The characters were: red (R) *v.* green (r) seedlings and mature plant colours; and black (B) *v.* brown (b) seeds. Plant colour can be readily scored in the hypocotyls of freshly germinated seedlings in petri dishes. Seed colour refers to testa colour; fruits are shed as such and the fragile pericarps must be rubbed off to reveal the underlying testas. Classification is good except that rare dark brown seeds may be mis-scored as black.

Plants heterozygous at the two loci were detected in a sample of the original population and the two more heterozygotes (R/r) were found in the progeny of glasshouse plants. Green plants (rr) yielded about one per two thousand heterozygous red progeny, so (since reds and greens are about equal) the outcrossing rate is about 0·1 per cent. The table shows that, apart from some slightly aberrant segregation for R-r, the breeding results are straightforward.

3. CONCLUSIONS

Cañáhua is an easy and convenient plant to handle but the impossibility of making reliable crosses rules it out as an experimental plant. It would, however, provide excellent material for elementary genetic teaching because it is hardy, responds well to crowding, is reliably selfed and because seedling colours can be easily scored in petri dishes. A bulk stock of F_2 R-r seed is available and samples will be sent on request.

4. REFERENCE

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STABILITY OF CHROMOSOMAL POLYMORPHISM IN POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA*

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1. INTRODUCTION

NUMEROUS experiments with *Drosophila pseudoobscura* have demonstrated that metastable equilibria are usually attained when carriers of different third chromosome gene arrangements of similar geographic origin are bred in population cages at 25° C. (Dobzhansky, 1947*a*, 1948; Levene, Pavlovsky and Dobzhansky, 1954). When flies come from different geographic regions, equilibria may or may not be attained; monomorphism or stable polymorphism may become established (Dobzhansky and Levene, 1951; Dobzhansky and Pavlovsky, 1953; Lewontin, 1958). Equilibria have been attributed to superiority of inversion heterozygotes over corresponding homozygotes.

Most population cage experiments have been terminated soon after an apparent equilibrium has been attained, usually in 12 to 18 months; long-term stability of the polymorphism is debatable in such cages. If, indeed, the chromosomal polymorphism is adaptive, then one might expect both inversion types to remain in the population so long as the experimental conditions remain selective for this adaptive mode. Levine and Beardmore (1959) studied the stability of an equilibrium in an experimental population containing Arrowhead (AR) and Chiricahua (CH) chromosomes of different geographic origin. They maintained the population for about 53 months (66 generations), and, although fluctuations in relative frequencies occurred, the polymorphism persisted for the duration of the experiment. The present report deals with another instance of the retention of polymorphism. One of the populations involved (No. 173) is the oldest *Drosophila pseudoobscura* experimental population in existence.

2. THE EXPERIMENTAL POPULATIONS

Two populations were started in 1957 with AR and CH strains derived from flies collected at Pinon Flats, Mount San Jacinto, in California, Population No. 173 was started in January, and No. 181 in May, each

TABLE 1

Frequency of CH in Populations 173 and 181 at 25° C.

Months	Per cent. CH No. 173	Per cent. CH No. 181
0	80·0	80·0
1	60·7	59·3
2	55·0	58·7
3	50·0	44·7
5	39·3	...
6	42·7	...
9	...	32·3
10	35·7	...
12	35·7	32·3
16	...	31·0
20	27·3	...
22	...	33·7
26	25·3	...
29	...	39·3
33	28·0	...
41	...	38·0
45	25·3	...
53	25·9	...
62	19·0	...
67	...	33·0
74	19·0	...
81	26·3	...
96	12·0	...
99	18·3	...
101	22·7	...

having initial gametic frequencies of 0·2 AR and 0·8 CH. The populations were periodically examined by sampling 300 chromosomes obtained from 150 larvae grown under optimal conditions. The populations were maintained in the laboratory of Professor Th. Dobzhansky until 1962, and equilibrium frequencies had seemingly been attained. In 1962, the populations were moved to Syracuse and were placed in wooden cages similar to those designed by Barker (1960). A cornmeal-agar-molasses medium was substituted for the previously-used cream of wheat-molasses medium

(Demerec and Kaufmann, 1964). Information concerning populations Nos. 181 and 173 can be found in Beardmore, Dobzhansky and Pavlovsky (1960) and Levine and Van Valen (1964). Table 1 summarises the progress of selection to date. Population No. 181 was terminated after 67 months (80 generations), whereas No. 173 is still in existence after more than 101 months (121 generations) at 25° C. Despite fluctuations, the persistence of the polymorphism is apparent. Due to a mite infection, population No.

TABLE 2

Comparison of observed frequencies of inversion types with frequencies expected according to Hardy-Weinberg formula

	Zygotic frequencies			χ^2	Gametic frequencies in per cent.	
	AR/AR	AR/CH	CH/CH		AR	CH
I. *Larvae uncrowded*						
Observed	87	58	5		77·3	22·7
Expected	89·7	52·6	7·8			
Difference	−2·7	+5·4	−2·8	1·64		
II. *Adult females from crowded cups*						
Observed	39	31	4		73·6	26·4
Expected	40·1	28·8	5·2			
Difference	−1·1	+2·2	−1·2	0·48		
III. *Adult males from crowded cups*						
Observed	31	33	3		70·9	29·1
Expected	33·7	27·7	5·7			
Difference	−2·7	+5·3	−2·7	2·51		
IV. *Adult males and females from crowded cups combined*						
Observed	70	64	7		72·3	27·7
Expected	73·7	56·5	10·9			
Difference	−3·7	+7·5	−3·9	2·58		

* Each χ^2 has one degree of freedom.

173 was maintained in bottles for about three months sometime between months 81 and 96, and when the cage was re-established at month 96, the frequency of CH was at its lowest point (12 per cent.). After five months, the frequency of CH increased to 22·7 per cent.

3. LIFE CYCLE AND SELECTION

Dobzhansky (1947*b*) found that when egg samples from cage populations containing AR and CH (or Standard and CH) chromosomes were taken, and larvae grown under uncrowded, optimal conditions, the proportions of inversion heterozygotes and homozygotes were close to those demanded by the Hardy-Weinberg formula; when adult flies that developed in crowded cages were tested, it was found that there was a significant excess of heterozygotes and a deficiency of homozygotes compared to Hardy-Weinberg expectations. Dobzhansky concluded that there was a differential mortality between the egg and adult stages under cage conditions in favour of heterozygote survival.

In view of the persistence of the polymorphism in population No. 173, it was of interest to determine whether the heterozygotes were favoured in the above manner in this population. In May 1965, after No. 173 had been maintained for more than eight years, egg samples were taken for six days and larvae were raised under uncrowded conditions. The frequencies of AR and CH inversion types among 300 chromosomes sampled were determined, and it was found that Hardy-Weinberg expectations were fulfilled in the egg sample reared under optimal conditions (table 2). At the same time the egg sample was taken, extra cups with food medium were placed in the cage and left there until shortly before hatching. Then the cups were removed, plastic chimneys were placed on each cup, and virgins were collected for several weeks until most of the hatching had been completed. Randomly chosen single females were then mated to males from an AR/AR stock; also, males that had developed in the crowded cups were mated to virgin females from the AR/AR stock. Ten glands were examined from each of a total of 141 crosses. If all ten glands were AR/AR, the tested parent was assumed to be AR/AR; if all ten glands were AR/CH, the tested parent was assumed to be CH/CH; when AR/AR and AR/CH glands were found, the parent was known to be AR/CH. Unlike the findings of Dobzhansky (1947*b*), there was no significant excess of heterozygotes, and the observed frequencies of inversion types did not differ significantly from Hardy-Weinberg expectations (table 2).

4. DISCUSSION

Long-term stability of chromosomal polymorphism in *Drosophila pseudoobscura* populations has been observed by Levine and Beardmore (1959), Dobzhansky (1960), and Strickberger (1963). The present article reports the longest known maintenance of chromosomal polymorphism in experimental cage populations of *Drosophila pseudoobscura*. The results thus far do not support Lewontin's (1958) view that monomorphism will ensue if a polymorphic population is maintained for a long time under " constant " conditions. However, cage conditions are certainly variable and may not provide sufficient constancy to test the argument adequately. Also, it may be argued that the populations have not been maintained long enough.

Maintenance of chromosomal polymorphism in experimental populations has been attributed to superiority of inversion heterozygotes over corresponding homozygotes. The apparent absence of a significant differential mortality in favour of heterozygotes in the present study differs from the findings of Dobzhansky (1947*b*). However, natural selection may operate in ways other than differential survival between egg and adult stages; factors such as differential longevity, fecundity, differences in sexual activity, etc., may also be important. Dobzhansky (1947*b*) did find that Hardy-Weinberg expectations were realised among young adult males from the AR and CH population, although both young and old females and old males did show an excess of heterozygotes. No samples of old males directly from No. 173

were taken, and it is possible that selection on males and/or females may be occurring at the adult level.

5. SUMMARY

Stability of chromosomal polymorphism was studied in two cage populations of *Drosophila pseudoobscura* containing AR and CH gene arrangements. The populations were maintained for $5\frac{1}{2}$ and $8\frac{1}{2}$ years respectively. The polymorphism was found to persist for the duration of the experiment.

Examination of chromosomes from No. 173 larvae grown under optimal conditions, and determination of the chromosomal constitution of adult flies grown under crowded cage conditions revealed a Hardy-Weinberg distribution of heterozygotes and homozygotes in both instances. Significant differential mortality between egg and adult stages favouring the heterozygotes was not observed.

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