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A Contribution to the Genetics of 'Hybrid Desynapsis' in Common Wheat, *T. aestivum* L.

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With 6 Figures

Introduction

Meiosis of allohexaploid as well as allotetraploid wheat is normally characterized by bivalent formation. This pairing of homologous chromosomes is controlled by a number of genes, preventing the homoeologous association which should be expected from the genomatic constitution (Sears and Okamoto, 1958; Riley and Chapman, 1958; Riley, 1966; Sears, 1976).

The level of meiotic irregularities, resulting in pollen mother cells containing a few unpaired chromosomes is low in homozygous cultivars, ranging from 0 to 10%. However, the frequency of such aberrations due to desynapsis increases considerably in heterozygous material and may affect up to 70% of the cells (Hollingshead, 1932; Riley and Kimber, 1961; Watanabe, 1962; Gaidalenok, 1973; Schlegel, 1976). These pairing failures seem to occur at random and there is, so far, no indication that this particular type of desynapsis is affected by major structural differences in the karyotypes of the hybridized wheats.

It has been argued that the optimal level of pairing is related to the predominant mating system of wheat, favouring a genetic balance which is based on homozygosity (Riley and Law, 1965). So, in wheat any expansion of heterozygosity induces similar effects which are, in the opposite direction, known in inbred rye (Rees, 1961). It was Person (1956) who observed the decrease of pairing irregularities with increasing recovery of homozygosity during the backcross procedure to establish wheat monosomics, although the relationships were not strictly linear. From these and other data Riley and Law (1965) concluded the balanced chromosome pairing in hexaploid wheat being probably due to nonallelic gene interactions rather than being a direct function of homozygosity.

In order to obtain further information on the genetic basis of this 'hybrid desynapsis' some intervarietal hybrids have been analyzed in successive generations on a single plant basis.

Materials and Methods

For screening purposes a total of 64 intervarietal wheat crosses were performed using the cultivar 'Chinese Spring' as the common female parent. The male parents were taken from the Zentralinstitut für Genetik und Kulturpflanzenforschung Gatersleben germplasm collection, and represented hexaploid wheats from all over the world. The F_1 hybrids were grown in the field at the same season.

Feulgen-stained pollen mother cells having two or more univalents at metaphase I were scored as desynaptic. Approximately 30 cells were found to be sufficient to characterize a particular plant for desynapsis frequency after preliminary experiments. Possible experimental errors, such as premature anaphase separations and squash effects, were avoided.

As a result of the screening two cultivars were chosen for detailed genetic studies in addition to 'Chinese Spring'; – 'Lundi' a spring wheat from Rhodesia, and 'Gaudenz' a spring wheat from the Federal Republic of Germany.

All of the genetic experiments were carried out under glasshouse conditions in order to minimize environmental effects.

Results

1. Intervarietal variation and modificability of the character

Because most of the results so far published were obtained from various cross combinations under different environmental conditions it seemed necessary for a genetic approach to survey the range of variation on a comparable basis. The cultivar 'Chinese Spring' as the conventional standard was chosen as the common female parent for two reasons; first to have a comparable cytoplasm in all hybrids, and second to use its monosomics for further analysis. Because most of the male parents differed from 'Chinese Spring' by a reciprocal translocation there was no problem to confirm the hybridity of the material.

The data obtained for the 64 intervarietal F_1 hybrids are graphically shown in Fig. 1. The variation of the character 'hybrid desynapsis' is obviously discontinuous, the

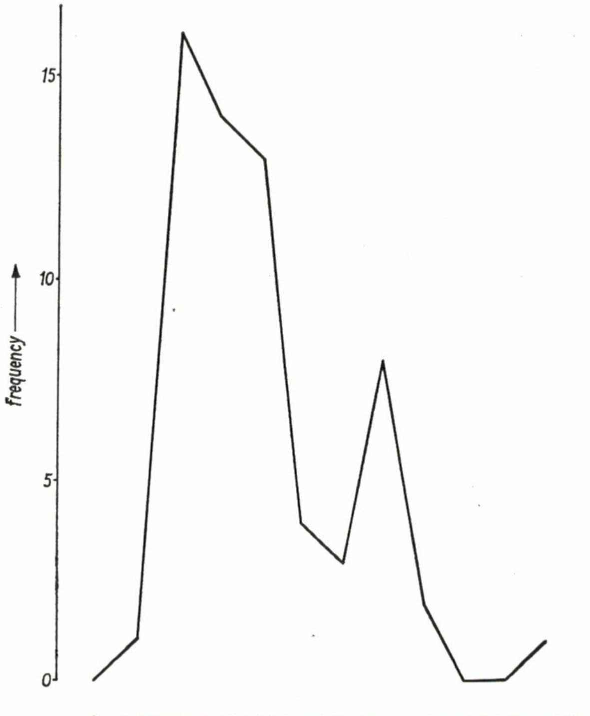

Fig. 1. Distribution curve of mean percentage of 'hybrid desynapsis' of 64 intervarietal F_1 hybrids

distribution curve showing two peaks at 20% and 40%, resp. The majority of the F_1 hybrids exhibit a frequency of desynaptic pairing failures around 20%. According to the top cross system used in this study it can be concluded that, at least, two genes being involved in the expression of the character. It should be added that this distribution curve is not affected by widely differing flowering dates and, hence, drastic temperature differences during meiosis.

Two of the hybrid combinations representing the extreme types of the overall distribution were chosen for a more detailed analysis of 'hybrid desynapsis' – namely the F_1

Table 1. Percentages of desynaptic cells of two selected F_1 hybrids, in different years (pooled data of several plants after test of homogeneity)

F_1 combination	Year	Number of PMC	Desynaptic cells (%)
Chinese Spring × Lundi	1973	30	10.0
	1974	170	12.3
	1975	295	10.8
Chinese Spring × Gaudenz	1973	30	60.0
	1974	150	45.3
	1975	280	38.6

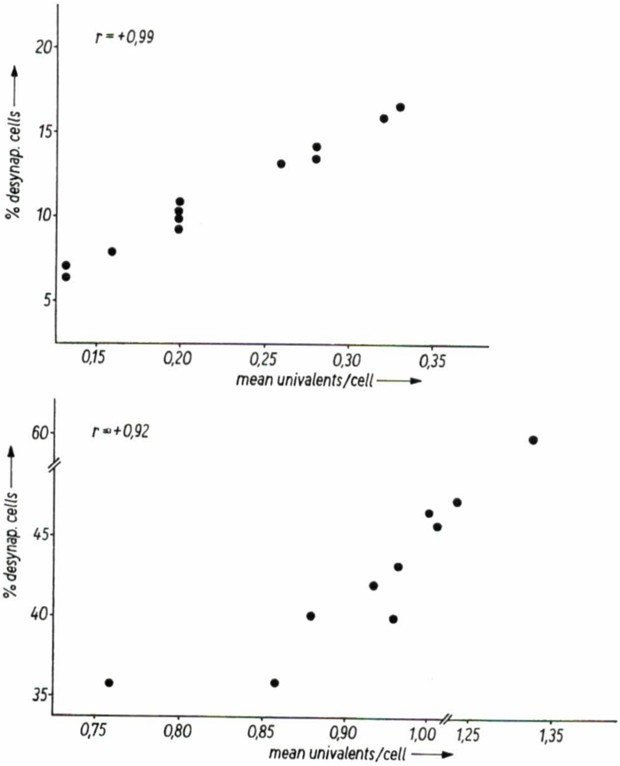

Fig. 2. The relationship between the percentage of desynaptic cells and the number of univalents/cell, 2a (upper past of the fig.) – F_1 'Chinese Spring' × 'Lundi', 2b (lower past of the fig.) – F_1 'Chinese Spring' × 'Gaudenz'

((Chinese Spring) × (Lundi)) and the F_1 ((Chinese Spring) × (Gaudenz)). The expression of the character has been analyzed over a three years period (Table 1). From these data it is very probable that the two selected types of 'hybrid desynapsis' are genetically distinct. The data also demonstrate a high stability of low level desynapsis, while high level desynapsis seems to be less stable. The experimental scores in both combinations indicate, in addition, a significant positive correlation between the total number of univalents/cell and the frequency of aberrant pollen mother cells/plant (Fig. 2). From these relationships it can be concluded that gene action is primarily directed on the behaviour of chiasmata.

The expression of the character 'hybrid desynapsis' is obviously related to the heterozygous condition of the F_1 hybrids. Comparing the level of F_1 desynapsis to the degree of pairing failures of the homozygous parents used there seems to be some connection; the figures for 'Chinese Spring', 'Lundi', and 'Gaudenz' amounted to 2.0%, 5.0%, and 12.2% resp.

2. The genetic behaviour of 'hybrid desynapsis'

Based on the different levels of F_1 desynapsis of the screening experiment the following intervarietal combinations were used for genetic investigations,

(a) 'Chinese Spring' × 'Lundi'
(b) 'Chinese Spring' × 'Gaudenz' and
(c) 'Gaudenz' × 'Lundi'.

From all of the hybrids, F_2 populations were grown and the plants individually scored. The results obtained for crosses (a) and (b) are graphically shown in Fig. 3. In both combinations a clearcut bimodal distribution was observed. About 50% of the plants in each population resembled the parental desynapsis, while the aberration frequency of the remaining part of the F_2 population was very close to the desynaptic behaviour of the F_1. The pattern of distribution in both of the F_2 populations allowed the classification of two phenotypes of desynapsis and, thus, a statistical analysis of the segregation pattern (Tables 2 and 3).

The actual segregation observed corresponds significantly to a 1:1 ratio. This mode can be explained best by assuming a monofactorial difference between 'Chinese Spring' on the one hand, and each of the varieties' Lundi' and 'Gaudenz' on the other. The 1:1 ratio seems to be really a 1:2:1 ratio, with 50% of the plants being heterozygous for a major gene, while the remaining 50% represent the two homozygous genotypes of the parents which, however, cannot be discriminated at the usual low level of varietal desynapsis (see arrows in Fig. 3).

It is obvious from crosses (a) and (b) that either different genes or different alleles of one particular gene must be involved to explain the differences in phenotypic expression of the two hybrids analyzed.

Cross (c) was used to discriminate the different modes of gene action. Assuming the expression of 'hybrid desynapsis' to be due to heterozygosity, cross (c) should segregate according to the 1:1 (= 1:2:1) ratio in case of multiple allelism. On the other hand, independent or interacting gene effects should result in a normal or modified digenic segregation. The actual results along with the F_1 behaviour are shown in Fig. 4. Again, the frequency distribution of the character is clearly bimodal, indicating a two gene system. Considering the F_1 phenotype of cross (c) F_2 segretation can be explained best

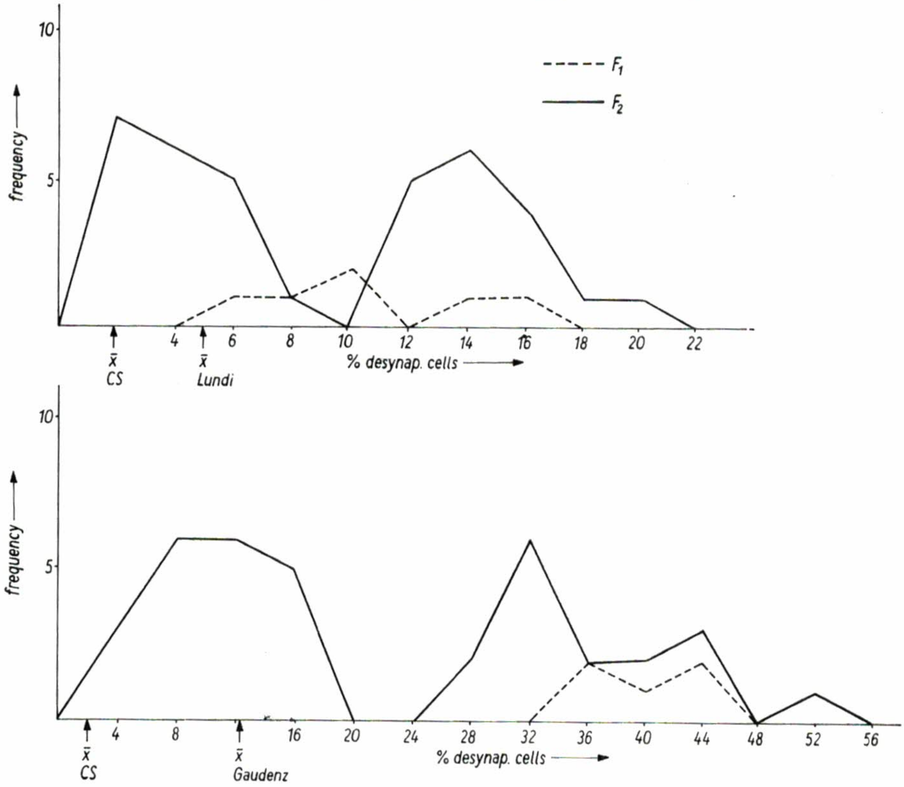

Fig. 3. F_2 segregation curves for percentage of desynaptic cells/plant in 'Chinese Spring' × 'Lundi' and 'Chinese Spring' × 'Gaudenz'

by some kind of gene interaction. Epistasis of the low level 'Lundi' gene over the high level 'Gaudenz' gene results in a 12:4 ratio, i. e., the large fraction involves the double homozygotes, the double heterozygotes, and the single 'Lundi'-type heterozygotes. The

Table 2. Statistical analysis of the F_2 segregation for percentage of desynaptic cells of the cross 'Chinese Spring' × 'Lundi'

Phenotypic expression	Segregation		χ^2	P (for 1:1)
	actual	expected		
parental-like	19	18	0.11	0.74
F_1-like	17	18		

Table 3. Statistical analysis of the F_2 segregation for percentage of desynaptic cells of the cross 'Chinese Spring' × 'Gaudenz'

Phenotypic expression	Segregation		χ^2	P (for 1:1)
	actual	expected		
parental-like	20	18	0.44	0.51
F_1-like	16	18		

statistical analysis revealed a sufficient agreement between actual and expected ratio (see Table 4). This is mainly due to some excess of low desynaptic plants which seems typical, however, for all populations analyzed.

Table 4. Statistical analysis of the F_2 segregation for percentage of desynaptic cells of the cross 'Gaudenz' × 'Lundi'

Phenotypic expression	Segregation		χ^2	P (for 12:4)
	actual	expected		
parental + low-type	50	45	2.21	0.15
high-type	10	15		

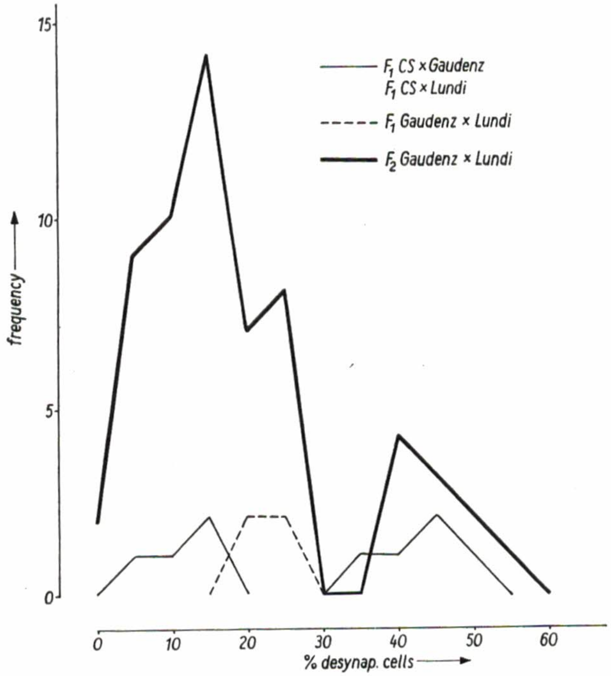

Fig. 4. F_2 segregation curve for percentage of desynaptic cells/plant in 'Gaudenz' × 'Lundi'

To confirm the hypothesis of the two gene difference between 'Lundi' and 'Gaudenz' a number of F_2 progenies from the low, medium, and high level segregants were checked. In all cases, the segregation pattern fitted with the theoretically supposed genotypes of the F_2 plants.

In addition to the extensively used crosses mentioned above a limited number of intervarietal combinations expressing the 20% level of 'hybrid desynapsis' have been investigated. The data obtained, though not yet fully clear, gave some evidence for a third gene controlling the degree of 'hybrid desynapsis'.

On the basis of the present results it is proposed to designate the genes being responsible for the expression of 'hybrid desynapsis' as *Hyd 1* ('Lundi'-type, low), and *Hyd 2* ('Gaudenz'-type, high) so that the genic formulae of the three varieties should be:

'Chinese Spring'	*hyd 1/hyd 1*	*hyd 2/hyd 2*
'Lundi'	*Hyd 1/Hyd 1*	*hyd 2/hyd 2*
'Gaudenz'	*hyd 1/hyd 1*	*Hyd 2/Hyd 2.*

3. Preliminary attempts to localize the genes by monosomic analysis

The observed mode of inheritance of 'hybrid desynapsis' and the use of 'Chinese Spring' as the female cross parent offered the chance for a monosomic analysis. The monosomics of 'Chinese Spring' were crossed to both varieties. Due to poor seed set and germination 15 F_1 combinations each have been established until now. Theoretically, all but one of the monosomic F_1 hybrids were expected to correspond in desynapsis frequency to the disomic hybrid provided that hemizygosity does not generally interfere with the expression of the character.

The results of the monosomic analysis, though not yet complete, are presented in Fig. 5. The data for both sets confirm the different levels of 'hybrid desynapsis'. But even in case of the more distinct 'Gaudenz' combination none of the 15 chromosomes tested exhibited the normal level of pairing failures of homozygous 'Gaudenz'. So further check crosses are needed with the monosomics still missing in order to ascertain the critical chromosome, or to prove the inefficacy of the hemizygous gene. On the other hand the

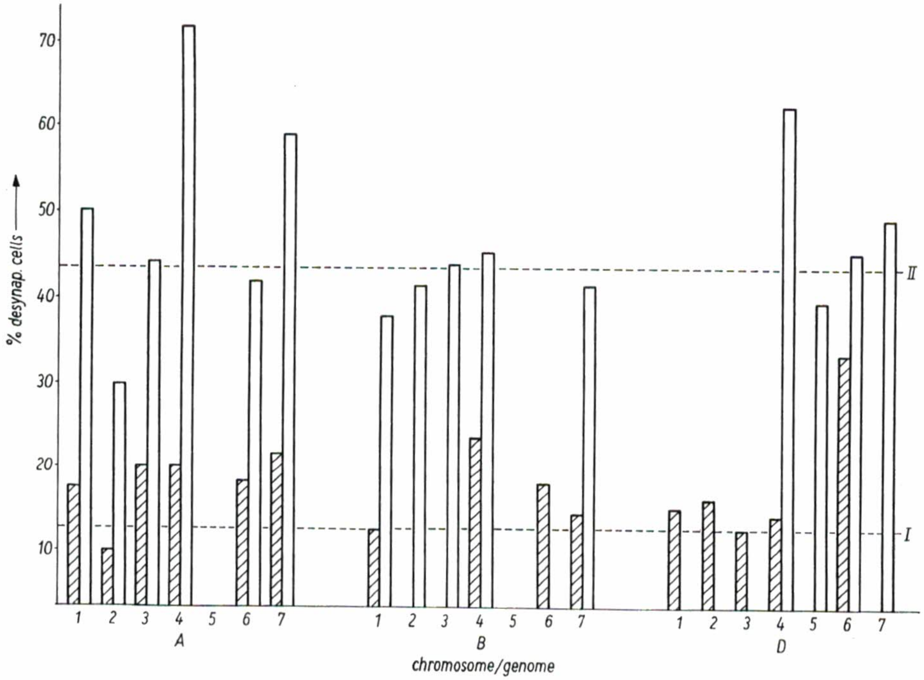

Fig. 5. The expression of the character 'hybrid desynapsis' in two incomplete sets of monosomic F_1 hybrids from 'mono-Chinese Spring' × 'Lundi' (solid columns) and 'mono-Chinese Spring' × 'Gaudenz' (open columns). I and II represent the disomic means

results in Fig. 5 also show the degree of variation of the percentage of 'hybrid desynapsis' which is already known and must be due to dosage effects of probably minor genes.

The comparison of the effects of corresponding hemizygous F_1 conditions indicates quite a number of similarities. So mono-4A and mono-7A hybrids obviously surpass the desynapsis frequency of the disomics, while the irregularities are less pronounced in mono-2A or even fully adversed in a few cases.

Discussion

In hexaploid wheat the increase of pairing failures following hybridization of more or less homozygous cultivars is a common feature. It cannot be questioned that the expression of the character is, in some way, related to heterozygosity. But until now a satisfactory explanation of the genetic basis of this special type of desynapsis is still lacking. While PERSON (1956) was not able to prove the relationships between desynapsis frequency and genetical status, the present results confirm his idea, without demanding the cogent linearity of aberration frequency and genic condition.

Another explanation for the cause of 'hybrid desynapsis' was given by WATANABE (1962). His suggestion is based on minor structural differences in the karyotypes of two parents which, after hybridization, result in cryptic hybrids. Such differences affecting either chiasma formation or activity cannot be ruled out perfectly. This argument is partly supported by experimental evidence which favours desynapsis rather than asynapsis, though an ultimative discrimination is not possible, at least in wheat (PERSON, 1956; RILEY and LAW, 1965; RÖBBELEN, 1968). Pre-metaphase I studies of the present material also revealed desynapsis to be more likely.

Discussing the possible cryptic condition of hybrids entails two consequences. First, small structural differences in the distal parts of one or a few chromosomes of the parental cultivars necessarily give rise to more or less effective structural heterozygosity in intervarietal hybrids which might affect chiasma terminalization. Such rearrangements or deficiencies behave like genes when distributed and transmitted at random. Another consequence of the cryptic condition would be preferential desynapsis of those bivalents carrying the structural difference. Since translocations are well known as a source of karyotype variation in wheat (RILEY et al., 1967; DIANNELIDIS et al., 1969; METTIN and KLEIN, 1974), the presence of chromosomal differences of the type mentioned seems conceivable. Until now no experimental evidence can be presented to prove preferential desynapsis of particular bivalents in wheat hybrids. The proportional participation of the chromosomes of the three basic genomes in the total aberration frequency of hexaploid wheat, as demonstrated by RILEY and KIMBER (1961), cannot be used to reject the argument. The present results can thus be explained either by genetical or structural hybridity, though rough measurements of the total chromosome lengths of the three varieties 'Chinese Spring', 'Lundi', and 'Gaudenz' revealed no differences. So it might be that these rearrangements are too small to be detected.

From the genetic studies it must be concluded that there are genotypical differences between varieties. The expression of the character is related to heterozygosity of at least two (possibly three) genes which are interacting. This means that 'hybrid desynapsis' is under oligogenic or polygenic control, as already suggested by RILEY and LAW (1965), and because wheat cultivars may differ in a few or several *Hyd* genes, segregation patterns in selfed or backcrossed progenies are getting obscure.

With these assumptions and considering the changing proportions of heterozygotes and homozygotes in successive generations the decrease of an initial desynapsis frequency in F_1 can be predicted for any offspring. So, e. g., in a monogenic model the population mean for percentage of 'hybrid desynapsis' after continuous selfing will follow the equation

$$\%\,\text{desynapsis}_n = \left[F \times \frac{1}{2^{n-1}}\right] + \left[\frac{P_1 + P_2}{2} \times \frac{2^{n-1} - 1}{2^{n-1}}\right] \tag{1}$$

(the symbols F, P_1, and P_2 mean the initial desynapsis frequencies of the F_1 and both parents, n means generation).

The decrease of ‚hybrid desynapsis' for the predominant levels of F_1 desynapsis observed in this study (low, medium, high) is graphically shown in Fig. 6 for unselected populations. These estimates are, of course, the most simple and neglect all kinds of nonallelic interaction in varietal crosses involving two or even more gene differences.

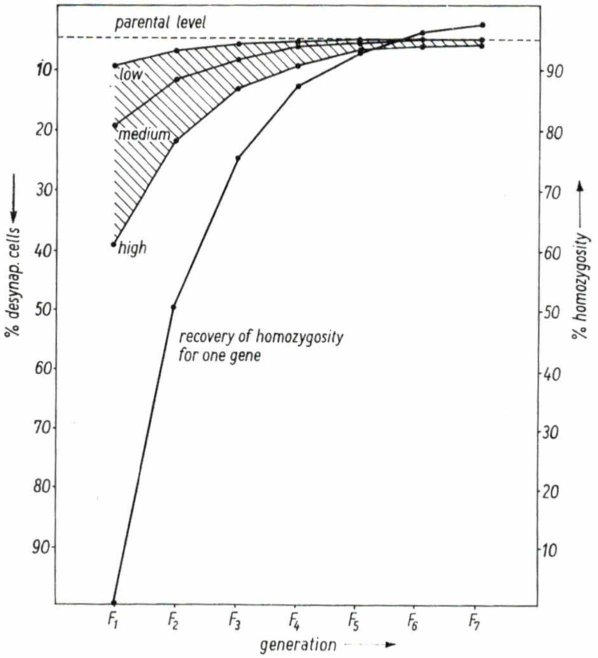

Fig. 6. Theoretical estimates for the decrease of mean 'hybrid desynapsis' in successive generations after selfing, for three levels of initial F_1 desynapsis. All estimates are based on a 5% level of parental pairing failure (see text)

Similar to the curve presented by PERSON (1956) the estimates confirm that his hypothesis of 'hybrid desynapsis' is correlated to heterozygosity, but not as a linear function. The curves given in Fig. 6 hold true only for populations; individual desynapsis covers the range of variation to be expected from each genotype. PERSON's (l. c.) records agree to this expectation, though superimposed by additional effects of monosomy.

RILEY and KIMBER (1961), based on the above considerations, have demonstrated the relationship between the level of pairing failures and the occurrence of aneuploids in wheat. While homozygous wheat cultivars exhibit about 1% aneuploids, this figure raises up to 6.8% in a F_2 population. Similar data were observed by METTIN et al. (1973). In both cases, however, no scores are available on the degree of desynapsis. In the present experiments somatic chromosome counts of more than 100 F_2 seedlings of the combinations 'Chinese Spring' × 'Lundi' and 'Chinese Spring' × 'Gaudenz' revealed 2.0% and 2.8% aneuploids, resp. Both figures are much lower than those reported in literature (l. c.). Due to the small absolute number of aneuploids no test of homogeneity of the differing ratios was applied. From additional F_3 counts of F_2 plants with a known desynapsis frequency, it is likely that there is no relationship between the two characters. It is plausible that 'hybrid desynapsis' should not be restricted to hexaploid wheats but is to be expected in tetraploid wheats and in triticales, too. THOMPSON and ROBERTSON (1930) reported on hybrids of tetraploid wheats and observed an increase of desynapsis. But until now only a few data are available which are based on comparable material. For that reason some preliminary crosses were performed using 'Chinese Spring' as the female and a small collection of tetraploid wheats of widely differing origin. Discounting the expected D genome univalents the pentaploid F_1 hybrids showed 'hybrid desynapsis', ranging from 10% to 26%. The distribution curve for desynapsis of ten hybrids analyzed was found to be continuous. The lack of high level desynapsis may be due either to sampling size or to the missing D genome pairing failures.

The increase of pairing irregularities in hexa- and octoploid triticale after hybridization of more or less homozygous parents is very common (MÜNTZING, 1939; MERKER, 1973; POHLER et al., 1978). In this connection it must not be emphasized that rye chromosome pairing failures are prevailing. In a special approach and by using the Giemsa staining technique POHLER et al. (1978) gave comparable estimates for the participation of wheat and rye chromosomes in desynapsis of reciprocal F_1 hybrids and their parents. The frequency of desynaptic cells including wheat univalents was in the hybrids about twice the parental figure and amounted to 12%. This is within the range of pairing failures of the tetraploid AABB level mentioned above.

Most of the results mentioned refer to euploid wheat. Special attention has, however, to be given to 'hybrid desynapsis' in monosomics. There is obviously considerable interaction between the major genes in disomic condition and modifying factors in the hemizygote state of monosomes. The variation of 'hybrid desynapsis' in monosomic F_1 hybrids, as shown in Fig. 5, is very common (SASAKI et al., 1963; COUCOLI and SKORDA, 1970; METTIN, 1970; GAIDALENOK and MAYSTRENKO, 1973; BANNIER 1978). The overall data give, however, no clear indication for the participation of particular hemizygous chromosomes, though mono-4B hybrids quite often surpass the disomic control in 'hybrid desynapsis'. On the other hand there seems to be one monosomic analysis which fits into the model of gene action presented in this study. COUCOLI and SKORDA (1970) analyzed the complete series of mono- 'Chinese Spring' × 'G 38290' hybrids and reported on 20 monosomic F_1 hybrids being with regard to 'hybrid desynapsis' more or less close to the disomic control, while mono-7B hybrids resembled the normal level of desynapsis of the parents. So the interference of desynapsis and monosomy needs further investigation.

Summary

1. Meiotic pairing failures most probably due to desynapsis are very common in heterozygous hybrids of wheat and triticale, while the more or less homozygous cultivars

show a nearly complete bivalent formation. Until now the genetic basis of this 'hybrid desynapsis' was not fully understood.

2. A screening of 64 intervarietal F_1 hybrids using 'Chinese Spring' as the common female parent revealed the existence of distinct levels of desynapsis which proved to be relatively stable in different years.
3. Progenies from F_1 hybrids with different levels of 'hybrid desynapsis' were scored individually. F_2 and F_3 segregations for desynapsis frequency can be explained best by assuming a monofactorial inheritance. The different levels of phenotypic expression are due to heterozygosity of at least two (possibly three) genes which have been designated *Hyd 1* and *Hyd 2* with the former being epistatic.
4. Attempts to localize the major genes *Hyd 1* and *Hyd 2* by monosomic analysis hitherto failed which might be due either to incompleteness of the two series analyzed or to some interference of character expression and hemizygosity of the major genes and a number of modifying minor factors.

Zusammenfassung

Ein Beitrag zur Genetik der „Hybrid-Desynapsis" bei *T. aestivum* L.

1. Heterozygote Bastarde von Weizen und Triticale weisen sehr häufig durch Desynapsis verursachte meiotische Paarungsanomalien auf, während homozygote Sorten nahezu vollständige Bivalentbildung zeigen. Über die genetischen Grundlagen dieser ‚Hybrid-Desynapsis' gibt es bisher noch keine klaren Vorstellungen.
2. Nach Herstellung und Durchsicht der F_1-Bastarde von 64 Sortenkreuzungen mit ‚Chinese Spring' als weiblicher Partner konnten deutlich verschiedene Ausprägungsgrade dieser Desynapsis ermittelt werden, die sich mehrjährig als weitgehend stabil erwiesen.
3. Die Nachkommen von F_1-Bastarden mit unterschiedlicher Ausprägung der ‚Hybrid-Desynapsis' wurden einzelpflanzenweise analysiert. Die in den F_2- und F_3-Generationen gefundenen Aufspaltungsverhältnisse können durch Annahme monogener Unterschiede am einfachsten erklärt werden. Das Merkmal manifestiert sich nur bei den Heterozygoten. Für die unterschiedlichen Ausprägungsgrade sind mindestens 2, vermutlich 3 Gene verantwortlich, für die die Symbole *Hyd 1* und *Hyd 2* vorgeschlagen werden. Das erstgenannte Gen wirkt epistatisch.
4. Die bisherigen Versuche, beide Gene mittels Monosomenanalyse zu lokalisieren, blieben erfolglos. Als Ursache kommt entweder die Unvollständigkeit der getesteten F_1-Serien oder die Überlagerung der Merkmalsausprägung durch Hemizygotieeffekte der major- oder weiterer minor-Faktoren in Frage.

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