

A BALANCED INVERSION POLYMORPHISM OF $\text{In}(2\text{L})\text{B}_1\text{D}_5$ IN *DROSOPHILA ALBOMICANS*¹

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Hwei-Yu Chang, Yi-Fei Yin, Yue-Ling Yang and Fei-Jann Lin (1988) A balanced inversion polymorphism of $\text{In}(2\text{L})\text{B}_1\text{D}_5$ in *Drosophila albomicans*. Bull. Inst. Zool., Academia Sinica 27(4): 245-248. Heterozygosity of $\text{In}(2\text{L})\text{B}_1\text{D}_5$ of 19 polymorphic isofemale stocks has been examined for three successive years. The average heterozygosity of these polymorphic stocks for 1985, 1986, and 1987 is 0.47, 0.49, and 0.48, respectively. These results indicate that these laboratory maintained isofemale stocks have reached genetic equilibrium for this gene arrangement. This polymorphic equilibrium is probably maintained by the overdominant selection force.

Key words: *Drosophila*, Chromosomal inversion, Polymorphism.

How to maintain the polymorphism in natural population has been an issue between selectionists and neutralists. From the view of the selectionists, the polymorphism in natural populations should be in balance and is maintained principally by all kinds of selection forces. The neutralists, on the other hand, suggest that the observed variation is essentially neutral and the frequencies of these neutral alleles in natural populations are resulted by mutation, migration and random genetic drift. The fixation or the loss of neutral alleles fits in stochastic models. The neutralists also consider that certain polymorphic loci, composed of alleles with differential selection pressure, are usually at a transient state.

An inversion in *Drosophila* represents a supergene in natural populations, because there is no recombination within the heterozygous inversion region. It is due to that a single crossing over between the homologous chromosome segments with heterozygous inversion usually produces lethal gametes. Thus, the heterozygous inversion provides a useful model to investigate the mechanism of polymorphism maintenance in population. We have previously reported that inversion $\text{In}(2\text{L})\text{B}_1\text{D}_5$ shows heterosis in both natural population and laboratory-maintained isofemale stocks of *Drosophila albomicans* (Chang, *et al.*, 1987). However, whether those isofemale stocks had reached equilibrium was uncertain when they were subjected for the inversion analysis. The investigation of the

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inversion $In(2L)B_1D_5$ at a balanced or a transient state is of fundamental importance to determining whether this inversion polymorphism is maintained by the selection forces or just a temporal phenomenon or even a neutral variation. In this communication, we compared the heterozygosity data of laboratory-maintained isofemale stocks of *Drosophila albomicans* in 1986 as well as 1987 to those in 1985 in order to see if the frequency of heterozygous $In(2L)B_1D_5$ is stable.

MATERIALS AND METHODS

The isofemale stocks of *Drosophila albomicans* from Wulai were established in 1977 and 1978 (Chang, *et al.*, 1987). They have been maintained by a standard procedure described previously (Lin and Chang, 1986).

At least thirty larvae were randomly sampled and sacrificed to prepare salivary gland chromosome slides for each of the 32 laboratory-maintained stocks in 1986 and again in 1987. The salivary glands removed from the third instar larvae were successively submerged in 45% acetic acid for one minute, in 1N HCl for 15 to 30 seconds and in lacto-aceto-orcein for 20 minutes. The stained salivary glands were then squashed on a slide with a drop of 75% lacto-acetic acid (1:1.5). The heterozygous inversion $In(2L)B_1D_5$ was identified microscopically according to the standard map of the giant chromosomes of *Drosophila albomicans* (Lin, *et al.*, 1974). The heterozygosity of each stock was the frequency of heterozygous individuals in the sample examined.

RESULTS AND DISCUSSION

The heterozygosity of $In(2L)B_1D_5$ for each of the 32 isofemale stocks was determined by examining a total of 1,024 and 1,109 larvae in 1986 and 1987, respectively. No heterozygous inversion of $In(2L)B_1D_5$ was observed in 13 monomorphic isofemale stocks from the survey of the three consecutive

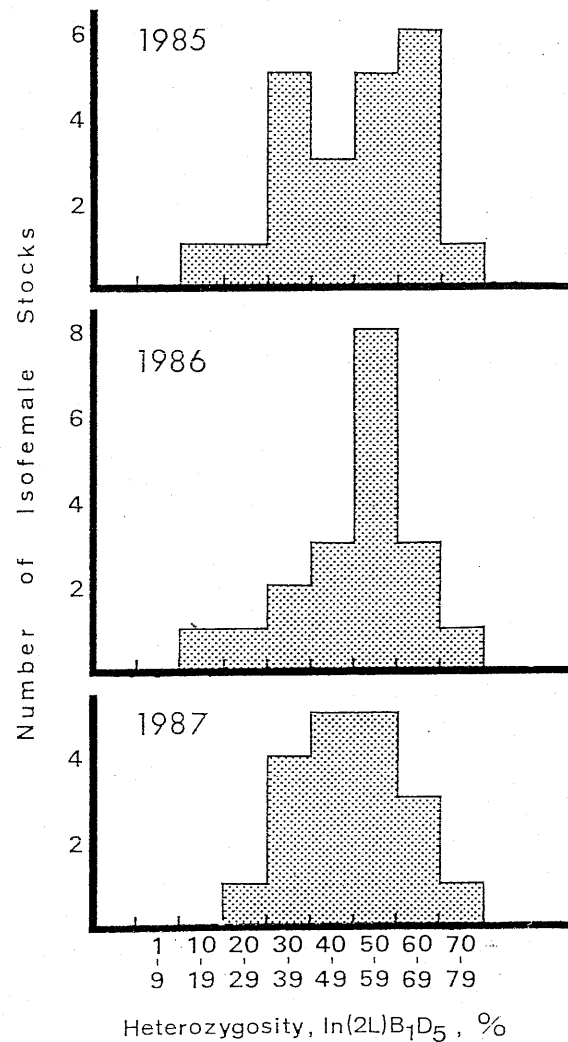


Fig. 1. The distribution of the 19 polymorphic isofemale stocks on heterozygosity in 1986 and 1987. The 1985 data, used for comparison was quoted from a previous paper (Chang, *et al.*, 1987).

years. This result is consistent to our previous view that the successful mutation rate of an inversion type is very low (Lin and Chang, 1986). The mutation rate of a non-deleterious inversion is so low that it is supposed to happen only once during the evolutionary history of *Drosophila*. Based on this assumption inversion data supply information to reconstruct the relationship among populations or even among species (Lin and Chang, 1986).

The distribution of heterozygosity of $In(2L)B_1D_5$ in the 19 polymorphic isofemale stocks is shown in Fig. 1. The average heterozygosity for these polymorphic laboratory stocks was 0.49 in 1986 and 0.48 in 1987 as compare to 0.47 in 1985 (Chang, *et al.*, 1987). These results suggest that the heterozygosity have reached equilibrium in 1985. Furthermore, the distribution of the heterozygosity is still centralized at a value close to 0.48 after two years. Since migration is almost impossible to happen in the laboratory stocks, the selection force may be a proper explanation for the maintenance of this inversion polymorphism in laboratory stocks of *Drosophila*. In fact, we have shown that in natural population the flies with heterozygous $In(2L)B_1D_5$ have better fitness to the cold and wet weather in winter (Chang, *et al.*, 1987). The laboratory temperature (22°C) and the relative humidity (75%) are coincidentally close to those in

winter of Wulai where the flies were collected.

Although genetic drift is also noticed during the two year's period (Fig. 2), the drift is obviously not the only factor influencing the heterozygosity of these stocks, since neither an increasing variation nor a tendency of fixation is observed. These results also support the view that the overdominance selection force is a simple explanation for the equilibrium in these polymorphic stocks in the laboratory. The heterozygotes may be adaptive and have selective advantages because over 1/2 stocks still show a heterozygosity value higher than 0.5.

In conclusion, our results agree to the hypothesis that the major polymorphisms are maintained by overdominant selection (Lewontin, 1985). The reason why the data of radiata pine failed to support this hypothesis (Strauss, 1987) could be explained that those populations were not at equilibrium

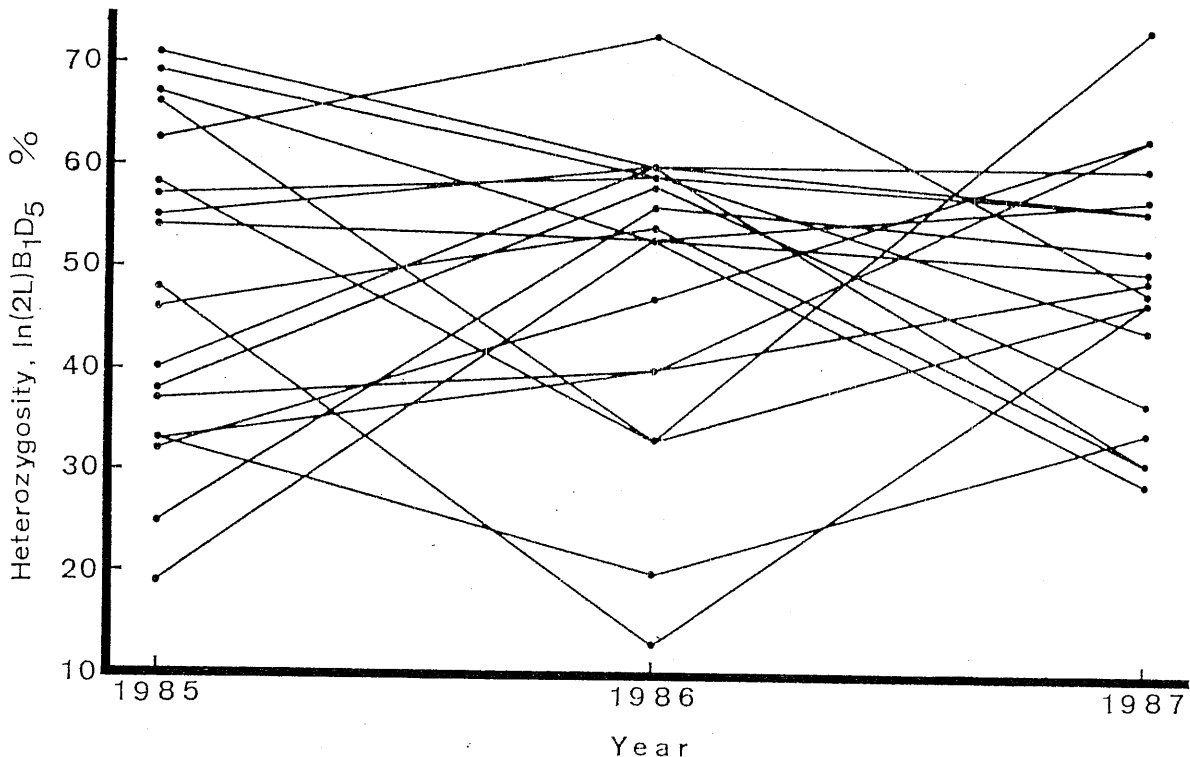


Fig. 2. The annual drifts heterozygosity of the 19 polymorphic isofemale stocks from 1985 to 1987.

and/or maintained by variable selection forces. The evidence showing that the inversion $In(2L)B_1D_5$ polymorphism is maintained by balanced selection forces does not falsify neutralism, because the neutralism and the selectionism are not mutually exclusive hypotheses. There may be different mechanisms to maintain the polymorphism of different genetic traits in natural populations.

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紅果蠅 (*Drosophila albomicans*) 染色體逆位 $In(2L)B_1D_5$ 的平衡多態性

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連續三年檢查 32 個紅果蠅單雌品系的染色體逆位 $In(2L)B_1D_5$ 異結合型比例 (heterozygosity)。其中 19 個多態性的品系在 1985, 1986 和 1987 的平均異結合型比例分別為 0.47, 0.49 和 0.48。該結果顯示這些實驗室培養的品系可能在 1985 年已達平衡，而此平衡極可能是由異結合型優勢 (overdominance) 的選汰壓力所維持。