THE MAINTENANCE OF SUPERNUMERARY CHROMOSOMES IN WILD POPULATIONS OF *LILIUM CALLOSUM* BY PREFERENTIAL SEGREGATION¹

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A CONSIDERABLE number of plant species have been reported to contain supernumerary or accessory chromosomes (B chromosomes) in some members of their population, and the list of such species is steadily increasing. Recently, MÜNTZING and his collaborators (MÜNTZING 1954) have carried out extensive cytogenetical investigations of supernumerary chromosomes in *Secale*, *Festuca*, *Centaurea*, *Poa* and *Anthoxanthum*. One of the most interesting points involved is that in such a case as in rye, the total effect of B chromosomes is predominantly deleterious but at the same time there is a special mechanism which effects a numerical increase of the B chromosomes in the functional male gametes, thus leading to a balance between two opposing forces. A similar result has been reported by the junior author (KAYANO 1956b, 1957) in *Lilium callosum*, in which a supernumerary chromosome denoted by f_1 (meaning long telocentric fragment) has a tendency to increase in numbers due to preferential segregation in embryo-sac-mother cells. Thus by crossing a plant with one f_1 chromosome as a seed parent and one with no f_1 chromosome as a pollen parent, he obtained plants with one f_1 and no f_1 in an approximate ratio of 80:20. This agreed well with the cytological observation that in about 80 percent of the cases f_1 goes to the micropylar side to be included in the egg cell. Pollen fertility and seed setting have also been investigated in plants with various numbers of f_1 chromosomes. As will be shown in the next section, f_1 chromosomes depress the reproductive ability of the possessor rather severely so that plants with more than two f_1 chromosomes are almost completely sterile. In order to investigate the distribution of the supernumerary chromosome among individuals of wild populations, samples were collected from several localities and examined cytologically. The pattern of distribution was quite clear, and it was realized by the senior author that with observational data on pollen fertility and seed setting it might be possible to analyse the mechanism of distribution of the f_1 chromosome by developing a mathematical model. In the present paper, the junior author is responsible for experimental and observational data, while the senior author is responsible for mathematical and statistical analyses.

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Experimental and observational data

Samples were collected from four colonies or populations denoted by I, II, III and IV.

Populations I, II and III are located on a calcareous terrain of Hirao-Dai near Kokura-shi, Fukuoka Prefecture and they are about two kilometers apart. Population IV was found on a slope in the suburbs of Karatsu-shi, Saga Prefecture and is quite far from the other three populations. In this area the soil is not calcareous. In all these places, *L. callosum* was found growing together with *Miscanthus sinensis*.

In Figures 1 a-d, the results of karyotype analysis are presented together with maps showing the spatial distribution of individuals within each population. It may be seen from these maps that the distribution of supernumerary chromosomes is quite striking, one type denoted by f_1 being found in a large majority of plants and yet its number per individual being restricted to one or two (for the description of the types of supernumerary chromosomes, see KAYANO 1956a). Frequency distributions of the number of f_1 chromosomes within the four samples are summarized in Table 1. Pollen and seed fertilities were investigated using individuals from population I and the results are summarized in Tables 2 and 3. These figures represent averages over two years in the case of pollen fertility (1953 and 1954) and over three years for seed fertility (1952, 1953 and 1954).

The characteristic mode of transmission of the f_1 chromosome has already been reported by the junior author (KAYANO 1956b), but it may be convenient to

TABLE 1
Frequency distribution of the number of f_1 chromosomes

Populations sampled No. of f_1	I (percent)	II (percent)	III (percent)	IV (percent)	Sum (percent)
0	17 (28.8)	10 (18.5)	18 (39.1)	29 (46.0)	74 (33.3)
1	30* (50.9)	33‡ (61.1)	26 (56.5)	31 (49.2)	120 (54.1)
2	12‡ (20.3)	11 (20.4)	2 (4.3)	3 (4.8)	28 (12.6)
Total no. of individuals observed	59 (100)	54 (100)	46 (100)	63 (100)	222 (100)

* Contains two individuals having $1f_1 + 1f_s$, and one individual having $1f_1 + 1F_1$. (f_s means a short supernumerary fragment).

‡ Contains one individual with $2f_1 + 1f_s$.

‡ Contains one individual with $1f_1 + 3f_s$.

TABLE 2
Pollen fertility of individuals with various numbers of f_1 chromosomes

No. of f_1	No. of plants investigated	No. of fertile pollen grains	No. of sterile pollen grains	Total no. counted	Fertility (percent)
0	24	17,621	879	18,500	95.25
1	38	26,739	3,761	30,500	87.67
2	21	8,521	7,479	16,000	53.26

FIGURE 1a-d.—Spatial distribution of individuals with various number of f_1 chromosomes within four colonies of *Lilium callosum*. a, b and c (populations I, II and III) were located on a calcareous terrain of Hirao-Dai near Kokura-shi, Fukuoka Prefecture; these are about two kilometers apart. d (population IV) was found on a slope in the suburbs of Karatsu-shi, Saga Prefecture; it is quite far apart from the others.

reproduce the experimental results in the form of Table 4, in which the figures given in parentheses are the approximate values used as bases for calculation.

A crossing experiment conducted in 1958 revealed that this lily was self-incom-

patible. The results of this experiment are listed in Table 5. Thus *L. callosum* may be regarded as an outbreeding species. Furthermore, it reproduces, at least in part, asexually through development of new bulbs.

Mathematical and statistical analyses

1. *Mathematical model:* In order to analyse the present case, we must take into account two new features which do not appear in the ordinary mathematical treatment in population genetics. Namely, (a) both sexual and asexual reproduction have to be considered and (b) the mode of segregation of the f_1 chromosome does not follow the simple rules characteristic of ordinary diploid loci. With these two points in mind, we will formulate the problem as follows, in which an abbreviated symbol f will often be used to represent the f_1 chromosome.

TABLE 3

Seed fertility of individuals with various numbers of f_1 chromosomes

No. of f_1	No. of individuals investigated	No. of fertile seeds	No. of sterile seeds	Total no. of seeds counted	Fertility (percent)
0	15	4,662	2,907	7,569	61.59
1	25	9,102	8,305	17,407	52.29
2	12	3,228	5,859	9,087	35.52

TABLE 4

Mode of transmission of f_1 chromosome in artificial crosses

No. of f_1 in the offspring No. of f_1 in the parents ♀ × ♂	0	1	2	3	No. of offspring observed
0 × 1	45(50)	54(50)	..	..	99*
1 × 0	16(20)	83(80)	1	..	100
1 × 1	8(10)	53(50)	38(40)	1	100
0 × 2	7	88	5	..	100
2 × 0	5	76	18	1	100

* One individual having chromosome $2n=24 + 1F_1$ is excluded.

TABLE 5

Comparison of the effects of outcrossing and selfing on the development of capsules

	No. of flowers pollinated	No. of capsules developed	No. of capsules failed to develop
Outcrossing			
Between individuals with no f_1	11	10	1
Between individuals with 1 f_1	21	19	2
Between individuals with different karyotypes	17	17	0
Total	49	46	3
Selfing	20	(2)*	18

* Development was incomplete and did not contain fertile seeds.

Let Φ_i be the relative frequency of mature individuals with i f-chromosomes ($i = 0, 1, 2, \dots$) in the population, and let w_i^* and w_i^{**} be the relative fertilities or reproductive values of individuals with i f's as pollen and seed parent respectively. We will designate by $g_{j/i}^*$ the relative proportion of pollen with j f-chromosomes among fertile pollen produced by individuals having i f-chromosomes, and by $g_{j/i}^{**}$ the proportion of fertile egg cells with j f-chromosomes produced by the same individual. Then we can write the male gametic array giving the frequency distribution of the number of f chromosomes in the male gametes which contribute to the next generation as

$$(1) \quad \sum_j G_j^* f^j \equiv G_0^* + G_1^* f + G_2^* ff + \dots + G_j^* f^j + \dots,$$

in which

$$G_j^* = \frac{\sum_i g_{j/i}^* w_i^* \Phi_i}{\sum_i w_i^* \Phi_i} \quad (j = 0, 1, 2, \dots)$$

is the proportion of pollen with j f's. Similarly the female gametic array may be written in the form:

$$(2) \quad \sum_k G_k^{**} f^k \equiv G_0^{**} + G_1^{**} f + G_2^{**} ff + \dots + G_k^{**} f^k + \dots,$$

where

$$G_k^{**} = \frac{\sum_i g_{k/i}^{**} w_i^{**} \Phi_i}{\sum_i w_i^{**} \Phi_i} \quad (k = 0, 1, 2, \dots)$$

is the relative proportion of egg cells with k f's in the totality of eggs which contribute to the next generation. If there were no asexual reproduction, the zygotic array immediately after fertilization could be generated by the product of male and female gametic arrays, i.e., by

$$\left(\sum_j G_j^* f^j \right) \left(\sum_k G_k^{**} f^k \right),$$

because self-sterility of the present material ensures outcrossing, making pollination approximately random. The above product may be rearranged to give

$$\sum_i \phi_i f^i \equiv \phi_0 + \phi_1 f + \phi_2 ff + \dots + \phi_i f^i + \dots, \quad (i = 0, 1, 2, \dots)$$

where

$$(3) \quad \phi_i = \sum_{j+k=i} G_j^* G_k^{**} \quad (j, k = 0, 1, 2, \dots)$$

is the relative frequency of zygotes with i f's immediately after fertilization.

However, we cannot neglect asexual reproduction and it is necessary to consider the relative contributions made by sexual and asexual reproduction to the next generation. Let M be the mean number of viable seeds per plant, and let b_i be the probability of a randomly chosen viable seed with i f's reaching maturity. Furthermore, we designate by A_i the mean number of plants which are produced asexually from a plant with i f-chromosomes and which reach maturity in the next generation.

With these definitions, the frequency of mature individuals containing i f-chromosomes in the next generation may be given by

$$(4) \quad \Phi_i' = \frac{Mb_i\phi_i + A_i\Phi_i}{\sum_j (Mb_j\phi_j + A_j\Phi_j)} \quad (i = 0, 1, 2, \dots).$$

Thus in order to calculate the expected frequency distribution at equilibrium, we have to know all the parameters involved in segregation and reproduction, namely, the w 's, $g_{j/i}$'s, b 's, A 's and M . If these are given, a set of equilibrium frequencies denoted by $\hat{\Phi}_0, \hat{\Phi}_1, \hat{\Phi}_2, \dots$

may be worked out by using relation (4) and applying the trial and error method, starting from a set of arbitrary frequencies and repeating calculations until we get

$$\Phi_i' = \Phi_i \equiv \hat{\Phi}_i, \quad (i = 0, 1, 2, \dots)$$

with desired accuracy. The stability of equilibrium will usually become evident in the process of iteration.

The equation (4) may be simplified if we assume that A_i is proportional to b_i , namely, genotypes with higher viability tend to have a higher rate of asexual reproduction. If we accept such an assumption, (4) is reduced to

$$(5) \quad \Phi_i' = \frac{b_i(\phi_i + \theta\Phi_i)}{\sum_j b_j(\phi_j + \theta\Phi_j)}, \quad (i = 0, 1, 2, \dots)$$

where θ is the ratio of the relative contributions by asexual and sexual reproduction to form the next generation such that

$$(6) \quad \frac{A_i}{Mb_i} = \theta$$

for all i , i.e., $i = 0, 1, 2, \dots$. Then at equilibrium we have

$$(7) \quad b_i = \frac{C\hat{\Phi}_i}{\hat{\Phi}_i + \theta\hat{\Phi}_i}$$

where $\hat{\Phi}_i$ is the equilibrium value of ϕ_i and C is a positive undetermined constant and may be adjusted so that b_0 is unity.

2. *Application of the mathematical model to the actual data:* We will first try to see whether the observed distribution of the f chromosome in natural populations (Table 1) may be explained satisfactorily from the observed mode of its transmission and its effect on fertility as shown in Tables 2, 3 and 4.

If we assume that different genotypes have the same viability, namely

$$(8) \quad b_0 = b_1 = b_2 = \dots$$

and that reproduction is almost exclusively sexual, i.e.

$$(9) \quad \theta = 0 \quad (i = 0, 1, 2, \dots)$$

then we can calculate the equilibrium distribution using (4) or (5), taking

$$(10) \quad \begin{array}{llll} w_0^* = 0.9525 & w_1^* = 0.8767 & w_2^* = 0.5326 & w_3^* = w_4^* = \dots = 0 \\ g_{0/0}^* = 1.00 & g_{0/1}^* = 0.50 & g_{0/2}^* = 0.07 & \dots \\ g_{1/0}^* = 0 & g_{1/1}^* = 0.50 & g_{1/2}^* = 0.88 & \dots \\ g_{2/0}^* = 0 & g_{2/1}^* = 0 & g_{2/2}^* = 0.05 & \dots \end{array}$$

with respect to the pollen parent, and

$$(11) \quad \begin{array}{llll} w_0^{**} = 0.6159 & w_1^{**} = 0.5229 & w_2^{**} = 0.3552 & w_3^{**} = w_4^{**} = \dots = 0 \\ g_{0/0}^{**} = 1.00 & g_{0/1}^{**} = 0.20 & g_{0/2}^{**} = 0.05 & \dots \\ g_{1/0}^{**} = 0 & g_{1/1}^{**} = 0.80 & g_{1/2}^{**} = 0.76 & \dots \\ g_{2/0}^{**} = 0 & g_{2/1}^{**} = 0 & g_{2/2}^{**} = 0.18 & \dots \\ g_{3/0}^{**} = 0 & g_{3/1}^{**} = 0 & g_{3/2}^{**} = 0.01 & \dots \end{array}$$

with respect to the seed parent.

After a considerable number of iterations, the equilibrium distribution (in %) turned out to be as follows:

$$(12) \quad \begin{array}{llll} \hat{\Phi}_0 = 20.2 & \hat{\Phi}_1 = 48.4 & \hat{\Phi}_2 = 28.9 & \hat{\Phi}_3 = 2.4 \\ \hat{\Phi}_4 = 0.1 & \hat{\Phi}_5 = \hat{\Phi}_6 = \dots = 0. \end{array}$$

This expected distribution may be compared with the observed distribution in population I, from which materials for the study of segregation and fertility were obtained. In Table 6, classes with the number of f_1 larger than two are

TABLE 6

Observed and expected frequency distributions in population I, assuming equal viabilities of individuals with different numbers of f_1 chromosomes. $\chi^2 = 5.2$, $df\ 3$, $0.1 < P < 0.2$

No. of f_1	Frequencies (numbers)	
	Observed	Expected
0	17	11.92
1	30	28.56
2	12	17.05
3 and over	0	1.47
Total	59	59.00

grouped together. Application of the χ^2 test gives the χ^2 value of 5.2. With three degrees of freedom, $0.1 < P < 0.2$, and therefore the deviation of observed frequencies from the expected is not significant. However, this does not prove that different genotypes have the same viability. On the contrary, Table 6 suggests that individuals having two or more *f* chromosomes are less viable than those having one *f* chromosome or none. In fact, if we add all the observed frequencies from four populations and compare the result with the expected, the deviation is now highly significant ($\chi^2 = 46.4$, df 3, $P < 0.01$). Observed frequencies of individuals having two or more *f*'s are definitely smaller than the corresponding expected frequencies.

However, it might not be desirable to add the observed frequencies from four populations, since the four samples from populations I, II, III and IV are heterogeneous ($\chi^2 = 19.3$, df 6, $P < 0.01$). The main source of heterogeneity comes from the fact that the two groups of samples I + II and III + IV have different distributions ($\chi^2 = 17.2$, df 2, $P < 0.01$), though within each group the difference between samples is not significant. If we test the observed frequency distribution of I + II against the expectation, the deviation of the observed from expected is significant ($\chi^2 = 7.84$, df 3, $P < 0.05$), again showing that those having two or more *f*'s have lower viabilities than those with one or no *f*.

Therefore, we have to reject the null hypothesis that individuals with different numbers of *f* chromosomes have the same viability, i.e., the assumption (8) must be abandoned. It may be noted here that though the expected distribution given in (12) is obtained by taking $\theta = 0$, actually the distribution is independent of the value of θ , unless $\theta = \infty$, i.e., the reproduction is entirely asexual.

Having rejected the above hypothesis, next step is evidently to estimate the relative viabilities of individuals with different numbers of *f*'s. For this purpose we assume that the observed populations I, II, III and IV are in equilibrium. The procedure is as follows:

For the sample from population I, we have

$$\begin{aligned}\hat{\phi}_0 &= 17/59 = 0.2881, & \hat{\phi}_1 &= 30/59 = 0.5085 \\ \hat{\phi}_2 &= 12/59 = 0.2034, & \hat{\phi}_3 &= \hat{\phi}_4 = \dots = 0.\end{aligned}$$

Then using relations (2) and (3), we obtain

$$\begin{aligned}\hat{\phi}_0 &= 0.2769, & \hat{\phi}_1 &= 0.4908, & \hat{\phi}_2 &= 0.2177, & \hat{\phi}_3 &= 0.0139, \\ \hat{\phi}_4 &= 0.0007, & \hat{\phi}_5 &= \hat{\phi}_6 = \dots & & & &= 0.\end{aligned}$$

The relative viabilities are computed from formula (7) if we know the value of θ , as exemplified in Table 7. Unfortunately no experimental or observational data are available which allow us to determine the value of θ with confidence. Indeed, we have never encountered a report that such a value was determined in any perennial plant species in its natural habitat. However, there are some reasons to believe that, in *L. callosum*, the average value of θ is of the order of a few percent. The senior author is informed by Mr. M. SHIMIZU, a lily specialist

in Japan, that most of the lily species, except for the triploid tiger lily, appear to propagate predominantly by seeds. He guessed that the relative contribution made by asexual reproduction might be around five percent in a wild state. It is interesting to find that this figure is substantiated by the following calculation based on our observational data.

From the inspection of Figure 1a, it becomes immediately evident that there is considerable similarity in chromosome constitution between neighboring individuals. By taking, rather arbitrarily, 40 random pairs of nearby individuals in Figure 1a (see Table 8) and calculating the intraclass correlation, we have $r = 0.347$. In order to get a more reliable estimate, the field observation must be specially designed to have a better sample of pairs.

Such a correlation is probably due to one of the following two causes: (a) The neighboring individuals are derived asexually from a same individual through division of bulbs, in which case the similarity is perfect, i.e., the correlation coefficient is unity. (b) The neighboring individuals are derived sexually but are close relatives, such as sibs or more likely half-sibs from the same seed parent.

If we assume, as a first approximation, that the adjacent individuals are either derived asexually from the same bulb or sexually from the same seed parent, the

TABLE 7

Relative viabilities of individuals with various numbers of f_1 's. In this table θ represents the ratio between the contributions made by asexual and sexual reproduction to form the next generation

Mode of reproduction No. of f_1	$\theta = 0$	$\theta = 0.1$	$\theta = 1$
0	1.000	1.000	1.000
1	0.996	0.996	0.998
2	0.898	0.907	0.947
3 and over	0.000	0.000	0.000

TABLE 8

Intraclass correlation in the number of f chromosomes between two nearby individuals randomly sampled from population I in Figure 1a. In this table, the symbol (i, j) denotes the pair of individuals with i and j f -chromosomes

Pairs	No. observed	
(0,0)	6	
(0,1)	7	$r = 0.347$
(0,2)	3	$z = 0.362$
(1,1)	13	$\sigma_z = 0.161$
(1,2)	7	
(2,2)	4	
Total n = 40		

correlation coefficient in the number of the f chromosomes between the adjacent individuals may be given by

$$(13) \quad r = \frac{\sigma_b^2}{\sigma_w^2 + \sigma_b^2},$$

where σ_b^2 is the variance between sibs (including the case of asexual reproduction which occurs at the proportion of $\theta/(1 + \theta)$ of the total), i.e.

$$(14) \quad \sigma_b^2 = \frac{\sum_i M_i^2 \Phi_i w_i^{**}}{\sum_i \Phi_i w_i^{**}} - \bar{M}^2 \quad (\bar{M}: \text{mean of } M_i\text{'s})$$

and σ_w^2 is the variance within sibs, i.e.

$$(15) \quad \sigma_w^2 = \frac{\sum_i \sigma_i^2 \Phi_i w_i^{**}}{\sum_i \Phi_i w_i^{**}},$$

in which

$$M_i = \frac{\sum_{j+k=0}^{\infty} (j+k) g_{j/i}^{**} G_k^* b_{j+k} + \theta i b_i}{\sum_{j+k=0} g_{j/i}^{**} G_k^* b_{j+k} + \theta b_i} \quad (i = 0, 1, 2, \dots)$$

and

$$\sigma_i^2 = \frac{\sum_{j+k=0}^{\infty} (j+k)^2 g_{j/i}^{**} G_k^* b_{j+k} + \theta i^2 b_i}{\sum_{j+k=0} g_{j/i}^{**} G_k^* b_{j+k} + \theta b_i} - M_i^2 \quad (i = 0, 1, 2, \dots)$$

are the mean and the variance of the number of f chromosomes among sibs reaching maturity and which are derived from individuals having i f -chromosomes.

Though the calculation involved is again laborious, it is possible to estimate θ using the above formulae: Using the values in (10) (11) and observed frequencies of

$$\Phi_0 = 0.2881, \quad \Phi_1 = 0.5085, \quad \Phi_2 = 0.2034, \quad \Phi_3 = \Phi_4 = \dots = 0,$$

the calculation is repeated until we get $r = 0.347$ from (13), the values of θ , and $b_1, b_2, \dots$ ($b_0 \equiv 1$) being adjusted at every cycle of iteration. The results obtained were as follows:

$$\theta = 0.07, \quad b_0 = 1, \quad b_1 = 0.996, \quad b_2 = 0.905, \quad b_3 = b_4 \dots = 0.$$

If we put all four samples (in Table 1) together, estimated values of θ and relative viabilities were approximately as follows:

$$\theta = 0.06, \quad b_0 = 1.000, \quad b_1 = 1.066, \quad b_2 = 0.691, \quad b_3 = b_4 = \dots = 0.$$

In Table 9, frequency distributions, relative fertilities and viabilities are summarized.

TABLE 9

Summary of frequency distributions, relative fertilities and viabilities. The estimated value of θ is approximately 0.06

No. of f chromosomes	0	1	2	3 or more
Observed frequencies (sum of four samples) Φ	0.333	0.541	0.126	0.000
Expected frequencies at fertilization ϕ (estimated)	0.323	0.489	0.180	0.008
Pollen fertility (observed) w^*	1.000	0.920	0.559	
Fertility as seed parents (observed) w^{**}	1.000	0.849	0.577	
Relative viability (estimated) b	1.000	1.066	0.691	0.000

DISCUSSION AND CONCLUSION

Although a considerable number of cases of supernumerary chromosomes have been reported in populations of various species, the present case is rather exceptional for its simplicity of frequency distribution and completeness of experimental and observational data which enable mathematical analysis based on a theoretical model.

The result of the present analysis has shown that individuals with f chromosomes are not only less fertile but also less viable than those with no f chromosomes. This deleterious effect of f chromosomes on viability is especially evident for the case of two or more f chromosomes: With two f's viability is about 70 percent and with more than two f's, it is practically zero. On the other hand for the case of one f chromosome, there is no definite indication of lowered viability. It is possible that even a slight increased viability may exist in plants with a single f, as suggested by the result of analysis on the four samples together. Furthermore, the difference in the details of frequency distribution between samples from different localities such as I + II *vs.* III + IV mentioned earlier, may very well be due to difference in ecologic conditions which influence viabilities of individuals with various numbers of f chromosomes. ROSEMARK (1956) reported

an interesting observation that in *Festuca pratensis*, there was a marked correlation between frequency of accessory chromosomes and the clay content of the soil in Sweden.

Whatever modification is made in the selective pattern by local ecologic conditions, the conclusion is inevitable that in *Lilium callosum* the *f* chromosome is predominantly deleterious and it may only be kept in the population by preferential segregation in embryo sac mother cells.

Analogous situations occur with the *t* allele found by DUNN in the mouse (DUNN 1957) and SD factor discovered by HIRAIZUMI in *Drosophila melanogaster* (HIRAIZUMI, SANDLER and CROW 1960). In the former, the *t* allele (actually consisting of multiple alleles) is a recessive gene located on an autosome and is lethal (or causes complete sterility) when homozygous. Nevertheless, it is found with very high frequencies in wild populations of mice sampled in USA, due to excessive frequency of the *t* allele among the sperms produced by heterozygous males (*t*/+). If we designate by *k* (> 0.5) the segregation proportion of *t* among the sperms produced from *t*/+ males, and if we assume that the heterozygotes, either male or female, have completely normal reproductive ability and that *t*/*t* is lethal, then it is possible to show that in equilibrium the proportion of *t* allele among the pools of male and female gametes are

$$k - \sqrt{k(1-k)} \quad \text{and} \quad \frac{1}{2k} \left\{ k - \sqrt{k(1-k)} \right\}$$

respectively. Thus the proportion of zygotes which fail to develop is

$$\frac{1}{2k} \left\{ k - \sqrt{k(1-k)} \right\}^2$$

or

$$\frac{1}{2} \left\{ 1 - 2\sqrt{k(1-k)} \right\}$$

In other words, this is the proportion of individuals which have to be eliminated to maintain the deleterious allele in the population. Recently the senior author proposed the term distortional load (or load due to meiotic drive) to designate such a load (KIMURA 1960). In the present case, this is given by

$$L_{SD} = \frac{1}{2} \left\{ 1 - 2\sqrt{k(1-k)} \right\}$$

According to DUNN, segregation percentage of *t* ranges from 89 percent to 99 percent ($k = 0.89-0.99$), so that $\hat{L}_{SD}$ lies between 0.19 and 0.40. This means that in wild populations of mice, even disregarding possible effects of overdominance of *t* allele, the load due to maintaining *t* amounts to about 20-40 percent.

A similar concept may be applied to the present case and the distortional load due to f chromosomes may be calculated as follows: From Table 9, the average loss of fertility for plants with one f chromosome is $1 - (0.920 + 0.849)/2$ or 0.115. Similarly for plants with two f 's it is 0.432. Thus the component of load due to fertility differences is $0.541 \times 0.115 + 0.126 \times 0.432$ or 0.117, when the population reproduces sexually. The component of load due to viability differences is $0.180 \times 0.309 + 0.08 \times 1$ or 0.064 under sexual reproduction, and 0.126×0.309 or 0.039 under asexual reproduction (see Table 9). In both cases we assume that plants with one f chromosome have the same viability as those with no f 's. Combining all these values and taking $\theta = 0.06$, the load becomes $(1 - 0.06)(0.117 + 0.064) + 0.06 \times 0.039$ or 0.1724. Thus in wild populations of *L. callosum*, the distortional load due to f chromosomes amounts to about 17 percent. If apparent increased viability of plants with a single f ($b_1 = 1.066$) is taken into consideration, this value may be increased by three percent.

Though the existence of the increased viability with a single B chromosome is not conclusive in the present case, there may be a considerable possibility for it in a population of organisms in which B chromosomes reach such a high frequency that the majority of individuals carry one or more of them. This is because, under such a circumstance, modifiers which improve viability in combination with B are more advantageous, other things being equal, than those which improve viability without B. If this modification goes on, fitness of individuals with one B will become higher than that with no B's. Through this process, the frequency of B in the population will be gradually enhanced and deleterious effect of B will be diminished. We may say that the B chromosome changes from "parasitic" to "symbiotic."

SUMMARY

1. In *Lilium callosum*, a supernumerary chromosome (B chromosome) denoted by f_1 has a tendency to increase its number due to preferential segregation in embryo-sac mother cells in such a way that in plants with one f_1 chromosome, it moves to the micropylar side in 80 percent of the cases to be included in the egg cells. No such tendency was found in its transmission through the pollen. (KAYANO 1956b, 1957).

2. By crossing experiments involving plants with various numbers of f_1 chromosomes, the mode of transmission and its effect on pollen and seed fertility were investigated. It was found that f_1 chromosomes, when more than one is present, markedly reduced both pollen and seed fertility (Tables 2 and 3).

3. In order to study the frequency distribution of the number of f_1 chromosomes among individuals in natural populations of this lily, samples were collected from four localities in Kyushu and their chromosome constitutions were determined.

The result of this study showed that the frequencies of f_1 are uniformly high: Individuals with one f_1 are most frequent and they together with those having two f_1 's compose nearly 70 percent of a population on the average. On the other hand, no individuals were found with more than two f_1 's (Table 1, Figure 1 a-d).

4. A mathematical theory was developed to analyse the mechanism of distribution of f_1 chromosomes in the population. The theory contains two new features which do not appear in the ordinary mathematical treatment in population genetics, in that it takes into account of (a) the existence of both sexual and asexual reproduction and (b) the fact that the mode of segregation of the f_1 chromosome does not follow the simple rules characteristic of diploid loci.

5. The analysis has shown that individuals with f_1 chromosomes are not only less fertile but also less viable than those with no f_1 chromosomes. This deleterious effect of f_1 chromosome on viability is especially evident for the case of two or more f_1 's. Namely, with two f_1 's viability is about 70 percent and with more than two, it is practically zero. For the case of one f_1 , there exists no definite indication of lowered viability and it is suspected that there is even a slight increase.

6. The concept of distortional load (or load due to meiotic drive) was applied to the maintenance of f_1 chromosomes in natural populations of *L. callosum* and it was estimated that this load amounts to about 17 percent. A mechanism was suggested by which the deleterious effect of f_1 chromosome may be reduced in the course of evolution.

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