GENOTYPIC CONTROL OF CHROMOSOME BEHAVIOUR IN RYE

X. CHROMOSOME PAIRING AND FERTILITY IN AUTOTETRAPLOIDS

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1. INTRODUCTION

IT is widely accepted that the infertility of autotetraploids is largely caused by irregular chromosome disjunction at anaphase of meiosis which, in turn, results from multivalent and univalent formation at prophase (Müntzing, 1936; Darlington, 1937; Darlington and Mather, 1949; Kostoff, 1940; Myers and Hills, 1942). If the frequencies of these multivalent and other chromosome configurations produced by chiasma formation are determined by the genotype it follows, on the above view, that selection for higher fertility in autotetraploids could be effected by increasing the frequencies of those chromosome configurations which permit of more regular disjunction. There is, however, little direct experimental evidence to confirm either a heritable component of variation in the pattern of chromosome pairing or that such variation influences fertility. What evidence there is is contradictory. For example, in the work of Morrison and Rajhathy (1960) on autotetraploids in a number of species there is no evidence for heritable variation in the chromosome pairing pattern and no indication, either, that variation in the pairing pattern affects fertility. McCollum (1958), on the other hand reports that high fertility in autotetraploid *Dactylis* is achieved in association with high quadrivalent frequency. Elsewhere in the Gramineæ, the data of Müntzing (1951) also show a higher quadrivalent frequency in autotetraploid rye plants with improved fertility. In sharp contrast Plarre (1954), Bremer and Bremer-Reinders (1954) and Hilpert (1957) all claim that selection for improvement in the fertility of autotetraploid rye was achieved by increasing the bivalent frequency at the expense of quadrivalents and of other configurations.

The conflicting and, generally, unsatisfactory nature of the available evidence relating to chromosome pairing and fertility in autotetraploids probably results largely from the difficulties inherent in investigations based on highly heterogeneous material derived directly from commercial varieties or from natural populations. The present work on rye was carried out on autotetraploids produced from inbred,

homozygous, diploid lines. This, as will be shown, greatly simplifies the investigation. The chief aims of the work were to determine:

1. The extent of variation in the pattern of chromosome pairing between autotetraploids of different genotype.

2. The relationship between chiasma frequencies and the distribution patterns of multivalent and other chromosome configurations at meiosis.

3. The relationship between variation in chromosome pairing at meiosis and the variation in fertility.

2. MATERIAL AND METHOD

The diploids ($2n = 14$) and induced autopolyploids used were derived from four inbred, homozygous, lines, P_1, P_8, P_{12} and P_{13} (see Rees, 1955). The advantage of using homozygotes is that while the heritable variation within lines is minimal the heritable variation between lines is of a high order as a result of segregation during inbreeding. Genotypic control over the variation in chromosome pairing can therefore be ascertained by straight-forward comparisons between lines. Further comparisons within and between lines serve to determine the influence of chromosome pairing upon fertility.

Tetraploidy was induced by treatment of seedlings in 0·2 per cent. colchicine solution for 4 hours at 20° C. After this treatment it was found that survival improved if the seedlings were grown for three days on Hoagland's nutrient solution in sterilised Vermiculite before transplanting to soil. Preliminary recognition of polyploids was based on the size of leaves and stomata and followed by chromosome counts.

For cytological analysis both diploids and tetraploids were sown in the field in two replicates. Chiasma frequencies and other chromosome characters were scored in twenty *p.m.c.* of each plant after fixing in Carnoy's solution and staining in aceto-carmine. For each plant the chiasma frequencies and the frequencies of multivalent and other chromosome configurations are expressed as the average per cell.

Fertility was measured as the proportion of seeds set in florets of two or more of the tallest tillers in each plant. Spikelets at the base and tip of each inflorescence were excluded from the scores and seeds were counted only in the lower florets of each spikelet.

3. CHIASMA FREQUENCIES

Because the associations of chromosomes at first metaphase of meiosis depend ultimately on chiasma formation it is clearly desirable to determine first the nature and extent of the variation in the frequencies and distributions of chiasmata between the different genotypes.

The chiasma frequencies in the diploid and autotetraploid plants for each genotype are represented in fig. 1. An analysis of variance of the data appears in table 1. For this analysis all diploid chiasma frequencies were multiplied by two so as to bring the means roughly to the same level as those of the tetraploids and, thereby, to eliminate differences in variances attributable to the magnitude of the means. We note from the analysis highly significant chiasma frequency variation between different genotypes ($P = <0·001$), a significant difference between twice the diploid values and those of the tetraploids ($P = <0·001$) and, finally, that the genotype/ploidy interaction item is not

significant. One concludes, therefore, that the chiasma frequencies are genotypically controlled, and that the increase in chiasma frequency from diploid to tetraploid values is consistent for all genotypes. As the histograms show, the tetraploid values are in all instances less than
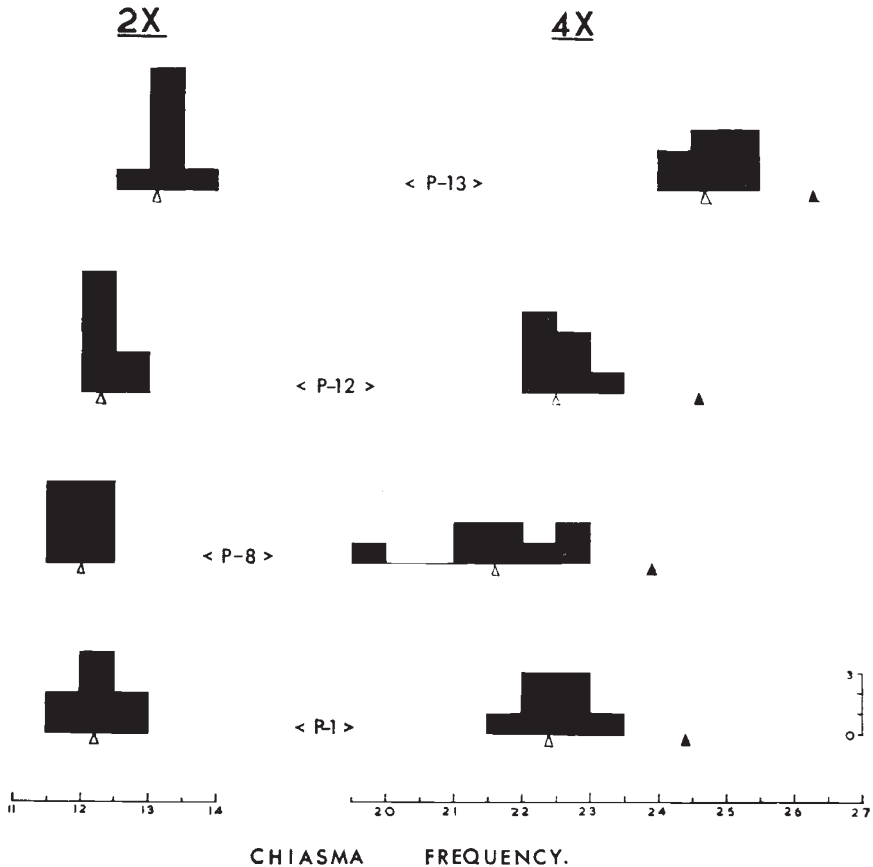

FIG. 1.—The distribution of mean plant chiasma frequencies in the four diploid inbred lines and their tetraploid derivatives. Data from replicates are pooled. Eight plants of each diploid and tetraploid genotype. Black triangles $= 2x$ means $\times 2$.

TABLE 1

The analysis of variance of the chiasma frequency variation between the diploid and autotetraploid lines

Item	S.S.	N	M.S.	V.R.	P
Between genotypes	67·99	3	22·66	66·26	<0·001
Between $4x$ and $2x \times 2$	63·70	1	63·70	186·25	<0·001
Genotype/ploidy interaction	0·85	3	0·28	0·82	>0·20
Between Replicates	0·17	1	0·17	—	—
Error	18·83	55	0·34	—	—
Total	151·54	63	—	—	—

twice the diploid frequencies. This relation varies for different species (see John and Henderson, 1962).

The consistent linear relationship between the chiasma frequencies of diploid and tetraploid genotypes (fig. 2) suggests that the tetraploid chiasma frequencies may be accurately predicted from observations on
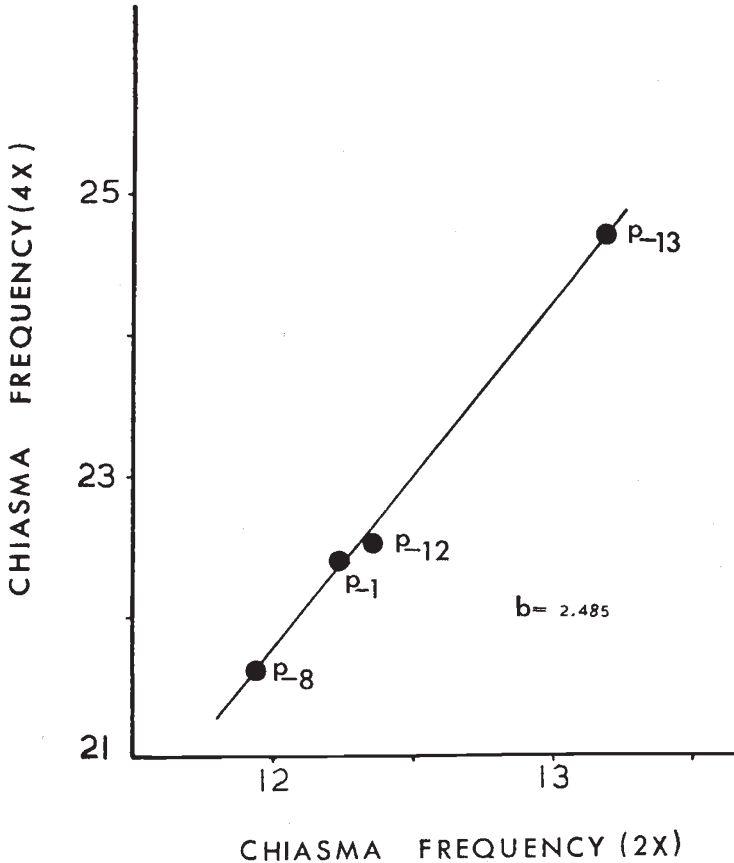

FIG. 2.—The relationship between the chiasma frequencies of diploid genotypes and their tetraploid derivatives.

their diploid progenitors. In view of the influence of chiasma frequencies on chromosome pairing and the fertility of tetraploids (see later section), this prediction may be particularly useful for practical, breeding, purposes.

4. THE CHROMOSOME PAIRING PATTERN

At first metaphase of meiosis the four representatives of each chromosome in an autotetraploid may be associated either in a quadrivalent (*iv*), a trivalent (*iii*) and univalent (*i*), two bivalents, one bivalent (*ii*) and two univalents or remain unpaired as four univalents. The relative frequencies of the different configurations will depend on

the frequency and distribution of chiasmata at prophase. Since the autotetraploid ryes have been shown to vary in respect of their chiasma frequencies we should consequently expect different frequencies of multivalent and other configurations in the different genotypes (see Durrant, 1960).

Where four univalents appear in a cell it is not possible in rye to ascertain whether they are homologous and represent the complete failure of pairing of one chromosome type or represent two pairs of homologues each formed along with a bivalent from two separate sets of four chromosomes. Bivalents and univalents are consequently classified without reference to homology.

There is considerable variation in the relative frequencies of *iv*'s, *iii*'s, *ii*'s and *i*'s between *p.m.c.*'s of the different genotypes (table 2). Analyses of variance of these data showed, first, that there was no significant variation between replicates and, second, that the mean frequencies of *iv*'s, *iii*'s, *ii*'s and *i*'s differed significantly between tetraploid genotypes (P $= <$0·001 for *iv*'s, *iii*'s and *ii*'s; P $= <$0·01 for *i*'s).

It is of course appreciated that the relative frequencies of the different configurations, although analysed separately, are not independent of one another. Nevertheless, that there are significant differences with respect to all four types leave no doubt of a significant influence of genotype on the pairing pattern at meiosis in these tetraploids Such variation, as will be considered later, is likely to influence fertility. In the meantime, however, it is necessary to inquire into the connection between the variation in respect of these chromosome configurations and that of the variation in the chiasma frequencies upon which, it has been inferred, they may depend.

5. CHROMOSOME PAIRING AND CHIASMA FREQUENCY

(a) *Dependence.* There is considerable variation in chiasma frequency and in chromosome pairing between plants within each tetraploid line as well as variation between plants between lines. The first kind of variation is of an entirely non-heritable or developmental origin, the second is at least partly of a heritable nature. Both kinds can be used to determine the relatonship between chiasma frequency and the pairing pattern at metaphase.

The results in table 2 show that *within* all lines the average frequencies of *iv*'s, *iii*'s, *ii*'s and *i*'s at metaphase are correlated with the average plant chiasma frequencies. The correlations are of the following kind:

1. *Quadrivalents.* Quadrivalents increase with increasing chiasma frequencies. A joint regression analysis of variance confirmed a significant positive regression (P $= <$0·01) and showed also that there was no heterogeneity with respect to the regressions between different lines (fig. 3).

X 2

TABLE 2

The average frequencies per p.m.c. of IVs, IIIs, IIs and Is, along with the mean chiasma frequencies, in each of eight plants in four tetraploid genotypes

		Replicate I					Replicate II					Pooled mean
		1	2	3	4	Mean	1	2	3	4	Mean	
P_1	Chiasmata	22·90	23·15	22·25	22·15	22·61	21·90	22·50	22·40	22·65	22·36	
	IV	3·70	3·90	3·55	3·60	3·69	3·40	3·75	3·50	3·55	3·55	3·62
	III	0·30	0·40	0·25	0·50	0·36	0·40	0·40	0·45	0·40	0·41	0·38
	II	5·90	5·35	6·30	5·65	5·80	6·05	5·55	5·95	5·95	5·87	5·83
	I	0·50	0·50	0·45	0·80	0·56	1·10	0·70	0·75	0·70	0·81	0·68
P_8	Chiasmata	21·45	19·60	21·40	22·85	21·32	22·55	21·80	21·50	22·25	22·02	21·67
	IV	3·65	2·20	3·10	3·35	3·07	3·25	3·50	3·00	2·95	3·17	3·12
	III	0·35	0·70	0·35	0·40	0·45	0·40	0·40	0·60	0·35	0·43	0·44
	II	5·90	7·65	6·80	6·45	6·70	6·60	6·15	6·65	7·35	6·68	6·69
	I	0·55	1·40	0·75	0·50	0·80	0·60	0·50	0·90	0·45	0·61	0·70
P_{12}	Chiasmata	22·45	23·05	22·90	22·40	22·70	22·15	22·30	22·60	22·75	22·45	22·57
	IV	3·40	3·70	3·30	3·25	3·41	3·45	3·15	3·70	3·55	3·46	3·44
	III	0·15	0·15	0·15	0·25	0·17	0·20	0·55	0·25	0·05	0·26	0·22
	II	6·60	6·10	5·95	6·80	6·61	6·45	6·50	5·90	6·50	6·33	6·47
	I	0·75	0·55	0·45	0·45	0·55	0·70	0·75	0·25	0·65	0·59	0·56
P_{13}	Chiasmata	24·10	25·00	25·30	24·75	24·78	25·20	24·15	24·85	24·70	24·72	24·75
	IV	3·60	3·70	3·70	4·00	3·75	4·10	4·05	4·40	4·10	4·16	3·96
	III	0·20	0·25	0·35	0·15	0·22	0·15	0·05	0·15	0·10	0·11	0·17
	II	6·40	6·00	5·85	5·80	6·01	5·50	5·65	4·85	5·60	5·40	5·70
	I	0·20	0·45	0·45	0·10	0·30	0·15	0·35	0·25	0·10	0·21	0·25

2. *Univalents*. There is a negative correlation between univalent and chiasma frequencies (fig. 4). The joint regression is significant (P = <0·01) and there is no significant heterogeneity between lines.
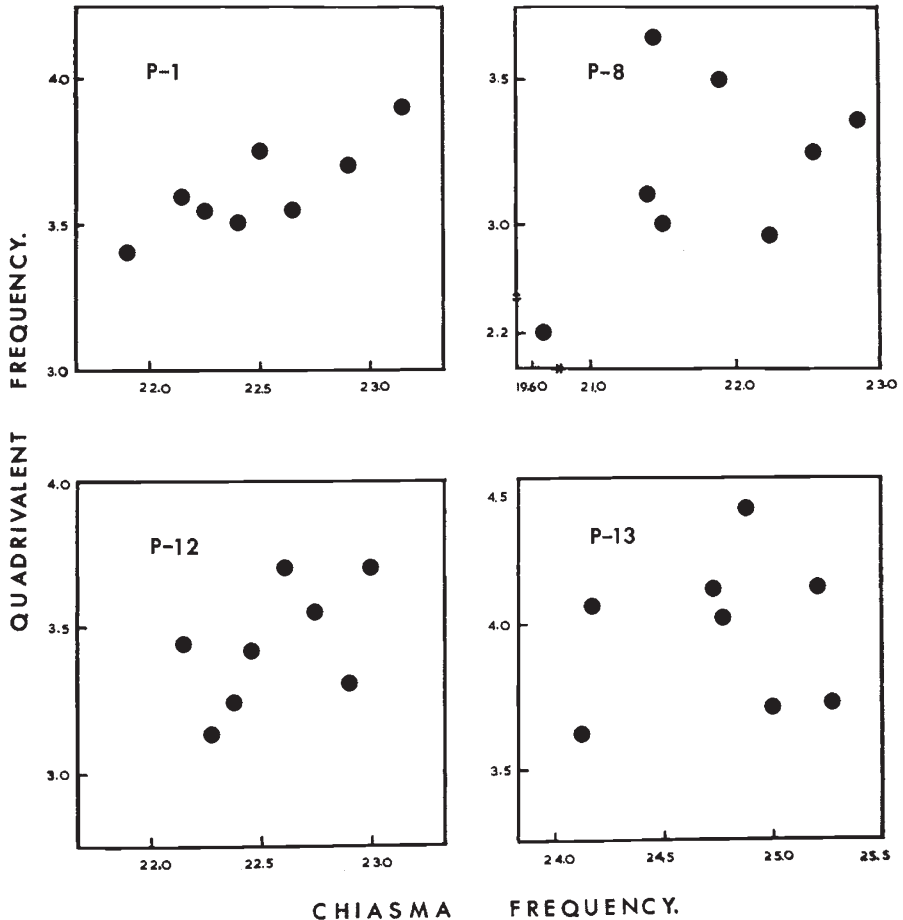

FIG. 3.—The *p.m.c.* quadrivalent frequency plotted against the mean chiasma frequency for plants within each tetraploid line.

3. *Trivalents and Bivalents*. The data show with respect to trivalents and bivalents the same dependence on chiasma frequencies. The correlations are negative and are significant at the 5 per cent. level.

From these results of comparisons within lines it would be expected that the heritable differences in chiasma frequencies reported between lines would be associated with differences in the frequencies of multivalent and other configurations. More precisely, the general expectation is that in lines with the highest chiasma frequencies the frequencies of quadrivalents would be highest and that of other configurations lowest. That this relationship holds is clearly established in fig. 5.
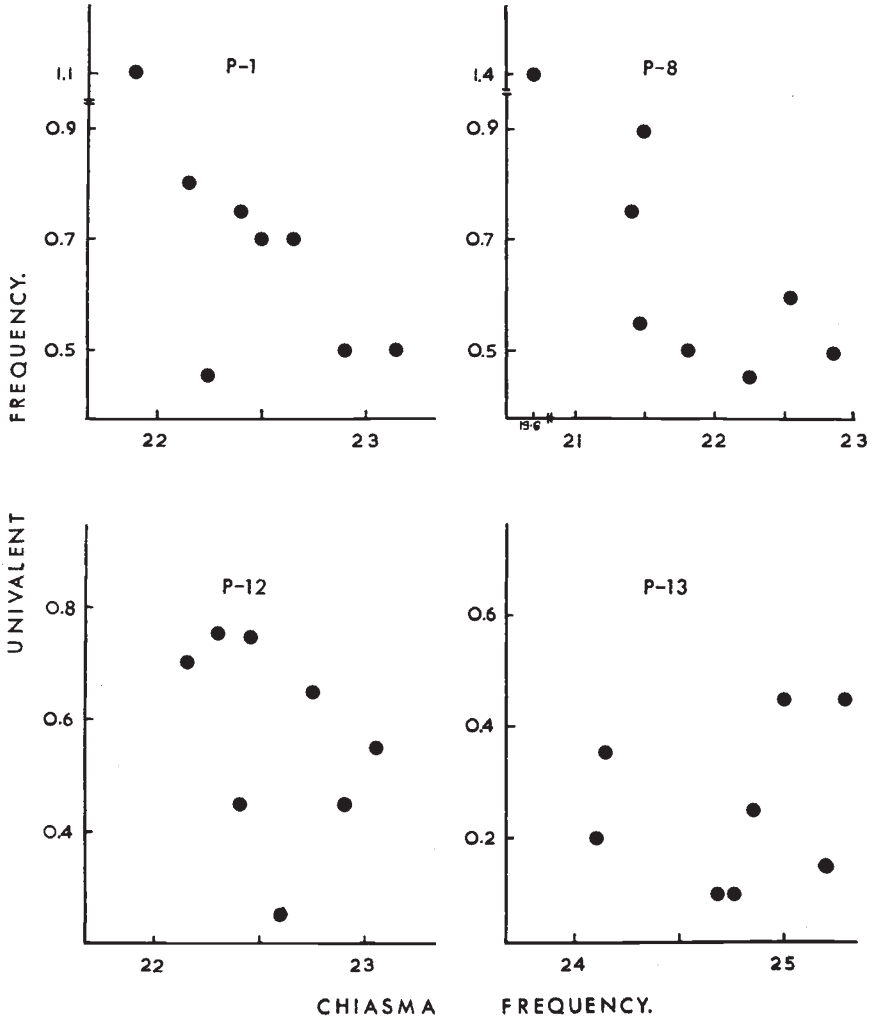
FIG. 4.—The *p.m.c.* univalent frequency plotted against the mean chiasma frequency for plants within each tetraploid line.
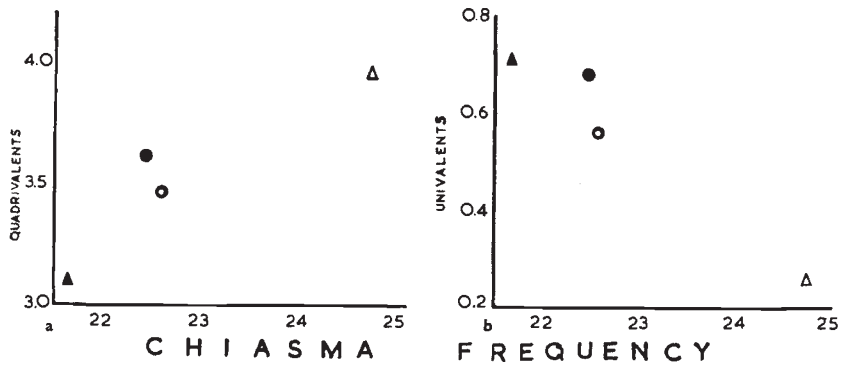

FIG. 5.—*a* The mean *p.m.c.* quadrivalent frequencies (*a*) and univalent frequency (*b*) for each genotype plotted against the mean chiasma frequency. Note the positive and negative correlations respectively. Blocked circles, P_1; blocked triangles, P_8; open circles, P_{12}; open triangles, P_{13}.

These results are in good agreement with those briefly reported by Roseweir and Rees (1962).

(b) *Independence.* The above results show that the chiasma frequency determines, at least to a large degree, the pattern of chromosome pairing at meiosis in autotetraploids and, also, that the variation in the pairing pattern is subject to control by the genotype as well as the environment. The following comparisons were designed to find out whether the genotype also determines a variation in the pairing pattern that is to some degree independent of the chiasma frequency. For example, are quadrivalents and other configurations more frequent

FIG. 6.—First metaphases of meiosis in *p.m.c.* of tetraploid rye with *a*, relatively high chiasma frequency (25) and high quadrivalent frequency (5), and *b*, fewer chiasmata (21) and a single quadrivalent, a trivalent and univalent.

in *p.m.c.*'s *of the same chiasma frequency* in different genotypes? The answer to this question can be found quite easily by comparing the average frequencies of *iv*'s, *iii*'s, *ii*'s and *i*'s in *p.m.c.*'s of specific chiasma frequencies in the different lines.

The results for *iv*'s show the expected increase in quadrivalent frequency with increasing chiasmata in all lines (fig. 7). But, for comparable chiasma frequencies, P_1 has the highest number of quadrivalents per *p.m.c.*; P_8, in general, has the least. The difference is significant (P = <0·01). From this one concludes that the control exercised by the genotype over the pattern of pairing in autotetraploids is achieved in two ways, first, by adjustment of the chiasma frequency and, second, by adjustment of the distribution of the chiasmata such that the same number of chiasmata may give rise to different configurations at first metaphase (*cf.* Roseweir and Rees, *loc. cit.*). The situation with respect to the control over the *distribution* of chiasmata is reminiscent of that in hexaploid wheat where an albeit more precise control over the chiasma distribution restricts the pairing to bivalents only (Riley, 1960).

Comparisons in respect of *iii*'s, *ii*'s and *i*'s gave essentially the same results as those for *iv*'s.

6. CHROMOSOME PAIRING AND FERTILITY

The relationship between the pattern of pairing at first metaphase and the fertility of the autotetraploids has been established from comparisons between the variation in the frequencies of the *iv*'s, *iii*'s, *ii*'s and *i*'s and the variation in seed set. It is appreciated that the data on pairing relate to meiosis in *p.m.c.*'s whereas the percentage seed set will depend largely on chromosome behaviour in the embryo sac
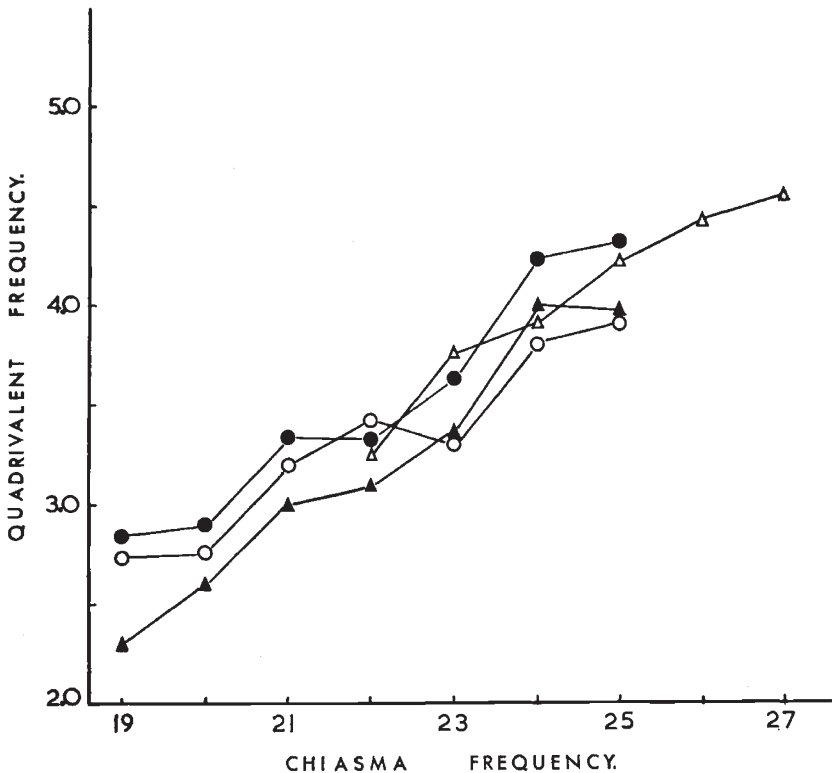

FIG. 7.—The mean quadrivalent frequencies in *p.m.c.* of specific chiasma frequencies in the four tetraploid lines. Symbols as in fig. 5. Note, in particular, the variation in quadrivalent frequency between genotypes for *p.m.c.* with identical chiasma frequencies. In general P_{13} has most, P_1 least. The mean quadrivalent frequencies are estimated from *p.m.c.* of *all* plants in each line for each chiasma frequency.

mother cells. There is, however, no reason for supposing that the events at male and female meiosis are unrelated, an assumption which is justified by the comparisons described below.

The results in respect of quadrivalents and univalents are summarised in figs. 8 and 9. These figures show that, in general, an increasing fertility is associated with an increase in quadrivalents and a decrease in univalents. P_{13} is somewhat exceptional in showing no obvious correlations. Nevertheless, joint regression analyses of variance show no significant heterogeneity of the regressions between lines and the joint regression for univalents on seed set is highly significant

(P = <0·01) and that for quadrivalents significant at the 5 to 10 per cent. level. These results fully confirm those of Roseweir and Rees (1962). As these authors pointed out, the increase in fertility with increasing quadrivalent frequency is on the face of it surprising and counter to the widespread belief that high fertility in autotetraploids can be achieved only by increasing bivalent frequencies at the expense of multivalents including quadrivalents. Admittedly rye is in a special,
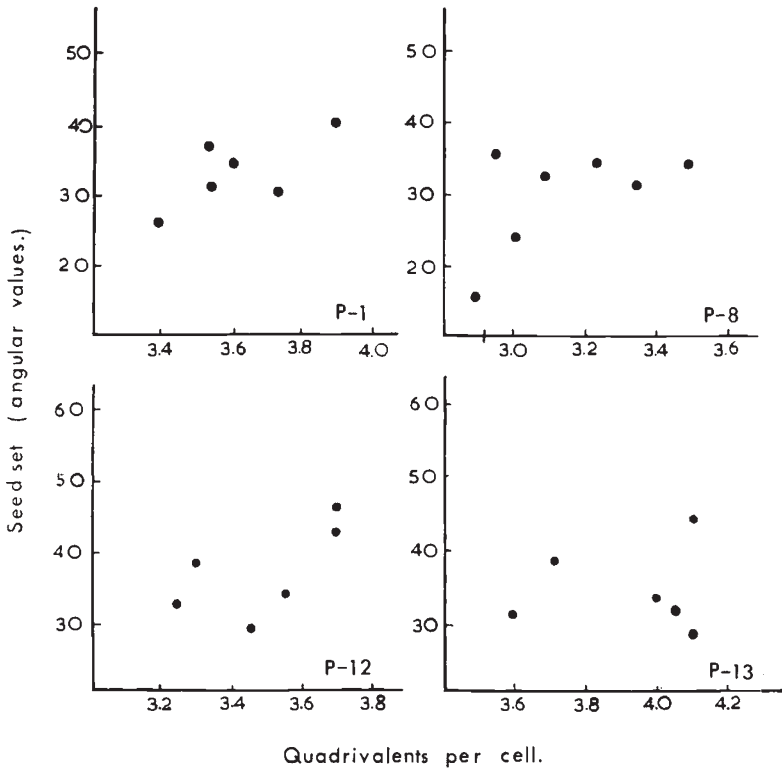

Fig. 8.—The proportion of seed set (in angular values) plotted against the quadrivalent frequency per plant in each of the tetraploid lines.

but by no means uncommon, cytological category in that the chiasma frequency of quadrivalents is low (usually 3 or 4) and, also, that they are located terminally or sub-terminally at metaphase. Both features facilitate a regular two-by-two disjunction at first anaphase (see Myers, 1945). The results for bivalents and trivalents show no significant correlations with seed set.

While these correlations between univalent and quadrivalent frequencies with seed set serve well enough to establish the dependence of fertility on the chromosome pairing pattern at meiosis, they do not in themselves provide an entirely satisfactory basis for describing completely those features at meiosis which affect the fertility. Moreover, the two variables, univalent and quadrivalent frequencies, are not independent of one another. They are negatively correlated and

both, it will be recalled, are determined largely by the chiasma fre-
quency. What is required is a single measure or index which takes
into account all those cytological features at meiosis that affect fertility.
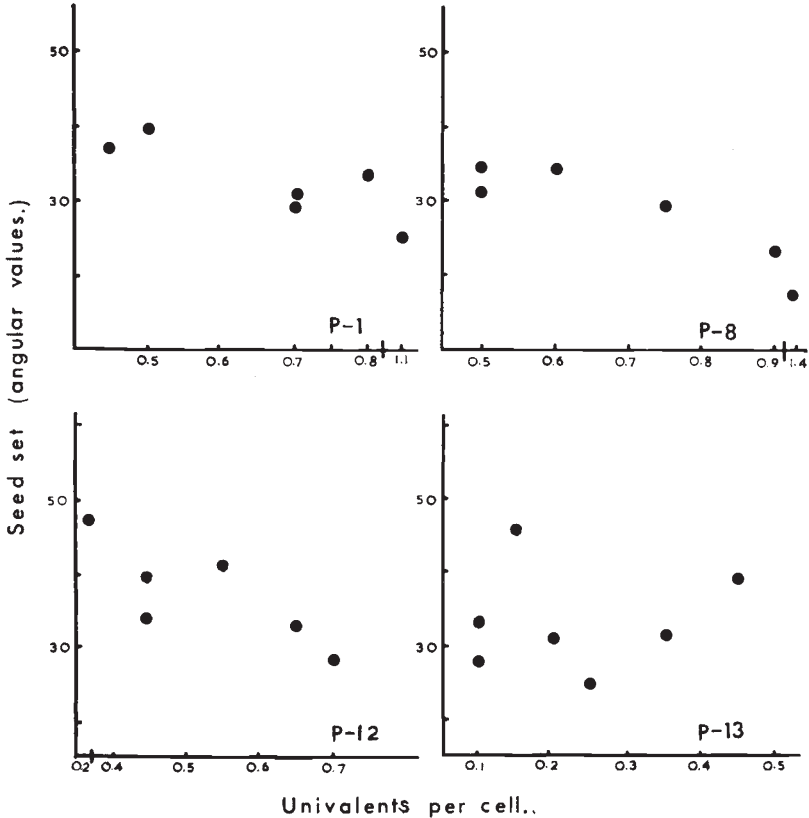This index is, in fact, quite easily obtained and is described below.

Fɪɢ. 9.—Seed set (angular values) plotted against the univalent frequency in plants within
the tetraploid lines.

7. THE DISJUNCTION INDEX

Because the quadrivalents disjoin regularly the two causes of
aneuploid gametes in rye autotetraploids are trivalents and univalents.
An estimate of the proportion of *p.m.c.*'s without trivalents or univalents
provides an index from which to predict the proportion of viable
gametes.

The disjunction index, calculated from the 20 *p.m.c.*'s in each plant,
is plotted against plant fertility in the four tetraploid lines in fig. 10.
The complete joint regression analysis of variance of the results is given
in table 3. From this analysis it will be seen that the joint regression
is significant ($P = < 0.001$) showing that seed fertility increases with
an increase in the *disjunction index*. There is no significant heterogeneity
between the regression slopes; the rate of change in fertility in relation
to the *disjunction index* is, therefore, constant for all genotypes. The

analysis also shows that the mean fertility varies significantly between genotypes ($P = <0.05$) which indicates that the fertility of different genotypes is partly independent of the *disjunction index*, as, indeed, is

TABLE 3

The joint regression analysis of variance of seed set against the disjunction index *in each line*

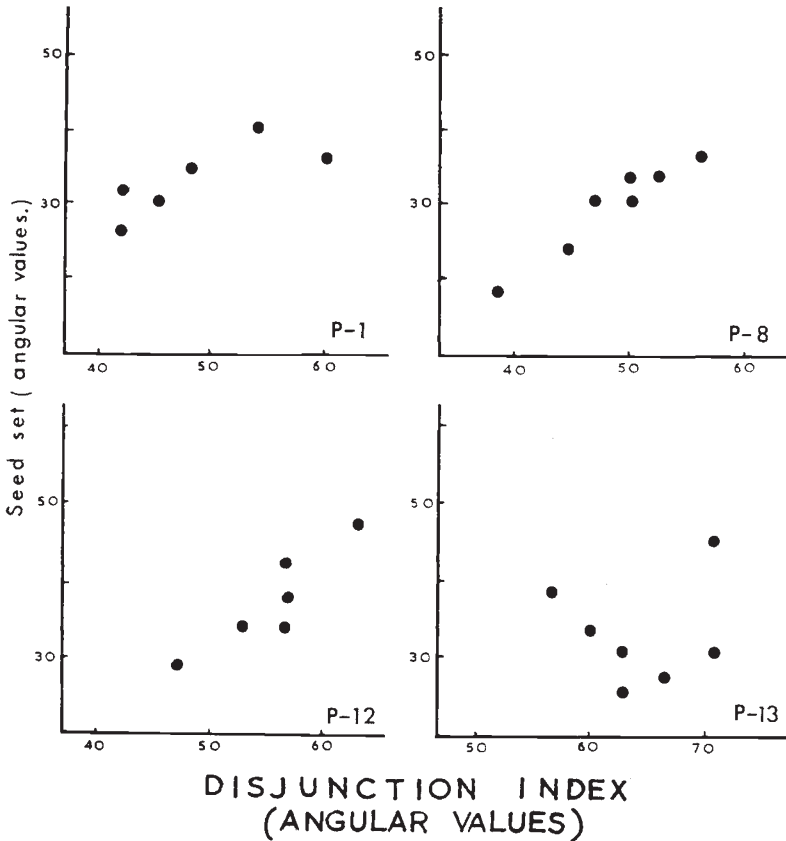| Item	S.S.	N	M.S.	V.R.	P
Joint regression	369·42	1	369·42	17·19	<0·001
Heterogeneity of regressions	129·36	3	43·12	2·06	>0·1
Heterogeneity of means	220·40	3	73·46	3·42	<0·05
Error	386·91	18	21·49	—	—
Total	1706·09	25	—	—	—

FIG. 10.—The seed set (angular values) plotted against the *disjunction index* (angular values) for each plant within the four lines.

made clear in fig. 10. Other factors of course affect the fertility of the autotetraploids. This analysis serves to show that these other factors are more important in some lines (e.g. P_{13}) than in others.

This simple analysis, based on the *disjunction index*, illustrates clearly the relation between the overall chromosome pairing pattern and fertility. Above all it takes into account all the relevant cytological features and one is spared the trouble and confusion of dealing with each feature in separate detail.

8. PREDICTION

In an earlier section it was shown that the pairing pattern giving a high disjunction index, *i.e.* with few trivalents and univalents, is largely dependent on high chiasma frequencies. It was also shown that the chiasma frequencies of the tetraploids were correlated with those of their diploid ancestors. It follows, therefore, that it should
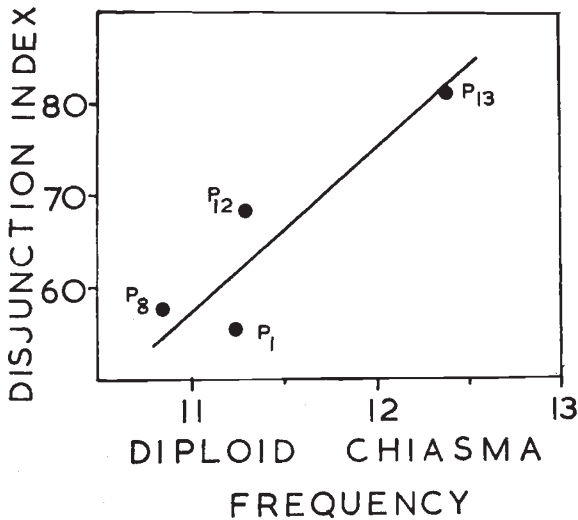

FIG. 11.—The *disjunction index* of tetraploid genotypes plotted against the mean chiasma frequency of their diploid ancestors.

be possible to predict from the chiasma frequencies of the diploids which tetraploid genotypes would have the highest *disjunction index* and, hence, the highest fertility.

In fig. 11 the mean *disjunction index* for each tetraploid line is plotted against the mean chiasma frequency of its diploid ancestor. The values are clearly correlated. In so far, therefore, as the fertility of autotetraploids is directly dependent on chromosome pairing, the chiasma frequencies of diploids should provide a useful basis for predicting the fertility of autotetraploids derived from them.

9. CONCLUSION

Bearing in mind that various " genic " factors affecting the development of gametes, endosperm and embryo contribute to the infertility of autotetraploids (Stebbins, 1949; Hakansson and Ellestrom, 1950; Kuckuck and Levan, 1951; Moore, 1963) it is confirmed by this work that the cytological consequences of doubling the chromosome numbers

also play a decisive role in controlling fertility. Apart from univalents, multivalents giving unequal disjunction account for the infertility. In rye and doubtless in other species with few and distally located chiasmata the culprits are the trivalents, the quadrivalents disjoining with respectable regularity. In species where quadrivalents do not disjoin regularly it would be expected that their frequencies must decrease to effect an improvement in fertility. They may disappear altogether as in *Lotus corniculatus* (Dawson, 1941).

It was established not only that chromosome pairing affects the fertility of autotetraploids but also that chromosome pairing is genotypically controlled. It follows that selection for improved fertility should be effective through adjustments in the pairing pattern. In rye it is clear what these would be. They would be changes that result in a high *disjunction index*, namely a high chiasma frequency, high quadrivalent, low univalent and trivalent frequencies.

Finally, the importance of the chiasma frequency in determining the pairing pattern, and hence fertility, in autotetraploids coupled with the observation that the chiasma frequencies of diploids and their tetraploid derivatives are highly correlated suggests the possibility of predicting from the chiasma frequency of diploid genotypes the probable fertility of autotetraploids derived from them. This prediction is quite well substantiated in the rye material described.

10. SUMMARY

1. The relative frequencies of multivalents and other chromosome configurations in *p.m.c.*'s of autotetraploid rye are largely dependent on chiasma frequencies. In general, with a higher chiasma frequency the number of quadrivalents increases whereas the frequencies of trivalents, bivalents and univalents decrease.

The chiasma frequency and hence the distributions of the different chromosome configurations at first metaphase of meiosis are genotypically controlled. The genotype also controls some variation in the distribution of chromosome configurations that is independent of the chiasma frequency. For comparable chiasma frequencies the frequencies of quadrivalents, for example, are higher in *p.m.c.*'s of some genotypes than of others.

3. Fertility, measured as the proportion of seed set, is correlated with the pattern of chromosome pairing at first metaphase. High fertility in rye is associated with high quadrivalent frequency and a low univalent frequency.

4. It is possible to predict with some accuracy the fertility of autotetraploids from observations of meiosis, viz. of chiasma frequencies, in the diploids from which they derive.

A *disjunction index* is described which takes into account those features of the chromosome pairing pattern in *p.m.c.* which affect fertility. This index can usefully be applied as a guide to assessing the fertility of autotetraploids.

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