determines the ebb and flow of evolutionary change.

SUMMARY

The sibling species, *Drosophila pseudoobscura* and *Drosophila persimilis,* both show chromosomal polymorphism in the populations of the Yosemite National Park region of the Sierra Nevada of California. Seven gene arrangements are recorded in the third chromosome of the former, and six in the latter species.

In *D. pseudoobscura* the relative frequencies of the ST and AR chromosomes show seasonal changes: ST chromosomes become more, and AR become less, common as the season progresses. Other gene arrangements evince no perceptible changes. No significant seasonal changes have been recorded in *D. persimilis.*

The populations of both species have suffered appreciable changes from year to year. In *D. pseudoobscura* the ST chromosomes waned and AR chromosomes waxed in frequencies between 1945 and 1950, but in 1951 the changes have become reversed. The PP gene arrangement was very rare in 1945 and 1946 but became fairly common in 1951. In *D. persimilis,* WH chromosomes waxed and ST and KL waned in frequencies between 1945 and 1950. Here, again, the year 1951 has brought an almost complete reversal.

There was a succession of drought years in 1946–1950, but the winter 1950–1951 had more than the normal amount of precipitation. It is considered probable that the genetic changes observed from year to year were causally related to the drought and to its abatement. However, the drought has not had a clear influence on the relative abundance of the three related species, *Drosophila pseudoobscura, D. persimilis,* and *D. azteca. D. persimilis* was, for unknown reasons, much less common in 1951 than ever before. *D. azteca* underwent regular seasonal changes in abundance, which were not appreciably different in 1950 and 1951, despite the genetic changes recorded in the other species.

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