Cytological Regulation of Recombination in *Pennisetum* and *Brassica*

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Bodmer and Parsons (1962) pointed out that chromosomal systems are to be considered while discussing the overall fitness of a species. One such system is the regulation of recombination through chiasma frequency. The release of cryptic genetic variability in outbreeding populations is sometimes substantially altered by genetically controlled internal regulation of chiasma frequency (Rees 1961, Riley and Law 1965). Moreover, the conflicting reports (Stebbins 1950, Zecevic 1958, Grant 1958, Rees 1961) on the nature of chiasma frequency under inbreeding are to be reconciled with reference to fitness-flexibility axis (Heslop-Harrison 1964). In the above studies, the degree of inbreeding has not been measured and only a limited number of lines derived from the same variety (Rees 1955a) were examined. Therefore, a comparison of the changes in chiasma frequency in a diverse germplasm with known degrees of inbreeding will be of immense utility.

While in *Pennisetum* inbreeding is easily manipulated, it becomes difficult in a self-incompatible population like *Brassica*. A material subjected to disruptive selection for flowering time promotes inbreeding to a limited extent. Such a material in *Brassica* is available for this study. This has permitted to verify the hypothesis that disruptive selection promotes recombination. Therefore, the changes in chiasmata in the selfed populations of *Brassica* and random mating population of the same material will be compared. Even among the cross-pollinated species, the cytological regulation may depend on the nature of the genetic control of breeding system. For example, the outbreeding mechanism in *Brassica*, is considered to be under the control of *s* locus, while a polygenic system is supposed to be operating in *Pennisetum*. Therefore, a comparison of the changes in chiasma frequency under different degrees of inbreeding in these crops may throw light on the extent of buffering mechanisms restricting recombination.

Material and methods

The changes in chiasma frequency under different degrees of inbreeding were studied in a) *Pennisetum typhoides* ($2n=14$) and b) *Brassica campestris* var. brown sarson ($2n=20$).

In *Pennisetum*, the studies were extended over two years. During 1965, four genetically and geographically diverse populations, their sibbed and selfed

lines were grown in February-May. During 1966, seven more cultures consisting of open-pollinated, their sibbed and selfed lines were grown during July-November. Two sibbed lines, the second derived from the former were included. Thus it was possible to compare material with $F=0$, 0.250, 0.375 and 0.500.

The material for cytological work on *Brassica* consisted of self-incompatible and self-compatible types that were subjected to five generations of disruptive selection for flowering time. Two early and two late lines from self-incompatible types and three early and two late lines from self-compatible type along with the base populations were grown during October-March, 1965-66. In addition to fixing buds for cytological examination, two plants in each line were selfed by natural as well as bud pollination, thus superimposing inbreeding on material already subjected to disruptive selection. These twenty-two lines together with the open-pollinated lines were raised in pots during October-March, 1966-67.

Entire ears in the case of *Pennisetum* and selected buds in the case of *Brassica* were fixed in Carnoy's (6 parts ethanol : 3 parts chloroform : 1 part acetic acid) and later transferred to 70% alcohol and stored in a refrigerator. The anthers were squashed in acetocarmine. Chiasma frequency counts were taken at diakinesis.

Results

With increase in inbreeding in *Pennisetum*, a consistent parallel change was observed in the mean chiasma frequency per cell of inbreds as compared

Table 1. Mean chiasma frequency per PMC at diakinesis under inbreeding in some populations of *Pennisetum* in 1965

Culture Country	Plant no.	Open-pollinated ($F=0$)	Sibbed ($F=0.250$)	Selfed ($F=0.500$)
IP 171 (Kenya)	1	12.15 ± 0.19 (40*)	12.10 ± 0.31 (40)	12.33 ± 0.26 (40)
	2	12.33 ± 0.23 (40)	12.75 ± 0.36 (32)	12.83 ± 0.27 (40)
		12.24 ± 0.92	12.42 ± 1.41	12.58 ± 1.18
IP 235 (Uganda)	1	10.70 ± 0.32 (40)	13.52 ± 0.26 (27)	12.03 ± 0.27 (30)
	2	12.23 ± 0.21 (35)	14.03 ± 0.24 (29)	12.64 ± 0.19 (28)
		11.83 ± 1.05	13.80 ± 0.93	12.44 ± 0.84
IP 238 (Uganda)	1	12.18 ± 0.28 (33)	12.82 ± 0.35 (34)	12.44 ± 0.35 (25)
	2	14.75 ± 0.59 (16)	12.73 ± 0.31 (40)	12.19 ± 0.24 (37)
		13.21 ± 1.49	12.78 ± 1.44	12.29 ± 1.11
IP 1244 (A.P., India)	1	8.25 ± 0.37 (36)	11.13 ± 0.35 (31)	13.12 ± 0.31 (26)
	2	7.55 ± 0.67 (31)	10.91 ± 0.68 (23)	14.45 ± 0.35 (31)
		7.93 ± 1.92	11.06 ± 1.69	13.66 ± 1.24

* No. of PMC's.

to the outbred lines under study (Fig. 2; Tables 1 and 2). However, IP 238, a selection from Uganda resisted such a change. The mean chiasma frequencies in the selfed line of IP 235 and in one of the sibbed lines of IP 81, IP 188 and IP 1079, although uncorrelated with the degree of inbreeding were substantially higher than in the open-pollinated lines (Table 3). A

Table 2. Mean* chiasma frequency per PMC in *Pennisetum* under different degrees of inbreeding during 1966

Culture Country	Plant number	Open-pollinated (F=0)	Sibbed-1 (F=0.250)	Sibbed-2 (F=0.375)	Selfed (F=0.500)
1	2	3	4	5	6
IP 81 (Ghana)	1	11.92±0.21	12.64±0.16	12.65±0.25	13.30±0.22
	2	9.58±0.29	12.24±0.21	14.26±0.18	13.60±0.21
		10.75±0.25	12.44±0.18	13.46±0.22	13.45±0.22
IP 82 (Ghana)	1	11.04±0.19	13.36±0.27	13.34±0.21	13.78±0.25
	2	10.38±0.31	11.42±0.19	13.32±0.19	13.60±0.26
		10.71±0.26	12.39±0.23	13.33±0.20	13.69±0.26
IP 173 (Kenya)	1	9.68±0.31	13.12±0.15	13.40±0.14	14.06±0.22
	2	10.56±0.29	12.32±0.16	13.42±0.13	13.54±0.18
		10.12±0.30	12.72±0.15	13.41±0.14	13.80±0.20
IP 209 (Kenya)	1	11.26±0.30	11.78±0.16	13.28±0.15	13.76±0.20
	2	10.92±0.29	11.90±0.18	13.19±0.14	13.12±0.14
		11.09±0.30	11.84±0.17	13.24±0.15	13.44±0.17
IP 188 (Nyasaland)	1	10.36±0.27	11.14±0.23	10.34±0.31	13.14±0.21
	2	10.88±0.24	11.74±0.26	11.34±0.22	12.18±0.18
		10.62±0.26	11.44±0.25	10.84±0.27	12.66±0.20
IP 261 (N. Rhodesia)	1	12.08±0.17	13.44±0.22	13.86±0.18	15.03±0.22
	2	12.08±0.16	13.42±0.23	13.16±0.16	14.87±0.20
		12.08±0.16	13.43±0.23	13.51±0.17	14.95±0.21
IP 1079 (India)	1	10.62±0.24	12.98±0.21	12.66±0.12	13.82±0.18
	2	11.28±0.16	14.18±0.28	12.24±0.18	13.55±0.21
		10.95±0.20	13.58±0.25	12.45±0.15	13.69±0.20

* Based on 50 PMC's in each case.

positive regression was indicated between the mean chiasma frequency and the inbreeding coefficient (Fig. 1).

Disruptive selection for half bloom in *Brassica* resulted in the appearance of two distinct groups, early and late within which the populations, although open-pollinated, would undergo some degree of inbreeding. This degree of inbreeding was reflected in an increase in the chiasma frequency of the early

Table 3. Changes in chiasma frequency under inbreeding in relation to genetic diversity in some *Pennisetum* populations

Culture		Open-pollinated (F=0) Mean Xta	Increase in Xta over O.P.			Genetic diversity (After Murty, Upadhyay and Manchada, 1967)									
Country	1		Sibbed-1 (F=0.250)	Sibbed-2 (F=0.375)	Selfed (F=0.500)	A	B	C	D	E	F	G	H	I	
			3	4	5										
a) 1965 studies															
	IP 171 (Kenya)	12.24	0.18	—	0.34	1	57	4	78	12	23	6	18	5	
	IP 285 (Uganda)	11.83	1.97	—	0.61	4	57	4	76	7	21	6	18	4	
	IP 238 (Uganda)	13.21	-0.43	—	-0.92	4	56	4	77	4	20	8	16	5	
	IP 1244 (A.P., India)	7.93	3.13	—	5.73	3	55	6	77	5	14	5	22	4	
b) 1966 studies															
	IP 81 (Ghana)	10.75	1.69	2.71	2.70	3	51	4	64	4	20	7	20	5	
	IP 82 (Ghana)	10.71	1.68	2.62	2.98	4	51	4	72	6	23	6	17	5	
	IP 173 (Kenya)	10.12	2.60	3.29	3.68	1	88	4	53	22	20	6	18	5	
	IP 209 (Kenya)	11.19	0.75	2.15	2.35	3	58	4	49	10	22	7	12	5	
	IP 188 (Nyasaland)	10.62	0.82	0.22	2.04	2	80	5	64	8	22	7	18	5	
	IP 261 (N. Rhodesia)	12.08	1.35	1.43	2.87	1	78	2	49	6	22	6	24	5	
	IP 1079 (Rajasthan, India)	10.95	2.63	1.50	2.74	3	61	2	73	7	16	5	19	5	

G=Ear girth (cm)

D=Height (in inches)

A=Early growth vigour
(Score: 1-poor, 5-best)

B=Days to 50% flowering

C=Drought resistance
(Score: 1-poor, 10-best)

E=Tiller number

F=Ear length (cm)

H=No. seeds/cm²I=Rust incidence
(Score: 1-resistant, 5-susceptible)

— Not available

and late groups as compared to the bulk in self-incompatible lines (Table 4). However, the early lines in the self-compatible group did not show an increase, although the late lines did register an increase in chiasma frequency as

Fig. 1. a, relation between inbreeding coefficient and mean chiasma frequency in *Pennisetum*.
b, regression between mean chiasma frequency and inbreeding coefficient in *Pennisetum*.

compared to the bulk. But when inbreeding was superimposed on these populations, the inbred lines in the self-compatible and self-incompatible lines did show an increase in the chiasma frequency over the open-pollinated plants (Table 5). Substantial increase in chiasma frequency was also observed within the early and late groups in the open-pollinated and selfed lines of self-compatible line. Although such a change was discernible in individual samples of the self-incompatible early and late groups, it was not reflected in the overall mean of the samples. In general, there was greater increase

in chiasma frequency in the late flowering group as compared to the early flowering group.

Fig. 2. Changes in chiasma frequency under different degrees of inbreeding in *Pennisetum*. a, $F=0$. b, $F=0.250$. c, $F=0.375$. d, $F=0.500$.

Discussion

The available evidence on the effect of inbreeding has indicated that the factors which promote recombination in the breeding system are often associated with factors which restrict it in the chromosomal mechanism and *vice versa*.

Stebbins (1958) considers that reduction in crossover frequency

will preserve variability in a cryptic form, thereby, reducing the recombination, particularly in unstable habitats and situations where fluctuations in population size are involved. Summarising the data from several families, Grant (1958) has concluded that a low chiasma frequency is correlated with outcrossing and a high chiasma frequency with selfing. Sun and Rees (1964) have also observed that the chiasma frequency of F_1 hybrids among a set of six *Secale* spp. including rye was lower than that of the parents. Further, a comparison of the chiasma frequencies between the self-compatible and self-incompatible species of *Secale* has also confirmed the observation of

Table 4. Mean* chiasma frequency per PMC in *Brassica* under disruptive selection during 1965-66

Group Line number	Days to 50% bloom	Plant number	Open-pollinated (F=0)
1	2	3	4
a. <i>Self-compatible</i>			
6 Bulk	63	I II	19.65±0.24 19.74±0.27
			19.70±0.26
6E-3-II-E4	58	I II	19.30±0.21 19.68±0.10
			19.49±0.16
6E-3-I-E1	58	I II	18.95±0.21 19.80±0.11
			19.38±0.16
6E-4-I-E1	60	I II	19.60±0.12 19.35±0.19
			19.48±0.16
6I-3-II-L3	71	I II	20.00±0.21 20.00±0.29
			20.00±0.25
6I-4-I-L4	75	I II	20.05±0.09 19.54±0.11
			19.80±0.10
b. <i>Self-incompatible</i>			
21 Bulk	61	I II	15.36±0.23 16.01±0.21
			15.69±0.22
21B-2-II-E4	57	I II	17.96±0.18 17.51±0.20
			17.74±0.19
21B-1-I-E1	58	I II	18.28±0.23 17.38±0.18
			17.83±0.21
21F-4-I-L3	60	I II	18.16±0.19 19.36±0.13
			18.76±0.16

Continued

Table 4 (Continued)

1	2	3	4
21G-3-II-L4	62	I	18.31±0.15
		II	18.52±0.18
			18.47±0.17

* Based on 50 PMC's in each case.

Grant (1958). Therefore, an outbreeding species will give rise to small but even flow of recombinants generation after generation unlike the self-pollinating species which release their variability in periodical bursts alternating with generation when little recombination occurs. The restriction of recombination, thus, appears to be a universal phenomenon related to mating system. Since chiasma frequency is under genotypic control, it is to be expected that outbreeding populations would try to resist recombination by buffering action towards any change in chiasma frequency under forced inbreeding by man.

As expected, a change in the genetic environment like forced inbreeding in allogamous material has shown an increase in chiasma frequency in both *Pennisetum* and *Brassica*. The specific but differential response of the genotypes confirmed the genotypic control of chiasma frequency. However, the changes in the magnitude of the chiasma frequency under inbreeding varied from population to population, in the populations from the same country and among the populations grown in different years. This differential response appears to be due to the past history of selection, the genetic diversity of the populations, and the ecological conditions under which they are grown which will be discussed later. The nature of the breeding system may also be important in other cases.

The polygenic control of outbreeding, polyphyletic origin (Swaminathan and Nath 1956, Chandola 1959) and the balanced genetic load (Harinarayana 1965) have helped *Pennisetum* to accumulate considerable genetic diversity including the alleles for differential fertility and viability controlled by orderly pairing, recombination and separation. These differences in the genetic architecture can be responsible for different degrees of buffering in chiasma frequency among *Pennisetum* populations. Inbreeding can also result in the change of genetic background. This change in the genetic background substantially alters the recombination frequency which will be reflected in the rate of gene segregation and recombination. Some data taken from Murty *et al.* (1967, Table 3) indicates that the *Pennisetum* populations chosen for this study are considerably diverse, particularly with respect to days to flower and grain density. The number of days to bloom appears to have considerable influence on the changes in chiasma frequency. For example, the increase in the chiasma frequency of late lines under inbreeding in *Pennisetum* is higher than in the early lines. However, material of same origin under different degrees of inbreeding could be cytologically examined at the same

Table 5. Mean* chiasma frequency per PMC in *Brassica* under disruptive selection with inbreeding during 1966-67

Group Line number	Days to 50% bloom	Plant no.	Sample number	Open-pollinated (F=0)	Selfed (F=0.500)
1	2	3	4	5	6
a. Self-compatible					
6 Bulk	61	I	1	17.90±0.18	18.54±0.13
			2	13.62±0.17	17.97±0.21
		II	1	14.82±0.15	17.82±0.27
			2	18.66±0.17	18.02±0.18
				18.25±0.17	18.09±0.20
6E-3-II-E4	58	I	1	16.40±0.18	19.12±0.15
			2	17.44±0.25	16.80±0.30
		II	1	17.35±0.12	18.12±0.18
			2	17.68±0.15	19.04±0.19
				17.22±0.18	18.27±0.21
6E-3-I-E1	58	I	1	16.30±0.25	17.14±0.28
			2	18.08±0.17	17.95±0.19
		II	1	16.94±0.22	18.20±0.23
			2	15.92±0.25	17.62±0.27
				16.81±0.22	17.73±0.24
6E-4-I-E1	56	I	1	15.42±0.41	19.24±0.12
			2	16.62±0.22	18.42±0.16
		II	1	16.21±0.21	18.21±0.23
			2	15.58±0.23	19.30±0.14
				15.96±0.27	18.79±0.16
6I-3-II-L3	79	I	1	17.89±0.21	18.98±0.12
			2	18.94±0.14	19.32±0.15
		II	1	18.40±0.20	18.20±0.30
			2	17.60±0.17	18.28±0.33
				18.21±0.18	18.70±0.23
6I-4-I-L4	77	I	1	17.12±0.11	17.16±0.21
			2	16.43±0.19	17.88±0.26
		II	1	16.40±0.24	17.88±0.12
			2	17.72±0.17	18.31±0.11
				16.92±0.18	17.81±0.18
b. Self-incompatible					
21 Bulk	60	I	1	17.72±0.22	18.72±0.14
			2	17.58±0.19	17.64±0.27

Continued

Table 5 (Continued)

1	2	3	4	5	6
		II	1	14.40 ± 0.29	18.30 ± 0.16
			2	17.02 ± 0.21	17.98 ± 0.21
				16.68 ± 0.23	18.16 ± 0.20
21B-2-II-E4	58	I	1	17.26 ± 0.27	14.89 ± 0.27
			2	13.78 ± 0.25	15.90 ± 0.22
		II	1	17.36 ± 0.20	18.13 ± 0.21
			2	17.16 ± 0.23	18.62 ± 0.12
				16.39 ± 0.24	16.89 ± 0.21
21B-1-I-E1	60	I	1	14.12 ± 0.18	17.62 ± 0.23
			2	13.84 ± 0.28	18.12 ± 0.11
		II	1	17.12 ± 0.23	17.50 ± 0.31
			2	16.98 ± 0.27	18.01 ± 0.11
				15.52 ± 0.24	17.81 ± 0.19
21F-4-I-L3	62	I	1	13.45 ± 0.29	18.64 ± 0.15
			2	15.72 ± 0.16	18.66 ± 0.11
		II	1	16.44 ± 0.18	18.34 ± 0.18
			2	16.46 ± 0.19	18.20 ± 0.23
				15.52 ± 0.20	18.46 ± 0.17
21G-3-II-L4	62	I	1	17.34 ± 0.24	17.72 ± 0.15
			2	18.40 ± 0.13	18.60 ± 0.18
		II	1	18.38 ± 0.21	16.30 ± 0.20
			2	17.08 ± 0.17	18.52 ± 0.16
				17.80 ± 0.19	17.79 ± 0.17

* Based on 50 PMC's in each case.

time permitting a more precise comparison within a base population. The differences in flowering time also account for the differences in chiasma frequencies of the populations from the same region. IP 173 and IP 209 are from Kenya, but the latter has, to some degree, resisted increase in chiasma frequency. It is earlier in flowering than IP 173 by 30 days. Moreover, the *Pennisetum* material of 1965 season was of similar maturity as compared with the diverse lines included in 1966. Even among the *Brassica* populations, the early lines in the self-incompatible group resisted an increase in chiasma frequency under disruptive selection, while the late lines registered an increase over the bulks.

The seasonal variation in the chiasma frequencies appears to be due to the fluctuations in the environment like temperature as reviewed by Wilson (1959) from data on several crops and organisms. The differences among the Indian cultures could be due to the moisture conditions under which they are

grown. For example, IP 1244 from Andhra Pradesh is grown under non-stress environment, while IP 1079 is from the arid zone of Rajasthan. The open-pollinated populations of IP 1079 showed much higher chiasma frequency than IP 1244. Therefore, the material grown under stress environment is likely to be eroded of certain alleles in low frequencies because of the fluctuations in population size. Under such conditions, the populations counterbalance against external environmental stress through internal genetic buffering mechanisms like chiasma frequency. The differences in the chiasma frequencies of the open-pollinated populations appear to support this.

While the increases observed in chiasma frequencies of pearl millet and mustard populations under inbreeding are easy to explain, the decrease in chiasma frequency in rye (Rees 1955a,b, 1957 Rees and Thompson 1958) appears to be due to the uncovering of drastic and deleterious recessives hitherto sheltered under heterozygous condition, resulting in many meiotic abnormalities (Lamm 1936, Müntzing and Akdik 1948) and in extreme cases high asynapsis (Prakken 1943). Moreover, the studies on diallel analysis of chiasma frequency in rye (Rees and Thompson 1956) and wheat (Watanabe 1962) have revealed that non-allelic interactions and the combination of adaptive parental genes (Sun and Rees 1964) are important in controlling the chiasma frequency. In view of these findings and those of Kempanna (1963) in wheat, Riley and Law (1965) have argued that the changes in chiasma frequencies are not due to homo- or heterozygosity of the populations as supposed hitherto, but these changes are the products of the interaction of homozygous loci in inbreeders and heterozygous loci in outbreeders. Granted this, the increase in chiasma frequency in pearl millet and mustard can be attributed to the increasing proportion of homozygous loci under inbreeding. The findings of Watanabe (1962) in wheat also fall in line with this argument. On the other hand, Müntzing (1963) has shown that differential selection has occurred for heterozygosity in rye under natural selection which may be responsible for the decrease in chiasma frequency.

The present investigations have brought out yet another mechanism of variability control, namely, the cytological homeostasis which acts to reduce the potential variation in outbreeders, but at the same time enhances the flow of variation in the inbreeders and in extreme cases leaves it distributed in the homozygous lines. In terms of Darlington's (1958) recombination index, under the influence of cytological homeostasis, cross-pollinating species are endowed with a low recombination index as observed in pearl millet and mustard, while the self-pollinating species are equipped with a high recombination index. The haploid number of chromosomes, another component of recombination index, in pearl millet ($n=7$) and mustard ($n=10$) as compared to wheat ($n=21$) also confirms such a contention. This appears to be a natural corollary to the findings of Stebbins (1950), Grant (1958) and Sun and Rees (1964) for the very cross-pollination in outbreeders acts like a high

recombination index in outbreeders, while another mechanism like cytological homeostasis is needed in inbreeders. Hence, cross-pollination and cytological homeostasis are complementary in promoting the flow of variability and these two mechanisms are regulated in different breeding systems in such a way so as to ensure immediate fitness and future survival of a species.

How the cytological homeostasis brings a compromise between fitness and flexibility depends upon the breeding system. Broadly, the inbreeders and the outbreeders differ in the way their variability is distributed, stored and released. In outbreeders, a high recombination index will be of no avail since from the evolutionary point of view cross-pollination gives flexibility at the expense of continuous destruction of any gene combinations giving fitness in the prevailing genetic milieu. Naturally a low chiasma frequency is selected for and is inevitable in outbreeders to maintain certain degree of fitness. The present findings in *Pennisetum* and *Brassica*, the outbreeders, substantiate that a compromise between the two components of fitness and flexibility is arrived at essentially by an adjustment of the recombination and the breeding system so that the advantage of close adaptation are balanced against the disadvantages of concomitant restriction of variability and hence low adaptability. By analogy, a similar balance might have also been achieved in self-pollinating crops. Self-pollination preserves any existing state of fitness and enhances the genetic stability over a succession of generations at the sacrifice of future adaptive potential. Consequently, a high chiasma frequency and hence a high recombination index will be of advantage for the redistribution of the new variability brought in by cross-pollination, although it is limited (Jain and Allard 1960, Allard and Jain 1962). Under natural selection, therefore, cross-pollination and low recombination index go together, while self-pollination is associated with high recombination index.

On the other hand, the success of human selection depends on the recovery and building up of desirable polygenic combinations in a short possible time. Obviously, a high recombination index augments the rate of progress under human selection. Then, here lies the secret of the success of the hybridization programme in a wide array of crops. Through inbreeding, a constellation of genotypes are produced by recombination which are selected and recombined into new desirable combinations or hybrids.

Summary

The restriction of recombination through chiasma frequency was investigated in *Pennisetum* and *Brassica* where outbreeding is controlled by two different genetic mechanisms. Lines with known inbreeding coefficients were utilised for this purpose. Self-compatible and self-incompatible *Brassica* material subjected to five generations of disruptive selection for flowering was also included.

A consistent increase was observed in the mean chiasma frequency per

cell of *Pennisetum* and *Brassica* inbreds as compared to the outbred populations. The increase was parallel with the degree of inbreeding in *Pennisetum*. Disruptive selection for flowering increased chiasma frequency in *Brassica* populations with the exception of late self-incompatible group.

The buffering mechanism of chiasma frequency under inbreeding, referred to as cytological homeostasis, was examined from the viewpoint of the genetic diversity of the populations, the past history of selection, the ecological conditions under which the material is grown, the nature of the breeding system and the fitness-flexibility axis. It is concluded that a compromise between fitness and flexibility is arrived essentially by regulation of recombination through cytological homeostasis and the breeding system.

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