estrus reappeared every 4th day in 6-OHDA animals as in intact animals (fig. 2). The 4-day estrous cycle continued in LD 12:12 after the 6-OHDA injection (experiment 3). Following destruction of the retinal dopaminergic neurons, persistent estrus could not be induced by LL.

DA turnover in the retina is mediated through a stimulation of photoreceptors by light[15,16] and undergoes a circadian rhythm[17]. The role of the retinal DA system might be to mediate continuous light information which induces the persistent estrus. Since 6-OHDA animals showed a normal estrous cycle in LD 12:12, the retinal DA system might not transmit periodic light information to which the reproductive system entrains.

In summary, our results suggest that the retinal dopaminergic neurons are involved in the induction of the persistent estrus in LL.

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Genetic load and effective size of natural populations of *Drosophila melanogaster* in Korea

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Summary. The effect of 750 second chromosomes of *Drosophila melanogaster* on viability was studied. 19.3% of them proved lethal or semilethal (= drastics) in homozygous condition. Compared to data obtained in previous years at the same sampling site, a significant frequency decrease of drastics during the past decade could be observed. The dynamic processes taking place in the Korean wild populations of *D. melanogaster* are discussed.

Key words. Drosophila melanogaster; second chromosome; drastics; genetic load; population size.

Information concerning the amount of genetic load hidden in natural populations of *Drosophila* is available for a few species; *D. pseudoobscura*[2], *D. subobscura*[3,4], *D. willistoni*[5], and *D. melanogaster*. Natural populations of *D. melanogaster* from various localities in the USA[6,7], Europe[8], Japan[9] and Korea[10-12] hav been studied in more detail.

There are two main hypotheses regarding the maintenance of genetic load in natural populations of *Drosophila*; 1) The balance theory: the genetic load is assumed to be maintained primarily by balancing selection. 2) The classical theory: the existence of the load is primarily due to mutation pressure. Although it is not easy to discriminate between these alternative hypotheses, a number of population parameters can be used for the estimation of the proportions of the balanced to the mutational components of the load[13,14].

Genetic load and viability variation in the population of *D. melanogaster* in Anyang, Korea, was already measured in 1969[10] and 1978[11]. The purpose of the present paper is to provide further information about the mechanisms maintaining the genetic burden in natural populations.

Materials and methods. Samples of wild male and female flies of *Drosophila melanogaster* were taken from the same trapping site as in 1976 and 1981[11,12]. Wild females were transferred individually to separate vials to establish isofemale lines. Wild males or one male of each isofemale line were crossed to *Cy/Pm* females from a strain whose genetic background (X- and III-chromosomes) had been previously substituted by chromosomes from the wild Anyang population. The usual crossing procedure[15] results in a F_3 generation composed of heterozygous *Cy/+* and homozygous +/+ genotypes (+0 = identical wild second chromosomes). Cy (Curly) and Pm (Plum) are dominant markers of second chromosomes traditionally used in this kind of experiment. They prevent crossing over effectively, and are lethal when homozygous.

In the test for homozygous viability, the expected F_3 offspring should consist of $\frac{2}{3}$ *Cy/+* individuals and $\frac{1}{3}$ +/+ flies. Hence, on the basis of the relative frequencies of +/+ flies in the test generation, the wild second chromosomes can be classified into the following five groups; complete lethals (less than 1% +/+ genotypes), semilethals (< 16.6%), subvitals (< 26.7%), quasinormals (< 39.9%), and supervitals (more than 39.9%)[12].

To estimate the viability of random heterozygotes the crossing procedure was performed in the same way as for homozygous viabilities, but in the last test crosses the *Cy/+* flies were taken from two different lines (e.g. $Cy/+^{n} \times Cy/+^{n+1}$). Thus, the normal individuals (+/+) in the F_3 test generation represented random heterozygotes for wild second chromosomes. The percentage of these normal genotypes was then employed as a measure of heterozygous viabilities as was done for the homozygotes.

For the estimation of effective population size, allelism tests were performed between the various different complete lethal chromosomes kept in balance over *Cy*. Those lethals of allelism crosses which yielded no normal individuals were considered to be allelic.

Results. The homozygous viabilities for the sample of 750 second chromosomes of *D. melanogaster* from Anyang 1982 are presented in table 1 and compared to those of previous investigations. The frequency of complete lethals is 14.8% in 1982 and that of semilethals 4.5% indicating a recent tendency to decrease. A homogeneity test between the three samples shows a significant deviation. The overall frequencies of drastics (lethals and semilethals) show this phenomenon even more clearly. An analysis of linear regression is presented in figure 1. The slope gradient deviates significantly from zero ($t_{(2)} = 16.45$, $p < 0.005$).

The average viabilities of all homozygotes, quasinormal homozygotes, and quasinormal heterozygotes are shown in table 2. The average viability of all homozygotes is 0.7138, and 0.8735, respectively excluding lethal and semilethals. That for quasinormal heterozygotes is 1.0012. As expected, random heterozygotes are less variable than quasinormal homozygotes ($F = 0.781$, $p < 0.01$). Mean viabilities of random heterozygotes can be subdivided into three classes according to the presence of lethal chromosomes (non-lethal/non-lethal', non-lethal/lethal and lethal/lethal' heterozygotes). The viability of non-lethal/lethal heterozygotes is 1.005, somewhat higher than that of the two other combination classes, but the differences are not significant.

The allelism rate deduced from the allelism test turned out to be about 0.0133 ± 0.0002 (= 50/3,770). Thus, the fluctuation of allelism rates for the period of 1967–1982 ranges from 0.01 in 1982 to 0.04 in 1976 in the population studied. A graphic representation of lethal-allelisms is given in figure 2. From this, it can be seen that five clusters of identical lethals (e.g. A–B with B–C–D, A–B–C with M–N, E–F–G with N–O–P–Q, etc.) exist. The frequencies of their multiple appearance are significantly different from those predicted by the Poisson distribution. Therefore, the present Anyang population seems to contain a certain number of persistent lethal chromosomes.

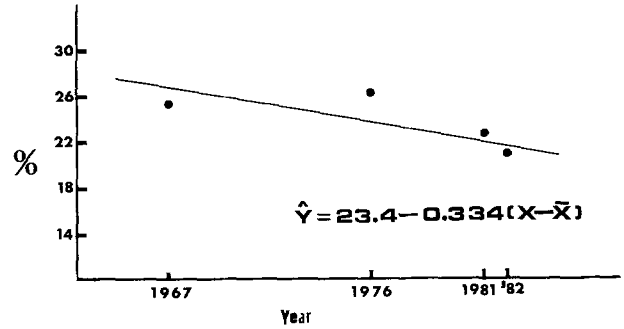

Figure 1. Linear regression analysis for detrimental frequencies in the Anyang population from 1967 to 1982.

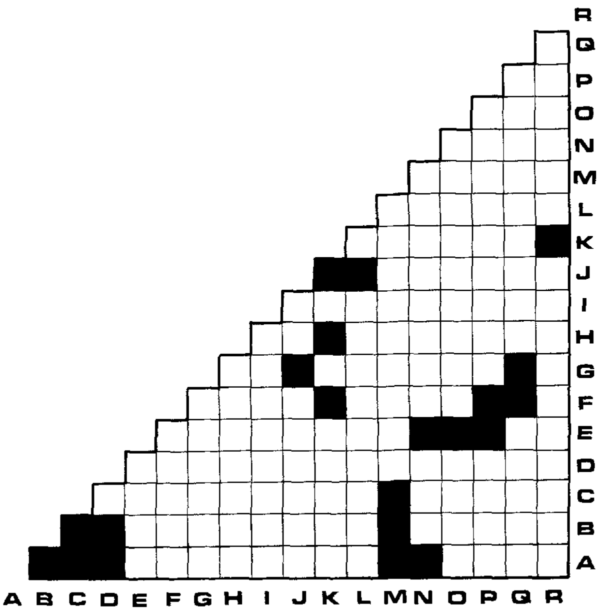

Figure 2. Graphic representation of allelic lethals having more than two occurrences in the Anyang population 1982 (allelic crosses are shown as black squares).

Finally, in order to obtain some information about whether a correlation exists between the viabilities of homozygotes and that of heterozygotes a correlation analysis was performed. All the heterozygotes having viabilities of more than 0.6 were used for the test ($n = 406$) in which it was examined whether the sum of the two viabilities of the corresponding homozygotes (e.g. $+^a/+^a$ and $+^b/+^b$) is correlated with the viabilities of their heterozygous combinations (e.g. $+^a/+^b$). The value of the correlation coefficient (r) proved to be 0.0071. This r value does not deviate significantly from zero, indicating the recessiveness of the genetic load in this material. This result is in agreement with our previous findings.

Discussion. From the present and the previous investigations, it is apparent that the frequency of semilethal second chromosomes has decreased significantly at Anyang, in the last 15 years. There are several cases of similar genetic changes, for instance a reduction in the frequency of drastics after a period of hot and dry summers in South Amherst[6] or a sudden increase of lethal frequencies in Japan[9]. Our data could be interpreted as a result of normalizing selection but could also be due to random drift events in these populations.

In table 3, a comparison is given for 'drastic' frequencies, allelism rates, and the calculated values for the elimination of lethals through allelism in the Anyang population for the years 1967–1982. The values for h were calculated from the following assumptions: $u - iq^2 = hpq + 2\,hq^2$, or mutation rate minus

Table 1. Relative viabilities of homozygotes for wild second chromosomes sampled in 1982, 1981 and 1976, respectively at Anyang, Korea

Viability class	1982	1981[12]	1976[11]	Total	Homogeneity tests 1982/81	1982/76
Lethal	111	81	71	263	0.2298	0.3771
%	14.8	13.8	16.3	14.8		
Semilethal	34	51	44	129	8.9414	12.8746
%	4.5	8.7	10.1	7.3		
Subvital	110	84	78	272	0.0289	1.7655
%	14.7	14.3	17.9	15.3		
Normal	489	362	237	1088	0	5.4294
%	65.2	61.7	54.2	61.3		
Supervital	6	9	7	22	1.5779	1.6209
%	0.8	1.5	1.6	1.2		
Total	750	587	437	1774	10.7780 $p < 0.05$	22.0675 $p < 0.001$

Table 2. Mean viabilities and variances for combinations of wild second chromosomes of *D. melanogaster* from the 1982 sample

Genotype	Mean viabilities	Number of crosses	Variances
All homozygotes	0.7138 ± 0.0130	750	0.1329
Quasinormal homozygotes	0.8735 ± 0.0070	605	0.0301
Quasinormal heterozygotes	1.0012 ± 0.0063	748	0.0308
$\frac{\text{Non-lethal}}{\text{Non-lethal'}}$	1.0007 ± 0.0072	529	0.0281
$\frac{\text{Non-lethal}}{\text{Lethal}}$	1.0051 ± 0.0123	198	0.0350
$\frac{\text{Lethal}}{\text{Lethal'}}$	0.9758 ± 0.0546	21	0.0628

Table 3. The frequencies of detrimentals and estimated elimination rates of lethal genes through allelism in the Anyang wild population of *D. melanogaster* for the period of 1967–1982

Year	detrimentals (le + sle)	allelism (i)	iq^2	pq	q^2	$hpq + 2hq^2$	h
1967	0.254	0.0179	0.0005	0.143	0.030	0.203	0.012
1976	0.264	0.0314	0.0008	0.136	0.027	0.190	0.012
1981	0.225	0.0210	0.0004	0.119	0.019	0.157	0.017
1982	0.193	0.0133	0.0003	0.126	0.022	0.170	0.016
average	0.234	0.0209	0.0005	0.131	0.025	0.180	0.014

Table 4. The estimated effective size[18] of the Korean populations of *D. melanogaster*

Year	q	I_c	I_g	*Ne* ($u = 10^{-5}$)
1967	0.1727	0.0179	0.0139	3,600
1976	0.1625	0.0314	0.0264	2,000
1981	0.1380	0.0210	0.0181	3,100
1982	0.1480	0.0133	0.0112	5,300

q, frequency of lethals; I_c, allelic rates; $I_g = \frac{-\ln(1 - I_c q^2)}{[\ln(1-q)]^2}$.

allelic elimination equals total genotypic elimination (see Wallace[16]). hpq stands for the fraction of elimination contributed by individuals carrying one lethal chromosome. 2 hq^2 for the fraction of those carrying two, non-allelic lethal chromosomes. The calculated value for lethal-elimination is 0.0003 for the present sample. Overall average dominance was calculated to be 1.6% in the 1982 population. All the other values for these elimination rates are smaller than the assumed lethal mutation rate, indicating a slight dominance effect of the deleterious genes. Crow and Temin[13] found an average of 3%. All our h-data are much smaller. Hoenigsberg et al.[17] hypothesized that the effects of dominance are of cyclical nature exerted by modifiers in larger and more relaxed populations. Our data could be interpreted along with this explanation.

The estimated sizes for effective population number of *D. melanogaster* are presented in table 4. The sample of 1982 turned out to give a value of 5300 individuals (= *Ne*). This indicates an expansion of the local population (*Ne* 1976 ≈ 2000, *Ne* 1981 ≈ 3000). It should be noted that Powell[19] has shown for *D. pseudoobscura* populations that in periods of population flush a relaxed selection occurs. Our allelism rate of 1.33% could be in accord with this hypothesis.

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The evolutionary history of *Drosophila buzzatii*. V. Differential survivorship on *Opuntia* between *D. buzzatii* and *D. serido*[1]

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Summary. Survival time of *Drosophila buzzatii* adults on an *Opuntia* (prickly pear) medium was significantly longer than that of its nearest relative *D. serido*. A significant difference was also found between *D. buzzatii* adults from two experimental populations, one of them fed on *Opuntia* rots for more than two years and another one kept on standard *Drosophila* medium for the same period of time. These results suggest that adult selection may be taking place in cactiphilic *Drosophila* in their natural habitats and could be responsible for the niche differentiation between *D. buzzatii* and *D. serido*.

Key words. Drosophila buzzatii; Drosophila serido; Opuntia; survivorship, differential; feeding behavior; niche differentiation; *Drosophila,* cactiphilic.

The nutritional requirements of *Drosophila* adults are very simple; only sugar is necessary to keep the flies alive. In addition, a mixture of essential amino acids, salts and vitamins is required for normal egg production[2,3]. Accordingly, feeding sites for most *Drosophila* species seem to be unspecific, that is to say, adult flies are attracted and feed upon a wide variety of fermenting substrates[4]. Cactiphilic *Drosophila* species, however, might have a particular, rather different, feeding behavior. Fellows and Heed[5] reported that a large mortality took place when flies of different *repleta* group species from the Sonoran Desert (Arizona) were placed in population cages with rotting cacti as the only food source. Similarly, we observed that almost all *D. buzzatii* and *D. serido* adults placed in population cages with *Opuntia ficus-indica* (prickly pear) rots as food, died in a few days. There was, however, a big difference between these two species. The *D. serido* population became extinct after the first generation, while the two populations (P1 and P2) founded with *D. buzzatii* flies survived, and could be maintained on the same food for more than two years[6]. These observations make sense because although the two species are closely related, there is evidence that, at least in Argentina where the ancestors of the population founders were