

## EFFECTS OF CLIMATIC FACTORS ON THE HETEROZYGOSITY OF $In(2L)B_1D_5$ IN *DROSOPHILA ALBOMICANS*

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Hwei-Yu Chang, Su-Hua Chang and Fei-JannLin (1987) Effects of climatic factors on the heterozygosity of  $In(2L)B_1D_5$  in *Drosophila albomicans*. *Bull. Inst. Zool., Academia Sinica* 26(1): 39-45. The seasonal fluctuation of heterozygous inversion,  $In(2L)B_1D_5$ , was observed in natural population of *Drosophila albomicans* at Wulai, Taiwan. The heterozygosity of  $In(2L)B_1D_5$  was negatively correlated with the temperature, and positively correlated with the relative humidity. These results indicated that the flies with heterozygous  $In(2L)B_1D_5$  have better fitness to the cold and wet weather in winter. Heterosis might be the main mechanism for maintaining the polymorphism in the natural population, and laboratory maintained isofemale stocks.

Heterozygous inversion in *Drosophila* can maintain a sequence of genes on a particular chromosome and prevent them from crossing over with the alleles on the homologous chromosome carrying a different gene order. Thus, an inversion in natural population may represent a supergene. In fact, the frequencies of inversions have been demonstrated to fluctuate with the change of several ecological factors (Dobzhansky and Epling, 1944; Dobzhansky, 1948; van Valen, *et al.*, 1962; da Cunha, 1951; and Wagner, 1949). Although they do not cause morphological changes, this kind of variation is not neutral (Dobzhansky, 1974). The population of *Drosophila albomicans* at Wulai contains several chromosomal inversion types.  $In(2L)B_1D_5$  is the most conspicuous one among them (Lin and Chang, 1986). Therefore, in this communication, we investigate the fluctuation of the heterozygosity of  $In(2L)B_1D_5$  during the period from April, 1977 to February 1978, and the relationships between the inversion heterozygosity and climatic factors, including temperature, humidity and rain precipitation.

We find that  $In(2L)B_1D_5$  shows heterosis in both natural population and laboratory maintained isofemale stocks.

### MATERIALS AND METHODS

#### Flies

*Drosophila albomicans* were collected from a valley at Wulai (Fig. 1) every two weeks from April 22, 1977 to February 24, 1978. Fourteen female flies were cultured individually from each collection. Totally 308 isofemale stocks were established from 22 collections. One or two isofemale stocks from each collection were saved purely by chance. Thirty nine isofemale stocks of them had been maintained in the laboratory (22°C and 75% relative humidity) for more than 8 years until 1986, and the rest were discarded after the  $F_1$  generation. The flies were maintained by a standard procedure described previously (Lin and Chang, 1986).

#### Chromosome preparation

Six female  $F_1$  larvae from each newly established isofemale stock and 30 female

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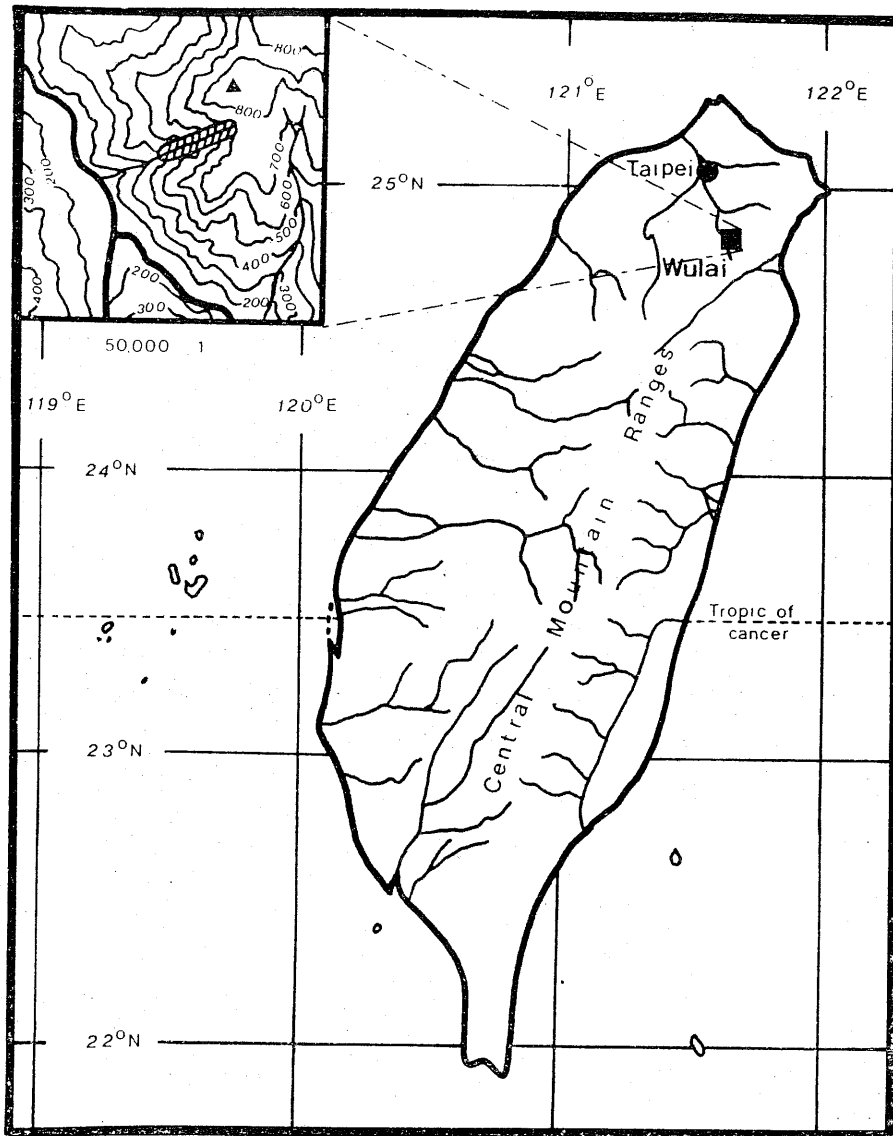


Fig. 1. The collecting site of *Drosophila albomicans*. Wulai is indicated on the map of Taiwan.

larvae from each laboratory maintained stock were sacrificed to make salivary gland chromosome slides. The salivary glands obtained from third instar female larvae were subsequently submerged in 45% acetic acid for one minute, in 1N HCl for 15 to 30 seconds and then in lacto-aceto-orcien for 20 minutes. The stained salivary glands were squashed on a slide in 75% lacto-acetic acid (1:1.5). The inversion types were identified microscopically according to the standard map of the giant chromosomes (Lin, *et al.*, 1974).

#### Heterozygosity of $In(2L)B_1D_5$

The heterozygosity (H) of  $In(2L)B_1D_5$  in natural population was estimated from  $F_1$  female larvae, because the larvae of *D. albomicans* are hard to be found and identified in nature. Let the frequencies of two homozygous forms in the natural population be  $a$  and  $b$ , and the probability that  $F_1$  heterozygosity=0 and the probability that  $F_1$  heterozygosity=1 be  $A$  and  $B$ , then  $A=a^2+b^2$  and  $B=2ab$ . Thus, the estimated heterozygosity,

$H$ , which is equal to  $1-(a+b)$ , can be calculated as follow:  $H=1-\sqrt{A+B}$ .  $A$  and  $B$  are estimated from the 14 samples for each collection. In order to reduce the sampling error,  $A$  and  $B$  are substituted by corrected values,  $A'$  and  $B'$ , respectively, where  $A'=A-C$ ,  $B'=B-C$ , and  $C=(1-A-B)\times 0.015626/0.958745$ . Heterozygosity of  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  in laboratory maintained stocks was determined directly from 30 female larvae.

### RESULTS AND DISCUSSION

From 1977 to 1978, 1,848 polytene chromosome slides had been examined. Total of eight inversion types were detected, but only  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  (Fig. 2) with the average frequency of 55% was a meaningful inversion type for further discussion (Brncic, 1972). Seasonal fluctuation of heterozygous inversion has been observed in several *Drosophila* species (Brncic, 1972; Dobzhansky, 1951; Dobzhansky, 1970; Patterson and Stone, 1952; Speiss, 1968). The seasonal fluctuation of climatic factors and

inversion heterozygosity of  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  during the experimental period (April, 1977 to February 1978) are showed in Fig. 3. According to Chi-square analysis, the frequency of  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  was significantly fluctuated during the year. Furthermore,  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  was negatively correlated to the temperature but positively correlated to the relative humidity (Fig. 4). However, no correlation was revealed between the inversion frequency and rain precipitation (Fig. 4). For the convenience of further analysis, we pooled our data into 3 groups, i.e. from April 22 to July 15, July 30 to Nov. 5, and Nov. 19 to Feb. 24. As shown in Table 1, the average temperature was declining, but the average relative humidity and the heterozygosity were increasing during this period. In the first two groups (from April to November), the average temperature was over 25°C and the relative humidity is less than 70%, and the heterozygosity of  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  was around 50%. However, in the third group, the average temperature was 17°C and the average relative humidity

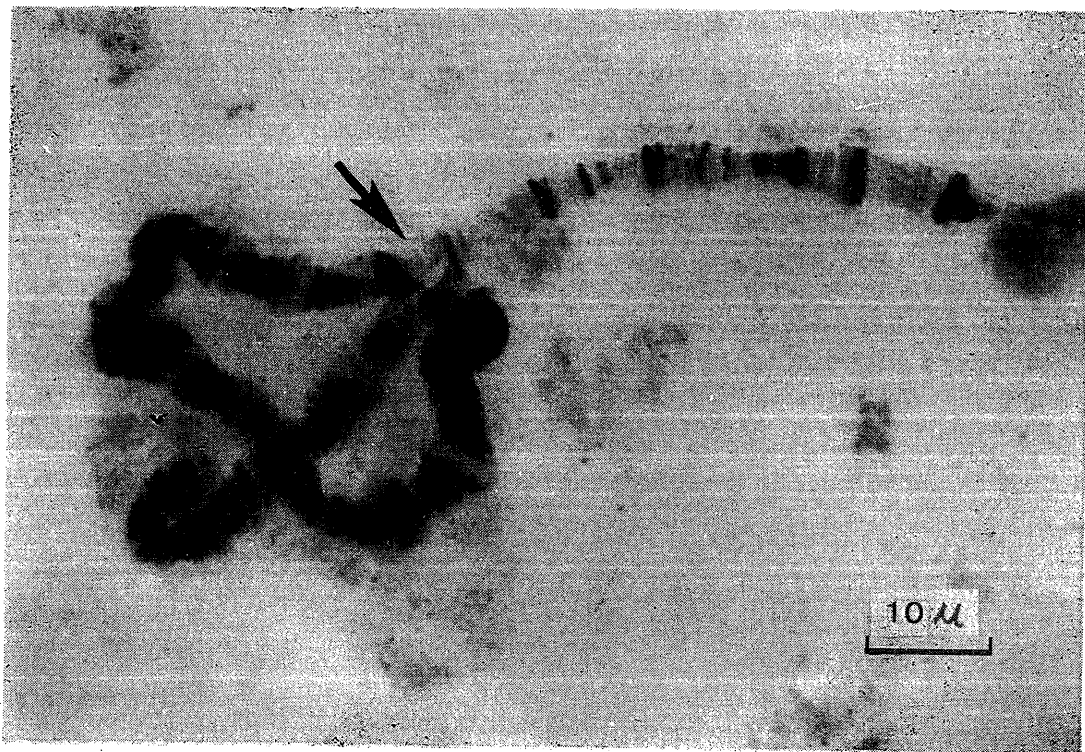


Fig. 2. The heterozygous  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  of *Drosophila albomicans*.

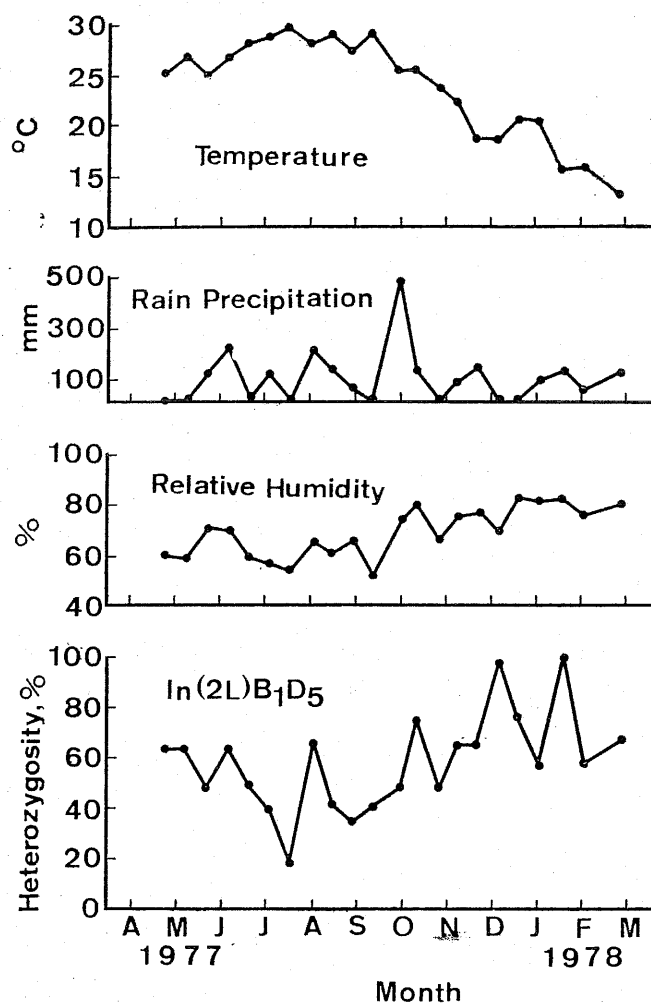


Fig. 3. The seasonal fluctuation of three climatic factors and the heterozygosity of  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  from April 22, 1977 to February 24, 1978.

was near 80%, whereas the heterozygosity of  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  was 66.1%, indicating that  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  showed heterosis in winter (Table 1). These results indicated that the flies with heterozygous inversion of  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  may have better fitness to the cold and wet winter.

$\text{In}(2\text{L})\text{B}_1\text{D}_5$  heterosis was confirmed in laboratory maintained stocks. We re-examined the heterozygosity of  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  eight years after the experimental period, i.e. approximately equivalent to 150 generations. Total of 1,166 polytene chromosome slides have been made. Seven of the 39 isofemale lines were monomorphic at beginning, and no spontaneously mutated inversion was observed

among them. This result is consistent to the general finding that mutation rate of inversion is very low. However, 10 out of 32 (31%) originally polymorphic stocks went fixation, i.e. no heterozygous  $\text{In}(2\text{L})\text{B}_1\text{D}_5$  was further detected, indicating a strong effect of genetic drift in isofemale lines. Therefore, isofemale lines, unless using a large number, are not ideal source to study the genetic variation in natural population. The remaining 22 isofemale stocks, which are originally polymorphic, are still polymorphic eight years after the stocks were established. The distributions of heterozygosity of  $\text{In}(2\text{L})\text{B}_1\text{D}_5$

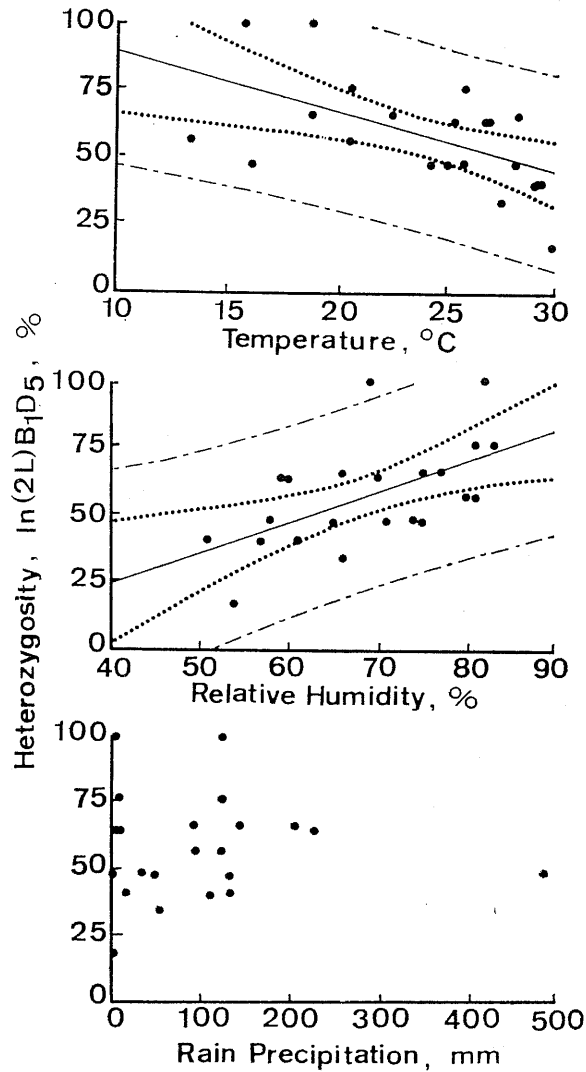


Fig. 4. The relationship between inversion heterozygosity and meteorological factors. Solid lines were obtained by the linear regression. Dotted and dash lines represent 99% and 95% confident interval, respectively.

TABLE 1  
Estimated heterozygosity of In(2L)B<sub>1</sub>D<sub>5</sub> in nature population

	April 22 to July 15	July 30 to November 5	November 19 to February 24
Heterozygosity (%)	46.8	52.6	66.1
Ave. Temp. (°C)	27.1	26.5	17.0
Ave. Rel. Humidity (%)	61.3	67.4	78.1

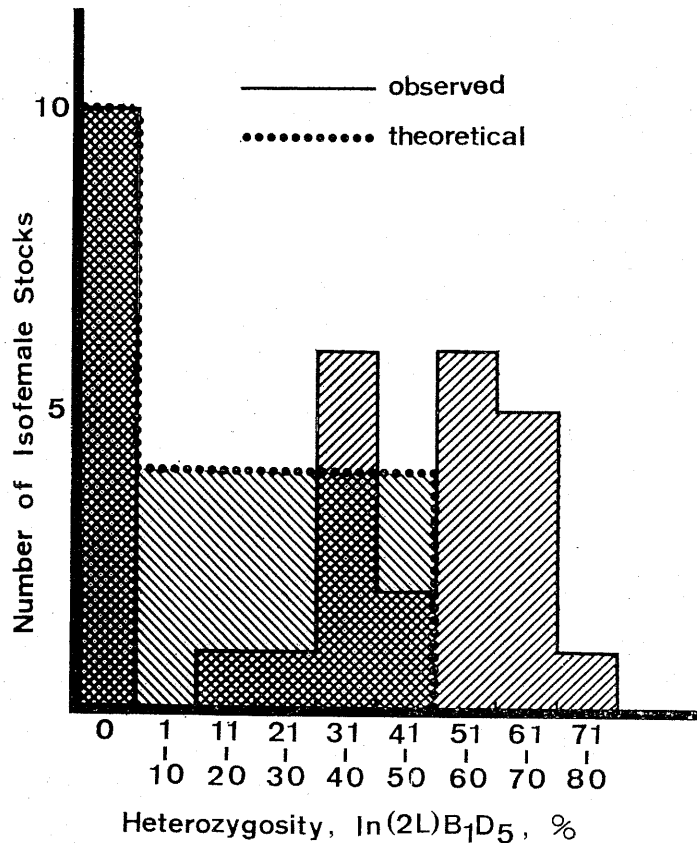


Fig. 5. The expected (considering genetic drift only) vs. observed distributions of 32 isofemale stocks on heterozygosity.

is shown in Fig. 5. According to Hardy-Weinberg's law, the heterozygosity should not be over 50% even in the presence of genetic drift. Our data show that 12 (55%) laboratory maintained stocks have the heterozygosity of  $In(2L)B_1D_5$  over 50%. These results indicate that heterozygous  $In(2L)B_1D_5$  did show heterosis in long-term culture in laboratory. In fact, the laboratory condition, which is constant during the years, is similar to the winter weather at Wulai as presented in Table 1.

In conclusion, although the frequency of heterozygous  $In(2L)B_1D_5$  was fluctuated during the year, heterozygous  $In(2L)B_1D_5$  shows heterosis in both natural population and laboratory maintained stocks in cold and wet condition. However, further investigation is needed to understand what genes located

within the segment of  $In(2L)B_1D_5$  are responsible for the heterosis.

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## 氣象因子對紅果蠅 (*Drosophila albomicans*) 染色體 逆位 In(2L)B<sub>5</sub>D<sub>1</sub> 異結合型比率之影響

張慧羽 張素華 林飛棧

在烏來地區紅果蠅異結合型染色體逆位 In(2L)B<sub>5</sub>D<sub>1</sub> 的比率呈現季節性變動。此異結合型比率與溫度成負相關，而與濕度成正相關。結果顯示具有異結合型逆位 In(2L)B<sub>5</sub>D<sub>1</sub> 的個體較能適應冷而濕的冬季氣候。在自然族羣及實驗室的單雌品系當中，雜結合型優勢 (heterosis) 或許是維持多態性的主要機制。

