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Cytogenetics of *Lolium perenne*

Part 1: Chiasma Frequency Variation in Inbred Lines

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Summary. A number of inbred lines of *Lolium perenne* have been developed as far as the fifth inbred generation and are being used for basic studies on the cytogenetics of the species. An analysis on variation in the pattern of chiasma frequency and distribution, including the parent plants and all generations down to the S5, reveals that the effect of inbreeding is to reduce chiasma frequency and to increase both the cell and bivalent variances. Evidence is presented for a genetic basis of polygenic control of chiasma formation and distribution, and a model is suggested for control over the three related components of variation which involves a two-stage level of regulation.

Key words: *Lolium perenne* – Inbred lines – Meiosis – Chiasmata

Introduction

Perennial ryegrass is widely grown as a cultivated diploid species and has received a considerable amount of attention from plant breeders since some of the first selections were made from permanent pastures in the early part of this century. Much of the work has concentrated on aspects of the genetic system that relate to quantitative characters and their response to selection. Interest has centered around developmental studies and towards an understanding of the genetic basis of such characters as inflorescence development and production (Cooper 1959; Hayward 1967); seed and seedling characters (Hayward and Breese 1966; Wilson and Cooper 1969, 1970) and variation is selfing and cross-fertility (Jenkin 1931; Beddows et al. 1962; Foster and Wright 1970; Jones and Jenabzadeh 1981). The genetics of the incompatibility system itself has been elucidated by Cornish et al. 1979.

Breeding activity has been concerned with the production of synthetic varieties and with the utilisation of *L. perenne* in interspecific hybridisation with the related Italian ryegrass, *L. multiflorum* (Breese et al. 1981).

Relatively little attention has been paid so far to fundamental aspects of the cytogenetics of the species; there is a lack of knowledge about the genetics of chromosome behaviour, and no linkage maps are in existence. The main investigations which have been carried out concern chromosome stability and segregation in the interspecific hybrids (Breese et al. 1981) and the regulation of homoeologous chromosome association by B chromosomes (Evans and Macefield 1972, 1973, 1974; Taylor and Evans 1976, 1977). There are some basic studies on chromosome pairing in autotetraploids, in relation to fertility (Crowley and Rees 1968), and on the adaptive significance of chiasma frequency variation in diploids at the population level (Jones and Rees 1966; Rees and Ahmad 1963; Rees and Dale 1974). Other evidence for the existence of genes controlling chromosome behaviour, mainly in relation to asynapsis, comes from investigations on inbred material (arising from intensive selection and sibmating) studied by Cooper and Thomas (1961) and Omara and Hayward (1978), and also from work on spontaneous desynaptics by Ahloowalia (1972). Some recent work on the transmission of trisomics, and on the use of trisomics to map isozyme loci, has been presented by Meijer and Ahloowalia (1981) and Lewis et al. (1980) respectively.

The present work is concerned with basic studies on the cytogenetics of the species, with particular reference to the genetics of meiosis. The classical method of inbreeding has been employed to expose recessive alleles affecting all aspects of meiosis, and the early phase of the work concentrates on the cytological aspects of recombination viz. genetic control of variation in chiasma frequency and distribution.

Materials and Methods

The material consists of several parent plants of *Lolium perenne* var. 'S23', together with their inbred descendents comprising pedigrees of families in the S1, S2, S3, S4 and S5 generations. Details of the ancestry of 'S23', the methods of growing and selfing the plants, and of the breeding scheme and pedigree structure of inbreds developed from each of the

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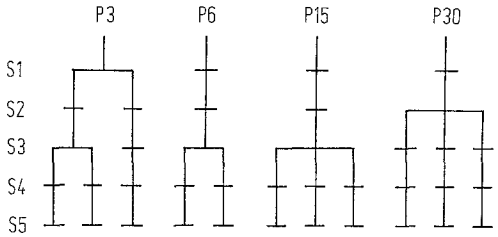

Fig. 1. Simplified diagram of the breeding scheme to show the structure of the four pedigrees and the relationships between the families at each generation of inbreeding. Families are denoted by the horizontal lines

parents, are given in Jones and Jenabzadeh (1981). An outline only of the pedigree scheme is given here (Fig. 1), to show the lines of descent which have reached the S5 and the generation at which the different lines and families within a pedigree diverged from one another. Each of the eleven S5 families is represented by ten plants (or less in some cases), and these families of plants, both within and among pedigrees, are each characterised by their distinctive morphological and developmental phenotypes. For cytological procedures the inflorescences were fixed in Carnoy's fluid and meiotic chromosome preparations were stained in acetocarmine.

Results

Chiasma frequency variation was determined at metaphase I of meiosis and the mean pollen mother cell (pmc) chiasma frequency, as well as the between-cell variance and the bivalent variance, was calculated from a sample of twenty pmcs/plant. Chiasma variation was thus studied at three levels of analysis: the level of the individual plants, the between-cell level within plants and the within-cell level in terms of the bivalent variance. The question of chiasma localisation within the bivalents themselves will be dealt with in a subsequent paper.

Data were collected for all individuals in each generation of inbreeding from the parent plants down to the S5. The parents were scored in both 1979 and 1980 and the results were found to be constant over the two years. The S1, S2, S3 and S4 data, which were collected from plants fixed in 1979 can therefore be directly compared with the S5 which were first fixed in 1980.

The Parent Characteristics

The mean pmc chiasma frequency of the four parents, taken over the two years, was 11.8. The metaphase I cell from a representative parent plant, shown in Fig. 2, is typical of the bivalent configurations in outbred population *L. perenne*. Of the seven bivalents in this pmc six are di-chiasmate rings and one is a rod bivalent with a single chiasma. Nearly all the bivalents of the parent material were of this kind; rings with more than two chiasmata and univalents were rarely found. Thus in the parents the chiasmata are characteristically found at the ends of the chromosome arms and are evenly distributed between the pmcs and among the bivalents within cells. The mean values for both cell and bivalent variances are of a low order of 1.224 and 0.2206 respectively (cf. Table 1).

Inbreeding Effects

The changes in chiasma frequency means from the parents down to the S5, for the four pedigrees of plants, are shown in Fig. 3a. In all cases there is a decrease in mean pmc chiasma frequency with inbreeding. A joint regression analysis of variance, combining results of the four pedigrees, is significant at the one per cent level, but when the pedigrees are taken individually significance is found for the P3 (<0.01) and P30 (<0.05) pedigrees only.

In the case of cell variance the relationship is positive (Fig. 3b), showing progressive loss of uniformity of distribution between cells with inbreeding, and is again significant at the 1 per cent level for the joint regression. For individual regressions only the P3 (<0.01) and P6 (<0.05) regressions are significant.

Bivalent variance (Fig. 3c) also increases over the generations, indicating less regular distribution of chiasmata between bivalents within cells as inbreeding progresses. The joint regression is significant at the 5 per cent level, and the individual regressions for the P3 and P15 pedigrees at the 1 and 5 per cent levels respectively.

Patterns of Variation due to Segregation

As the inbred lines have been developed on a pedigree basis it is possible to examine the patterns of variation for the three characters in relation to segregating families and lines arising from heterozygosity within

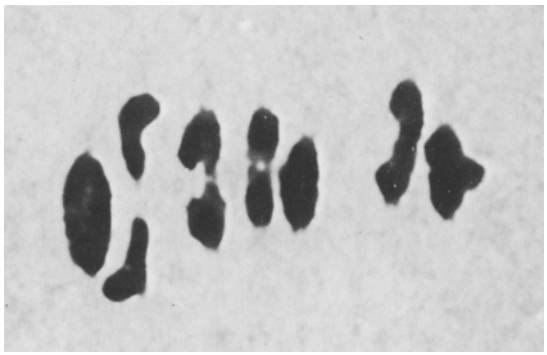

Fig. 2. Metaphase I of meiosis showing the typical configurations of the seven bivalents in a cell of a representative parent plant

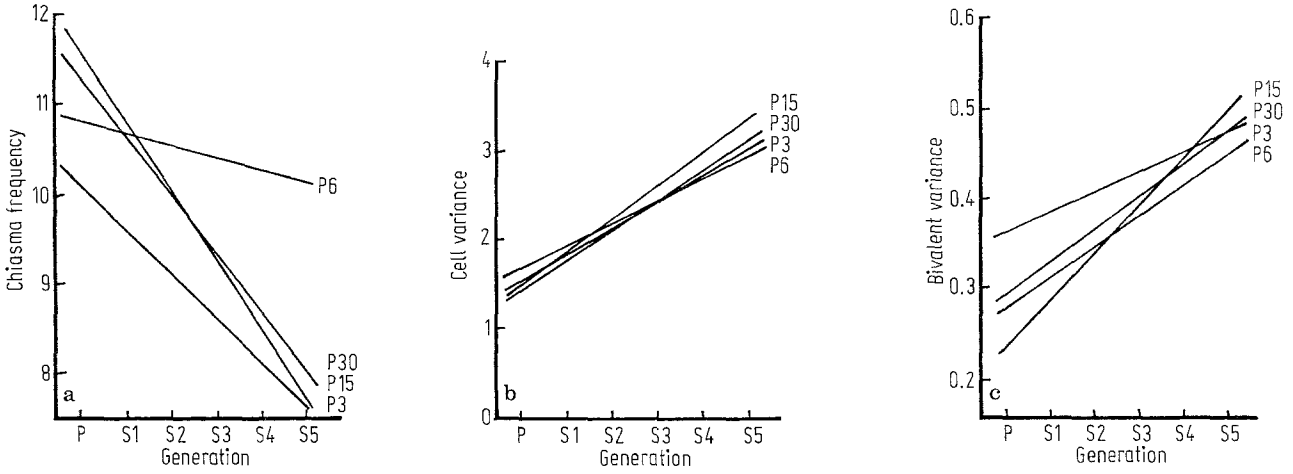

Fig. 3a–c. Graphs showing the relationship between inbreeding and the three components of chiasma variation, in each of the four pedigrees

Table 1. Data on chiasma frequency variation for the eleven lines (family means, and numbers of individuals (n)) at the S5 in 1980, grouped under the four pedigrees

Pedigree and family means	Mean chiasma frequency	Cell variance	Mean bivalent variance
P3 a)	8.36 (8)	2.996	0.4328
b)	6.76 (9)	2.933	0.4736
c)	7.97 (9)	2.311	0.4589
Mean	7.67 (26)	2.737	0.4663
P6 a)	10.56 (10)	3.156	0.4941
b)	10.30 (10)	2.307	0.4303
Mean	10.43 (20)	2.732	0.4622
P15 a)	8.66 (10)	3.222	0.4272
b)	7.84 (9)	2.705	0.4722
c)	8.79 (8)	3.421	0.4435
Mean	8.43 (27)	3.109	0.4470
P30 a)	7.96 (7)	3.417	0.5041
b)	8.94 (9)	2.245	0.4267
c)	7.68 (10)	3.503	0.4665
Mean	8.19 (26)	3.045	0.4628

individual parents, and also to analyse variation among the pedigrees which results from genotypic differences between the parents. Data are given for the S5 generation only, in Table 1, but one-way analyses of variance were performed on all the inbred generations from the S1 down to the S5 (Karp 1981).

When the S5 data for chiasma frequency are examined it can be seen that there are differences in family means within some of the pedigrees, and also that there are differences between some of the pedigree means as well. Results of the analysis show highly significant differences for families overall ($P < 0.001$), and that this variation can be partitioned into a between pedigrees item ($P < 0.01$), and into a between families within pedigrees item as well ($P < 0.05$). Separate analyses of variance on the individual pedigrees show the within pedigrees item resides in variation among families of the P3 pedigree only ($P < 0.01$).

The pattern of variation in chiasma frequency observed in the S5 has been developed over the earlier generations of inbreeding. In all of these early generations significant differences were found between families overall (Karp 1981), and there is firm and convincing evidence for the widespread segregation of polygenes controlling mean pmc chiasma frequency. Variation between pedigrees implies genotypic differences between the original parents and variation within pedigrees implies segregation of heterozygous gene combinations from within the parents. Most of the variation was found amongst the S1 and S2 individuals of the early segregants, and the amount of variation decreased after the S3. The use of individual plants in any one generation to provide seed for progeny plants in the next generation was quite arbitrary, but 'natural' selection for effectiveness at meiosis screens out the more extreme forms of chromosome behaviour and narrows down the variation among the more advanced lines. Heterogeneity within families also decreases as inbreeding advances.

Variation in cell variances for the S5 is much less pronounced than that for chiasma frequency, in so far as there are no differences between the pedigrees, and significant differences between families are found for those within the P30 pedigree only ($P < 0.05$). Uniformity of between-cell variance is found in all the generations except the S3, where there are differences within the P3 ($P < 0.01$) and the P6 ($P < 0.05$) pedi-

grees. Evidently the parent plants do not exhibit such wide genotypic differences for this character, but there is still convincing and clear-cut evidence for gene segregation coming from three of the parents.

Bivalent variances in the S5 (Table 1) show a similar pattern of variation to the cell variances; significant differences are found only between families within the P6 pedigree ($P<0.05$). There is no significant variation between pedigrees, but in the S3 the families of P6 are again variable ($P<0.001$), and in the S4 those of P30 also show a significant difference ($P<0.01$). The evidence for genotypic control for this character therefore comes mainly from segregation from the P6 and P30 parent plants.

The analyses of variance for the different inbred generations reveal different patterns of variation and segregation for the three components of recombination control. For chiasma frequency there is evidence of extensive segregation and heterozygosity within individual parents as well as for genotypic differences between parents. For cell and bivalent variances the segregation pattern is more restricted. Furthermore the distribution of the variation, within and among pedigrees, does not always correspond for the three characters, and this distribution pattern has to be considered in relation to the structure of the pedigrees shown in Fig. 1. The P3 pedigree in fact is the only one in which the lines were separated from one another as early as the S1, and they thus have the widest degree of genetic divergence. This pedigree showed significant variation (at least in some generations) for both chiasma frequency and cell variance, but not (in any of the generations) for bivalent variances. Lines in the P6 and P15 pedigrees did not diverge until the S3, and are more closely related together than those of P3. The P6 pedigree showed evidence of considerable variation in both chiasma frequency and bivalent variance, but very little for cell variance. The P15 pedigree showed little variation for all three characters. For the P30 families the lines of descent can be traced back to separation at the S2. Homozygosity appears to have been attained early on and the P30 lines show little segregation for either chiasma frequency or cell variance, although there is significant variation for bivalent variances.

The outcome of these analyses and comparisons are revealing in terms of the genetic profiles of the parents, and are also of interest in that they suggest that, in some of the pedigrees at least, the components of recombination control are segregating independently of one another and that they may therefore be under separate systems of genetic control. Investigations into the relationships between these three components are considered below.

Relationships between the Components of Chiasma Frequency Variation

Relationships between the three components were studied down the generations of inbreeding and also among the segregating individuals within the different inbred generations (i.e. across the generations).

When the components are plotted against one another using overall means (for all individuals) at each generation of inbreeding (Fig. 4) it emerges that there is a positive correlation between cell variance and bivalent variance (Fig. 4c, $P<0.001$) and that both of these characters are negatively correlated with chiasma frequency (Figs. 4a, b, $P<0.001$ for both). When the four pedigrees are plotted separately the same trends are still found but not all of the regressions are significant (Table 2). A pedigree may show a significant regression for one component but not for another, which is not altogether surprising since, as already described, the components did not show significant changes with inbreeding for all the pedigrees (Figs. 3a–c), and this indicates that when these correlations are examined at a more critical level they begin to reveal different patterns of variation between the different pedigrees. Again this implies some independence between the three components of variation.

The detailed relationships between the characters across the generations of inbreeding are displayed in the form of correlation coefficients in Table 3. In the early generations the cell and bivalent variances are seen to be positively and significantly correlated with one another, and both are negatively and significantly correlated with chiasma frequency, except for cell

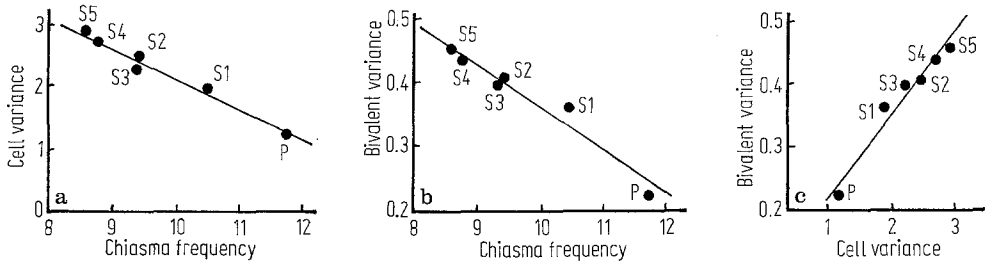

Fig. 4a–c. Graphs showing the interrelationships between the three components of chiasma variation

Table 2. Summary of regression analyses of variance for relationships between the three components of chiasma variation at the level of inividual pedigrees (cv = cell variance; bv = bivalent variance; Xta = pmc chiasma frequency)

	P3	P6	P15	P30
cv/Xta	<0.05	NS	<0.001	<0.01
bv/Xta	<0.001	<0.05	<0.01	NS
bv/cv	<0.01	<0.05	<0.05	<0.05

Table 3. Summary of correlations, across the five generations of inbreeding, for the relationships between the three components of chiasma variation (cv/Xta = cell variance against chiasma frequency; bv/Xta = bivalent variance against chiasma frequency; bv/cv = bivalent variance against cell variance)

Generations	Correlation coefficients and probabilities		
	cv/Xta	bv/Xta	bv/cv
S1	−0.1274 NS	−0.4202 <0.05	0.3953 <0.05
S2	−0.4786 <0.001	−0.3020 <0.05	0.3047 <0.01
S3	−0.3729 <0.001	−0.4556 <0.001	0.3588 <0.001
S4	−0.0232 NS	−0.1330 NS	0.0212 NS
S5	−0.1274 NS	−0.2988 <0.01	0.0350 NS

variance against chiasmata in the S1. The correlations are lost in the later S4 and S5 generations. It would appear that in the later generation, where the variation is on a much narrower basis anyway, that the components of variation have segregated out somewhat independently of one another and the relationships no longer hold.

The case for correlated responses, and also for a degree of independence between the three variables of chiasma variation, is complicated by the fact that we are dealing with variation in both means and variances, and it would strengthen the argument to have evidence of a rather more critical nature in support of the independent behaviour of these components. Such critical evidence is forthcoming in fact in respect of the bivalent variances and chiasma frequency variables over generations of inbreeding within the P3 pedigree. Confounding effects can be separated by making comparisons of mean bivalent variances taken from identical pmc chiasma frequency classes in each of the generations (by pooling all pmcs of a given chiasma frequency over all plants within a generation). The chiasma classes of 9 and 10 are widely represented among individual plants in all families and generations. Correlations of mean bivalent variances from both these pmc classes (as well as for their mean), against generations of inbreeding, are positive and significant ($P<0.05$). As it happens it is within this pedigree that the strongest correlations of bivalent variance with inbreeding ($P<0.01$), and chiasma frequency ($P<0.001$), exist anyway. Furthermore a joint regression analysis of variance, involving the same two variables in the P30 as well as the P3 pedigree ($P<0.01$), reveals an identity of slopes and, also, a significant heterogeneity of means ($P<0.01$). As far as these two variables are concerned there is not only confirmation of their partial independence upon one another, but also evidence for genotypic variation in their interrelationships between the pedigrees.

Additional evidence in support of the partial independence of bivalent variance upon chiasma frequency comes from segregation for mean bivalent variance among families within the S4 generation of the P30 pedigree. The significant difference in mean bivalent variance (0.4283 compared with 0.5304, $P<0.01$) is between two out of the three families, both of which have identical mean pmc chiasma frequencies (8.74). As explained in the discussion the data can best be interpreted on the basis of a controlling system, for the components of chiasma variation, which operates on two different levels of adjustment.

Discussion

In outbred S23 perennial ryegrass chiasmata are distally located at the ends of the chromosome arms and their distribution pattern is highly regular and uniform both between the different pollen mother cells within plants, as well as among the seven bivalents within the individuals pmcs. The question of chiasma localisation and distribution within bivalents will be dealt with separately at a later date.

Over generations of inbreeding there is a decrease in mean pmc chiasma frequency and an increase in the cell and bivalent variances. The depression of chiasma frequencies with inbreeding also results in the presence of univalents, and various aspects of their frequency and behaviour will also be treated and presented as a separate study.

Similar effects of inbreeding on chiasma frequency, and cell and bivalent variances, have been documented in rye (Rees 1955; Rees and Thompson 1958; Jones and Rees 1964), and the effect of inbreeding on chiasma frequency has also been described in radish (Dayal 1977). The evidence in *Lolium*, as in other species, is in support of a system of polygenic control which regulates both the frequency and the distribution of chiasmata.

One of the advantages of the breeding scheme used in the present work is that the lines and families have been developed on a pedigree basis and all the plants have been studied over all the generations of inbreeding, so that the relationships and patterns of segregation could be investigated at each of the generations from the parents down to the S5. From a study of these relationships it emerges that while there are inevitable consequences of inbreeding, in the form of correlated responses for the three components of variation, there are also independent patterns of segregation and variation that have their origins in the heterozygosity, and genotypic differences, that reside respectively within and between the parent plants themselves. The three components of chiasma variation have elements of both dependence and independence upon one another that leads to the suggestion that their regulation is operating on two levels of genetic control.

Earlier work on rye by Rees and Thompson (1958) also showed that there is a negative correlation between cell variance and chiasma frequency, and that there is some independence as well. Similar results have been demonstrated for the relationship between bivalent variance and chiasma frequency in rye (Jones and Rees 1964). Rees and Thompson (1958) suggested that the basis of the interrelationships may be the control of chiasma frequency itself; and that there may be an upper limit to the numbers of chiasmata in the pmcs of rye. An increase in cell variance will mean that more cells must deviate from this upper limit, and to accommodate this variation the chiasma frequency will have to be reduced. Decrease in chiasma frequency is therefore inevitably coupled with increases in both the cell and bivalent variances which are consequent upon inbreeding. They further suggested that some independence between the variables could arise from a change in the value of the upper limit itself. A study of a large number of rye genotypes of varied origin (including a commercial variety, a semi-inbred line and an F2 derived from a cross between a 'distributional' mutant and wild type rye), led Jones (1974) to the finding that there is a positive correlation between cell variance and bivalent variance. These components were also shown to be correlated with the distribution of chiasmata within bivalents; a matter that we will raise in a subsequent publication. In an earlier analysis (Jones 1967), a rye distributional mutant was described which showed a random variation of chiasmata both within and between cells, and probably also within bivalents; this system having a complex genetic basis. From these studies it was argued that the different levels of chiasma variation are under a single system of genetic control. The hypothesis was put forward that in rye, under normal circumstances, strict control is exercised at the level of individual bivalents, on a model postulating sites of high probability of chiasma formation at the ends of the chromosome arms. This leads to an even distribution of chiasmata between and within cells. Changes in the components of variation are correlated because they all constitute a degree of change, or 'relaxation', in the common basis of control. It was further proposed that the common underlying basis of the control is the error component of variation (Jones 1974).

The data presented for *L. perenne* shows general agreement with the findings and interpretations given for rye. There appears to be strict control operating in the parent material to limit the variation between and within cells, and the changes that accompany inbreeding result in part from a breakdown of a common underlying system of control. The main difficulty in accommodating the *Lolium* data entirely within a single system of control is the finding that segregation patterns for the three variables are not necessarily coincidental, and that the correlations between them do not invariably hold when tested at a critical level.

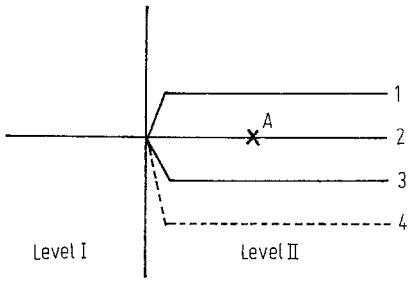

Fig. 5. Model illustrating the two-level system of control for the interrelated components of chiasma variation *1* Chiasma frequency; *2* cell variance; *3* bivalent variance; *4* distribution of chiasmata within bivalents

In order to interpret the *Lolium* data, as well as to take account of the previous findings for rye, we propose a model for chiasma frequency variation based on two levels of control, as shown in Fig. 5. Chiasma frequency, cell variance and bivalent variance are interrelated by a system which operates at a common level of control – level I. A mutation, or variation, in genes operating at level I results in a change in all three components, as in the rye distributional mutant. In addition to this overall control there are independent controlling systems operating at level II. When level I is operating normally a variation in level II will affect only one of the components; for example, a change in A will cause a variation in cell variance independently of chiasma frequency and bivalent variance. Inbreeding leads to the exposure of recessive alleles affecting both levels of control. Progressive increase in homozygosity for recessives affecting level I leads to a reduction in chiasma frequency and a correlated increase in the cell and bivalent variances, in the way envisaged by Rees and Thompson (1958). In addition to this there are patterns of variation that arise, and are evident, in the advanced S4 and S5 generations, due to the segregation of controlling genes affecting level II. The inbred pedigrees of *Lolium* may therefore show a correlation, or otherwise, for the components of chiasma frequency variation depending on the genetic profiles of the parents in respect of the genes operating at levels I and II.

Literature

Ahloowalia, B.S. (1972): Genetic control of the post-synaptic phase of meiosis in rye-grass. Chromosomes Today **3,** 93–103

Beddows, A.R.; Breese, E.L.; Lewis, B. (1962): The genetic assessment of heterozygous breeding material by means of a diallel cross. I. Description of parents, self- and cross-fertility and early seedling vigour. Heredity **17,** 501–512

Breese, E.L., Lewis, E.J., Evans, G.M. (1981): Interspecies hybrids and polyploidy. Phil. Trans. R. Soc. (Lond.) B. **292,** 487–497

Cooper, J.P. (1959): Selection and population structure in *Lolium*. 1: The initial populations. Heredity **13,** 317–340

Cooper, J.P.; Thomas, P.T. (1961): Cytological unbalance resulting from intensive selection in *Lolium*. Annu. Rep. Welsh Plant Breed. St. 1961, 115–118

Cornish, M.A.; Hayward, M.D.; Lawrence, M.J. (1979): Self-incompatibility in ryegrass. 1: Genetic control in diploid *Lolium perenne* L. Heredity **43,** 95–106

Crowley, J.G.; Rees, H. (1968): Fertility and selection in tetraploid *Lolium*. Chromosoma **24,** 300–308

Dayal, N. (1977): Cytogenetical studies in the inbred lines of radish (*Raphanus sativus* L. var. radicola Pers.) and their hybrids. 1: Chiasma frequency. Cytologia **42,** 29–35

Evans, G.M.; Macefield, J. (1972): Suppression of homoeologous pairing by B-chromosomes in a *Lolium* species hybrid. Nature New Biology **236,** 110–111

Evans, G.M.; Macefield, J. (1973): The effect of B-chromosomes on homoeologous pairing in species hybrids. 1: *Lolium temulentum*×*Lolium perenne*. Chromosoma **41,** 63–73

Evans, G.M.; Macefield, A.J. (1974): The effect of B-chromosomes on homoeologous pairing in species hybrids. 2: *Lolium multiflorum*×*Lolium perenne*. Chromosoma **45,** 369–378

Foster, C.A.; Wright, C.E. (1970): Variation in the expression of self-fertility in *Lolium perenne* L. Euphytica **19,** 61–70

Hayward, M.D. (1967): The genetic organisation of natural populations of *Lolium perenne*. 2: Inflorescence production. Heredity **22,** 105–116

Hayward, M.D.; Breese, E.L. (1966): The genetic organisation of natural populations of *Lolium perenne*. 1: Seed and seedling characters. Heredity **21,** 287–304

Jenkin, T.J. (1931): Self-fertility in perennial ryegrass (*Lolium perenne* L.) Bull. Welsh Plant Breed. St. Ser. H. **12,** 100–112

Jones, G.H. (1967): The control of chiasma distribution in rye. Chromosoma **22,** 69–90

Jones, G.H. (1974): Correlated components of chiasma variation and the control of chiasma distribution in rye. Heredity **32,** 375–387

Jones, G.H.; Rees, H. (1964): Genotypic control of chromosome behaviour in rye. VIII. The distribution of chiasmata within pollen mother cells. Heredity **19,** 719–730

Jones, R.N.; Jenabzadeh, P. (1981): Variation in self-fertility, flowering time and inflorescence production in inbred *Lolium perenne* L. J. Agric. Sci. **96,** 521–537

Jones, R.N.; Rees, H. (1966): Chiasma frequencies and the potential genetic variability of *Lolium* populations. Nature **211,** 432–433

Karp, A. (1981): The genetic control of meiosis in *Lolium perenne*. Ph. D. Thesis, University of Wales

Lewis, E.J.; Humphreys, M.W.; Caton, M.P. (1980): Chromosome location of two isozyme loci in *Lolium perenne* using primary trisomics. Theor. Appl. Genet. **57,** 237–239

Meijer, E.G.M.; Ahloowalia, B.S. (1981): Trisomics of ryegrass and their transmission. Theor. Appl. Genet. **60,** 135–140

Omara, M.K.; Hayward, M.D. (1978): Asynapsis in *Lolium perenne*. Chromosoma **67,** 87–96

Rees, H. (1955): Genotypic control of chromosome behaviour in rye. I. Inbred lines. Heredity **9,** 93–116

Rees, H.; Ahmad, K. (1963): Chiasma frequencies in *Lolium* populations. Evolution **17,** 575–579

Rees, H.; Dale, P.J. (1974): Chiasmata and variability in *Lolium* and *Festuca* populations. Chromosoma **47,** 335–351

Rees, H.; Thompson, J.B. (1958): Genotypic control of chromosome behaviour in rye. V. The distribution pattern of chiasmata between pollen mother cells. Heredity **12,** 101–111

Taylor, I.B.; Evans, G.M. (1976): The effect of chromosomes on homoeologous pairing in species hybrids. III. Intraspecific variation. Chromosoma **57,** 25–32

Taylor, I.B.; Evans, G.M. (1977): The genotypic control of homoeologous chromosome association in *Lolium temulentum*×*Lolium perenne* interspecific hybrids. Chromosoma **62,** 57–67

Wilson, D.; Cooper, J.P. (1969): Diallel analysis of photosynthetic rate and related leaf characters among contrasting genotypes of *Lolium perenne*. Heredity **24,** 633–649

Wilson, D.; Cooper, J.P. (1970): Effect of selection for mesophyll cell size on growth and assimilation in *Lolium perenne* L. New Phytologist **69,** 233–245

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