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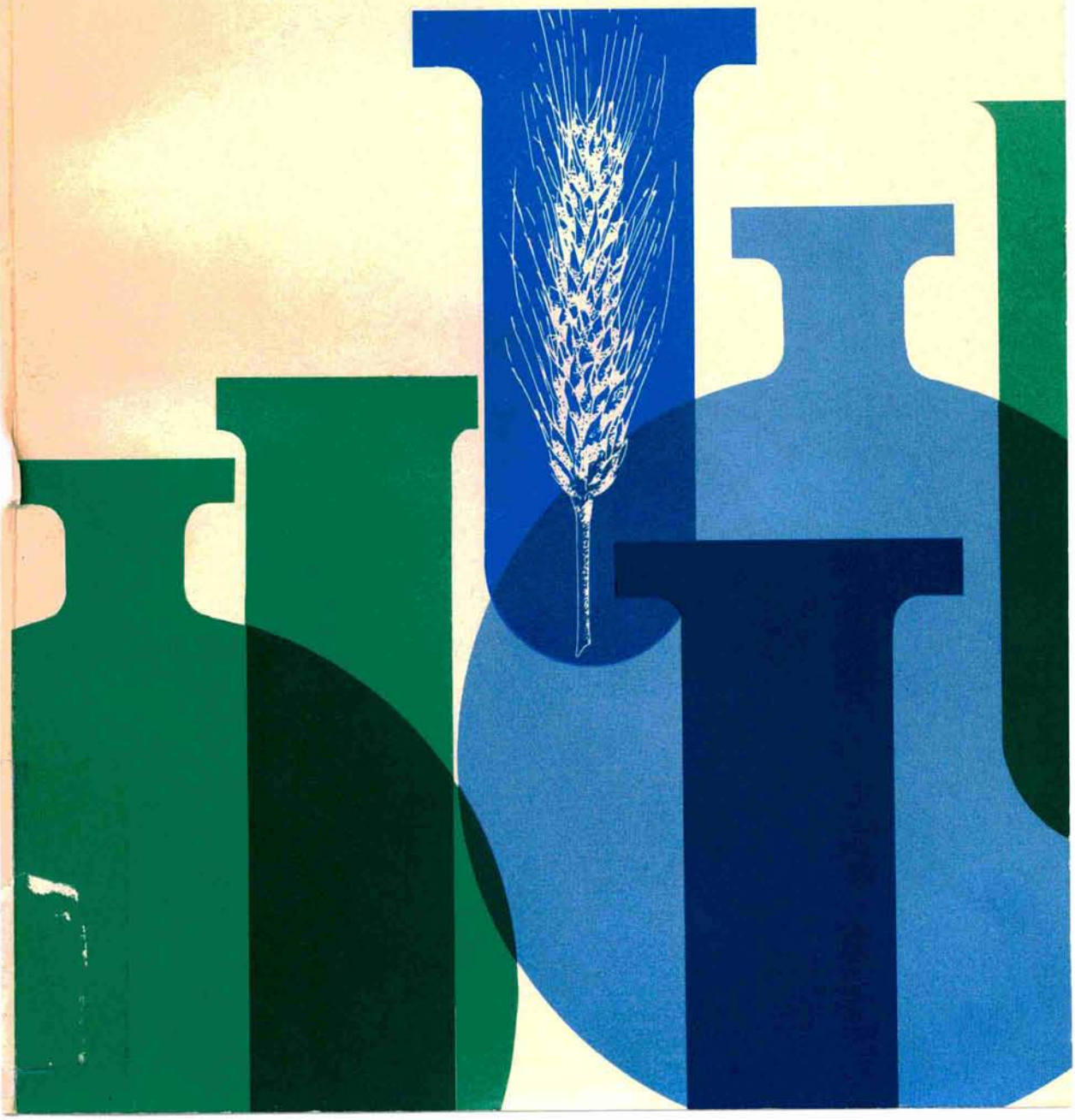
Editors: Reginald MacIntyre/Marilyn Campbell



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Editors: REGINALD MACINTYRE/MARILYN CAMPBELL

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Meiotic, Gametophytic, and Early Endosperm Development in Triticale

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Abstract Sterility in triticale may have several causes, including failure of meiotic and gametophytic development in either the anther or ovary, and failure of either embryo or endosperm development. Results are described showing that, in particular, failure of normal development in the ovary and the total abortion of early endosperm development contribute to sterility in triticale. Observations of nuclear and cellular behaviour are described in the young endosperm of Rosner triticale that are correlated with its total abortion (and hence sterility) in some florets, and may be correlated with the production of shrunken grain in other florets. A simple method is described for distinguishing between the chromosomes of rye (*Secale cereale*) and wheat (*Triticum aestivum*) in an octoploid triticale derived from them. There was a striking structural difference between the polynemic chromosomes of wheat and rye in mature antipodal cell nuclei. Each rye chromosome, but no wheat chromosome, had a prominent dark-staining body at one or both telomeres. The number and distribution of the dark-staining telomeric bodies in polynemic rye antipodal chromosomes appear to correlate with the number and distribution of telomeric Geimsa-staining bands in rye root-tip metaphase diploid chromosomes. The possible basis of genome incompatibility in triticale is discussed.

Résumé La stérilité du triticale peut avoir plusieurs causes, dont les accidents au cours de la méiose ou de l'évolution du gamétophyte, dans l'anthère, ou dans l'ovaire, et le non développement de l'embryon ou de l'endosperme. Selon les résultats des recherches, on constate notamment que le développement anormal de l'ovaire et l'avortement total du développement premier de l'endosperme contribuent à la stérilité chez le triticale. Selon les observations faites sur le comportement des noyaux et des cellules de l'endosperme jeune du triticale Rosner, ce comportement a un lien avec l'avortement total (et par conséquent la stérilité) de certaines fleurs, et peut en avoir un chez d'autres fleurs avec la production d'un grain ratatiné. L'auteur décrit une méthode simple permettant de reconnaître les chromosomes du seigle (*Secale cereale*) et ceux du blé (*Triticum aestivum*), dans un triticale octoploïde qui en est issu. On a constaté une différence structurale frappante entre les chromosomes polynémiques des noyaux d'antipodes adultes du blé et du seigle. Un ou deux télomères de chaque chromosome du seigle comportent une excroissance prenant une couleur sombre, mais non ceux du blé. Il semble que le nombre et la répartition de ces excroissances télomériques des chromo-

somes polynémiques des antipodes du seigle soient liés au nombre et à la répartition des bandes télomériques se colorant au giemsa des chromosomes diploïdes observés dans les méristèmes radiculaires du seigle lors de la métaphase. Le texte traite également de l'incompatibilité possible des génomes dans le triticale.

Two major problems have been encountered in triticale breeding. First, most allopolyploid triticale cultivars are "subject to reproductive disorganisation characterised by premature desynapsis of meiotic bivalents and aneuploid or inviable gametes" (Rupert et al. 1973). These result in sterility in some florets and consequently in reduced grain yield. Second, "triticale shows varying degrees of seed shrivelling" (Darvey 1973), and this too results in reduced grain yield. Cytological investigations of triticale chromosomes have been hampered by the lack of simple methods for distinguishing between wheat and rye chromosomes in somatic and meiotic cells. Rye chromosomes can be identified in a test plant from an analysis of chromosome pairing behaviour in F_1 plants obtained from crosses of the test plant with either wheat or rye (Gustafson and Zillinsky 1973; Mettin et al. 1973). A method for identifying rye chromosomes based on karyotype analysis of metaphase chromosomes in somatic cells has been suggested by Lelley (1973). Both methods are laborious and time consuming.

The objects of this paper are threefold: first, to describe observations of cell and nuclear behaviour in triticale possibly related to the causes of meiotic instability and grain shrinkage mentioned above; second, to describe a simple method for identifying the presence of rye chromosomes in test triticale and other genotypes; and third, to discuss briefly the possible basis of genome incompatibility in triticale.

Rates of Cell Development in Wheat, Rye, and Triticale

Studies of the total duration of the cell cycle in root-tip meristem cells of wheat, rye, and hexaploid triticale have not revealed any important differences. The cell cycle time at 20°C lasted 12.5 h in wheat (*Triticum aestivum*) (M. W. Bayliss, unpublished data); 12.0 h in hexaploid triticale (Kaltsikes 1971); and 11.5 (Kaltsikes 1971) and 12.1 h (M. D. Bennett, unpublished data) in rye (*Secale cereale*). Apparently the rates of somatic cell development in wheat and rye species are very similar. Consequently, differences between the developmental rates of wheat and rye chromosomes are unlikely to be a cause of genome incompatibility during somatic cell growth in triticale. As far as I am aware, no aberrant nuclear behaviour in somatic cells of triticale has been reported.

Studies of the rates of reproductive cell development, however, have revealed important differences between wheat, rye, and triticale genotypes (Bennett and Smith 1972; Bennett and Kaltsikes 1973). At 20°C meiosis in the diploid wheat *T. monococcum* (42 h) was shorter than in diploid *S. cereale* (51 h). Similarly, in the tetraploid wheats *T. dicoccum* (30 h) and *T. turgidum* var. *durum* (31 h) meiosis was shorter than in tetraploid *S. cereale* (38 h). Moreover, meiosis in hexaploid *T. aestivum* (24 h) was shorter than in the two hexaploid triticales, Rosner (34 h) and 6A190 (37 h). Thus, at the diploid, tetraploid, and hexaploid levels, meiosis was longer in plants containing rye genomes than in plants containing wheat genomes alone. The existence of these differences might lead one to expect aberrant nuclear behaviour during meiosis in triticale. Gross differences between the rates of meiotic prophase development of wheat and rye chromosomes in triticale as reported by Schkutina (1969) and Stutz (1962) are rare. However, the difference between the rate of meiotic development of rye chromosomes in *S. cereale* and the rate of development of the same chromosomes in triticale might be a major cause of meiotic instability in triticale.

For example partial chromosome pairing failure in octoploid triticale may be caused by the difference between the durations of zygotene and pachytene in octoploid triticale

and the durations required by rye chromosomes for normal meiotic behaviour (Bennett et al. 1971). Bennett and Kaltsikes (1973) also showed that in diploid and tetraploid rye and in hexaploid triticale the proportion of the total meiotic time taken by zygotene and pachytene together (about 40%) differed from the proportion of meiosis that they took in hexaploid wheat and octoploid triticale (about 25%). It was concluded, therefore, that such proportional differences may be causally correlated with differences in meiotic stability of rye chromosomes in triticales of different ploidy levels.

Female Meiosis and Embryo Sac Development in Triticale

In triticale, as in related species, each floret contains several hundred pollen mother cells (PMC) but only a single embryo sac mother cell (EMC). Consequently, meiotic failure in a single EMC inevitably results in a sterile floret whereas meiotic failure in a PMC merely reduces the number of pollen grains produced by four. Using nullisomic lines in *T. aestivum*, Sears (1954) showed that the absence of just a single chromosome can produce a high frequency of female sterility. Thus, the loss of even a single chromosome due to meiotic instability could cause female sterility in triticale.

Meiotic chromosomes behaviour and gametophyte development in triticale has usually been studied in anthers. However, because of the importance of female meiosis and embryo sac development, a pilot experiment to study these processes was carried out using an octoploid triticale (Chinese Spring × King II). Using the method described by Bennett et al. (1973), ovules were examined from florets at, or close to, anther dehiscence to see what percentage of embryo sacs had undergone normal development. In about 15% of the florets examined the embryo sac had failed to develop and the ovule contained only undifferentiated parenchymous cells. A further 10% of the embryo sacs contained no egg cell and the polar body consisted of three fused haploid nuclei instead of two (Fig. 1). Since the method used detected only grossly aberrant embryo sac development, the actual proportion of florets incapable of being fertilized was probably much higher than 25%. Detailed studies of the incidence of aberrant female meiotic and gametophytic development are needed so that the contribution of misdevelopment in these processes to the problem of sterility in triticales can be estimated.

Rates of Normal Endosperm Development

The rates of embryo and endosperm development were measured in plants grown at 20°C with continuous illumination (Bennett et al. 1973). In hexaploid wheat (Chinese Spring), diploid rye (Petkus Spring), hexaploid triticale (Rosner), and octoploid triticale (Chinese Spring × King II) the pollen tube penetrated the embryo sac about 30 min after pollination and sperm nuclei reached the egg nucleus and the polar nuclei about 40 min after pollination. Mitosis occurred in the primary endosperm nucleus about 6 h after pollination whereas in the zygote it occurred about 22 h after pollination. By 24 h after pollination the endosperm contained 16 or 32 nuclei in *T. aestivum* and *S. cereale*, whereas in the 6x and 8x triticales it contained 16 nuclei. Thus, the nuclear doubling times were very similar (between 4.5 and 5.5 h) in the endosperms of all four genotypes during this period.

During the first 5 days after pollination the pattern of endosperm development in rye and triticale is essentially similar to that described for *T. aestivum* var. Chinese Spring (Bennett et al. 1973). Initially the endosperm is coenocytic but after 3 days it becomes cellular. During the coenocytic phase nuclear development is highly synchronous but becomes progressively less so. The nuclear doubling time slowly increases from an initial time of 4.5–5.5 h to reach about 8–10 h by the onset of cell wall formation but thereafter it is greatly increased. The rates of embryo and endosperm development in florets of *T. aestivum* and hexaploid triticale Rosner with normal development were very similar (Table 1).

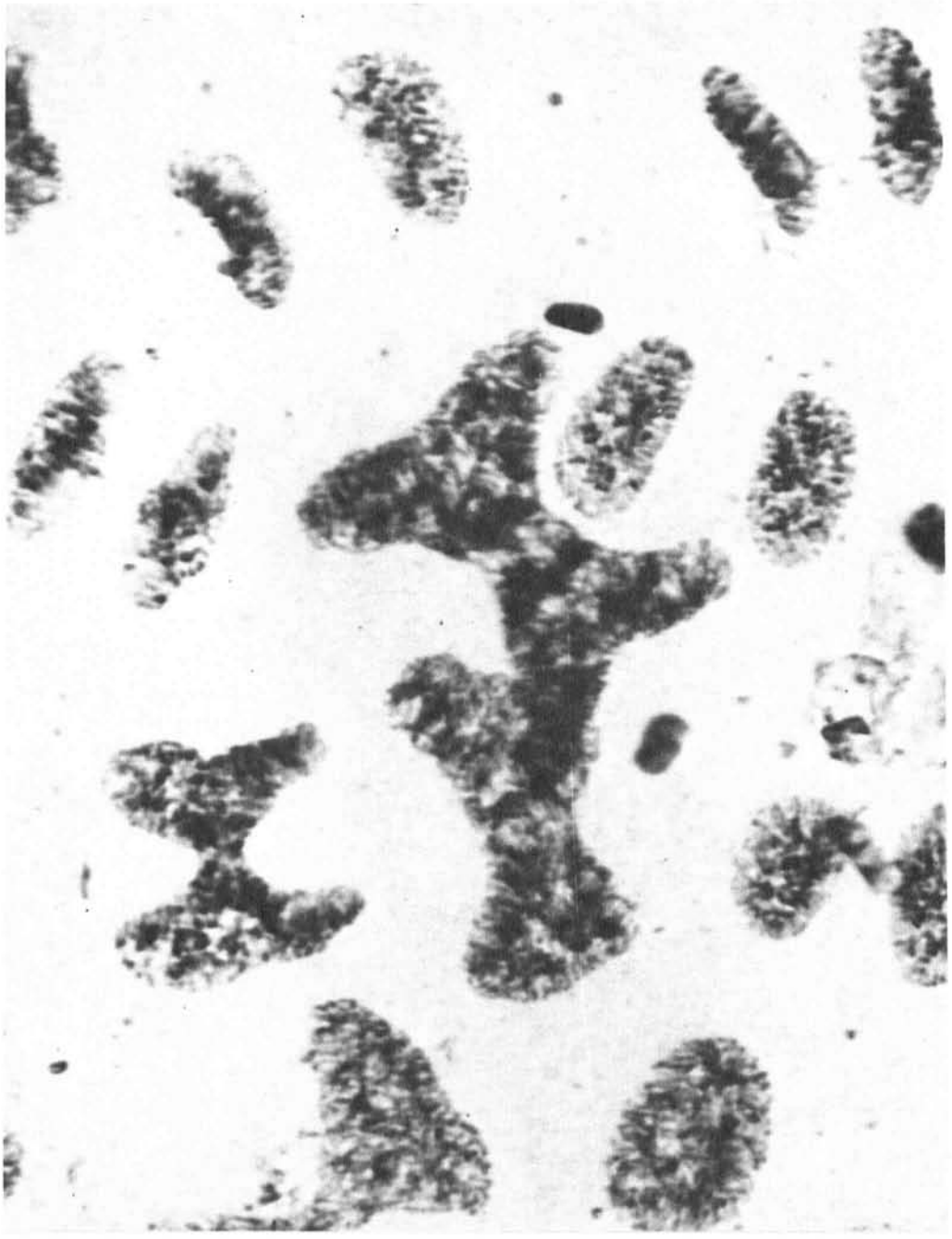

FIG. 1. Feulgen-stained Rosner triticale endosperm nuclei fixed 72 h after pollination. Normal nuclei, polyploid butterfly-shaped nuclei, and micronuclei are seen. Note the bridge of chromatin joining one pair of otherwise normal nuclei.

TABLE 1. Mean number of embryo and endosperm cells (or nuclei) at various times after pollination in hexaploid wheat and triticale grown at 20°C with continuous illumination.

Days after pollination	Genotype: *Triticum aestivum* (Chinese Spring) Embryo	*Triticum aestivum* (Chinese Spring) Endosperm	Triticale (Rosner) Embryo	Triticale (Rosner) Endosperm
1	2	16	2	16
2	8	276	4	128
3	16	876	15	1024
5	232	>10,000	153	>10,000

Aberrant endosperm nuclei containing more than the normal 6*C* DNA content occur at low frequencies in developing endosperm sacs of many cereal species (Moss 1970) especially in the neck of the endosperm near the proembryo. Examination of feulgen-stained endosperm sacs from florets fixed 3–4 days after pollination revealed the presence of a few such nuclei in some endosperms of Chinese Spring, Petkus Spring, and Rosner. The incidence and size of such nuclei was greatly increased in a significant number of florets in Rosner triticale but never in hexaploid wheat or diploid rye. A detailed study of the development of aberrant polyploid nuclei in Rosner endosperm was made.

Aberrant Endosperm Development in Rosner Triticale

In normal Rosner endosperm the nuclei remain synchronous in development until the 512 nuclear stage reached about 64 h after pollination. By 24 h after pollination a few Rosner endosperms exhibited abnormally asynchronous nuclear development, and by 48 h after pollination some endosperms displayed pronounced asynchronous nuclear development. Such asynchrony was never observed in Chinese Spring wheat or Petkus Spring rye, and did not occur in most florets of Rosner triticale. Aberrant polyploid endosperm nuclei were first observed in Rosner endosperms fixed 48 h after pollination. They were larger than the normal triploid endosperm nuclei and contained up to four times the normal 6*C* DNA content. Aberrant nuclei were sometimes sub-spherical but usually they were butterfly- (Fig. 1) or dumbbell-shaped and composed of two equal or unequal chromatin masses joined by one or more chromatin bridges (Fig. 2). At increasingly later times, between 48 and 120 h after pollination, aberrant endosperm nuclei were detected with increasingly greater sizes and DNA contents. Some endosperm sacs fixed 96 or 120 h after pollination contained one or two giant aberrant nuclei with at least 100 times the normal 6*C* DNA content of endosperm nuclei (Fig. 3). Some of these giant aberrant nuclei were so large as to be visible to the naked eye in feulgen-stained embryo sacs dissected from florets fixed 5 days after pollination. Observations of endosperm sacs containing giant aberrant nuclei showed that the remainder of the normal endosperm nuclei had either already aborted and disintegrated, or were in the process of doing so. The development of the associated proembryo was normal, however. It was concluded that the presence of giant aberrant nuclei causes the death of the endosperm but not necessarily of the embryo.

Aberrant nuclei, usually in groups, were observed throughout the endosperm. They were, however, most often found in the neck of the endosperm just below its junction with the proembryo. Cell wall formation often occurred later in normal endosperms than in endosperms containing aberrant nuclei with 2–16 times the normal DNA content. Thus, in florets fixed 72 h after pollination, cellular endosperms were found that contained 256–512 cells including some with aberrant nuclei. Normal endosperms contained about 1024 nuclei and were not yet completely cellular at this time.

Polyploid endosperm nuclei are formed after either the omission of mitosis between successive phases of DNA synthesis, or failure of anaphase during mitosis. The latter was frequently observed in Rosner triticale; how-

FIG. 2. A feulgen-stained Rosner triticale endosperm nucleus fixed 72 h after pollination. Two daughter nuclei that failed to separate at the previous telophase remain attached by several strands of chromatin.

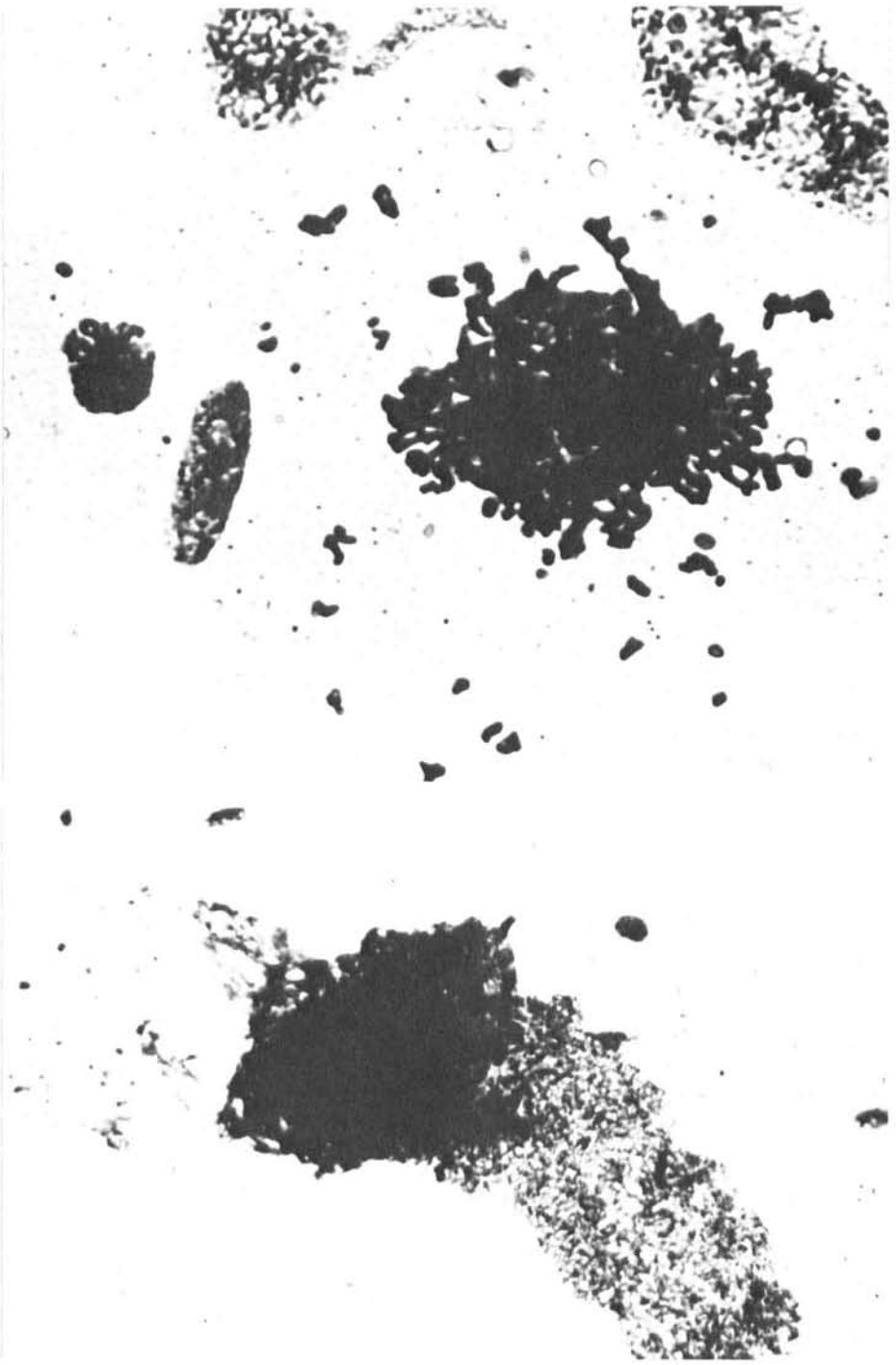

FIG. 3. Feulgen-stained Rosner triticale endosperms fixed 96 h after pollination showing an abberrant polyploid restitution nucleus containing about eight times the normal 6*C* DNA content (*top*), and a giant restitution nucleus containing at least 100 times the normal 6*C* DNA content of endosperm nuclei (*bottom*). Traces of aborted normal endosperm nuclei are seen.

ever, the former may also have occurred. Bridges connecting partially separated daughter nuclei formed at mitosis were often seen in the coenocytic endosperm of triticale. The formation of bridges between nuclei at telophase in a coenocytic tissue has different consequences for further development than their formation in a cellular tissue. In a cellular tissue, the bridges would be pinched off by the developing cell wall and the daughter nuclei would be isolated in single cells. In a coenocyte, however, the bridges remain unbroken so that restitution nuclei with double ploidy level are formed. Furthermore, the aberrant nuclei produced in endosperms are not isolated from normal nuclei by cell walls, nor from the supply of metabolites necessary for their further development.

Observations of aberrant nuclei in Rosner showed that once produced they continued to undergo DNA synthesis at normal intervals. Consequently, their size and DNA content doubled with each successive round of DNA synthesis. Thus an increasingly abnormal product of a single misdivision remained unisolated from normally developing endosperm nuclei until the time of cell wall formation. It seems, therefore, that the time of the initial misdivision during the coenocytic stage is important in determining its effect on subsequent endosperm development. If the initial misdivision occurs early in the coenocytic stage, so that many rounds of DNA synthesis are completed before cell walls are formed, then the resultant giant polyploid nuclei causes the death of the endosperm. If, however, the initial misdivision occurs late during the coenocytic stage, so that only a few cycles of DNA synthesis are completed before the aberrant nucleus is isolated by a cell wall, then the death of the entire endosperm need not result. Instead, the cells with polyploid endosperm nuclei may themselves die. Thus, in cellular endosperms fixed 120 h after pollination, patches of cells containing dead or aborting aberrant polyploid nuclei were seen, yet the surrounding cells appeared to be developing normally. The death during early seed development of a patch of endosperm cells would presumably result in reduced later development of a part of the endosperm. It is suggested, therefore, that the death of patches of cells with aberrant nuclei formed late in the coenocytic stage might be a cause of shrunken endosperm in triticale. Further experimental investigations of this hypothesis are required and are being undertaken at Cambridge.

The production of polyploid nuclei during the coenocytic stage of endosperm development is certainly a cause of sterility and may be a cause of shrunken grain in triticale and may therefore be the principal factor causing both the major problems facing triticale breeders.

The cause of aberrant polyploid nuclear development in endosperm appears to be the development of abnormal asynchrony between adjacent nuclei within the coenocyte. Such asynchrony can, and sometimes does, develop in the coenocytic endosperm of most cereals and results in the production of polyploid nuclei. However, in triticale it occurs earlier in development, and in a greater proportion of florets than in wheat or rye, probably because of increased stresses caused by genome incompatibility during coenocytic development in triticale compared with established nonhybrid genotypes.

Cytological Identification of Rye Chromosomes

Use of Antipodal Cell Nuclei

Bennett et al. (1973) made a detailed study of the development of antipodal cells in the embryo sac of *T. aestivum* var. Chinese Spring. In plants grown at 20°C the chromosomes in antipodal cell nuclei became highly polynemic during the 5 days prior to anther dehiscence. During this period the DNA content of antipodal cell nuclei increased from the haploid (2*C*) amount to between 64 and 256*C* amounts. In feulgen-stained ovules fixed shortly after pollination, each of the 21 chromosomes could be counted in some squashes of antipodal cells. Each polynemic chromosome consisted of a dense darker staining centromeric region with chromosome arms formed of less dense, loosely organized bunches of feulgen-positive

threads on either side. In intact, unsquashed, antipodal cell nuclei the chromosomes were always arranged in a constant pattern which the nucleus. The 21 denser centromeric regions were located at one pole of the nucleus whereas the less dense chromosome arms radiated toward the opposite pole over and around the centrally located nucleoli. Although the centromeric thickenings were denser than the chromosome arms, they were nevertheless completely composed of feulgen-positive threads.

Studies of antipodal nuclei in rye (*S. cereale* var. Petkus Spring and Prolific) revealed a similar pattern of antipodal cell development to that found in wheat. However, a marked difference was observed between the appearance and distribution of DNA in polynemic chromosomes of wheat and rye. Unsquashed antipodal cell nuclei from newly fertilized embryo sacs of rye contained not only the haploid number (7) of darkly stained centromeric regions grouped at one pole of the nucleus but also at least eight and sometimes nine spherical or sub-spherical feulgen-positive, heteropycnotic bodies. The bodies ("rye bodies") were located at, or near, the ends of the chromosome arms and hence near the opposite pole of the nucleus from that near the seven centromeric regions. Squash preparations of feulgen-stained antipodal cell nuclei showed that these bodies differed from the centromeric regions in several obvious respects. The rye bodies were denser and darker staining and had a more distinct outline; they were spherical or sub-spherical and appeared to be solid rather than composed of threads; often, however, they contained one or more small unstained vacuoles. The most obvious difference between the rye bodies and centromeric regions was that the rye bodies were located at or near telomeres whereas the centromeric regions were of median position. Estimates of the DNA content of the rye bodies showed that they each contained up to about 4% of the haploid rye genome so that together they may contain about 32% of the nuclear DNA.

It seemed possible that the presence or absence of rye bodies might prove useful in establishing a method for identifying the presence of rye chromosomes in triticale. The distribution of rye bodies was investigated in mature feulgen-stained antipodal cell nuclei of various wheat, rye, triticale, and other genotypes. The following results were obtained:

1. Rye bodies do *not* occur in hexaploid wheat (*Triticum aestivum* var. Chinese Spring and Holdfast). They *do* occur in some other diploid, tetraploid, and hexaploid wheats.
2. The presence of up to eight or nine rye bodies was demonstrated in several plants of *Secale cereale* var. Petkus Spring and Prolific and also in *S. montanum*. Observation of autotetraploid *S. cereale* revealed the presence of up to 16 rye bodies in antipodal cell nuclei.
3. Both a hexaploid triticale (Rosner) and an octoploid triticale (Chinese Spring × King II) were examined. Up to eight rye bodies were observed in antipodal nuclei of the former (containing 14 wheat and seven rye chromosomes) and the latter (containing 21 wheat and seven rye chromosomes). The development of rye bodies is therefore not suppressed in triticale hybrids.
4. Antipodal cells were examined from each of the seven disomic addition lines of known King II rye chromosomes to Holdfast breadwheat. In these plants the haploid antipodal nuclei should contain 21 wheat chromosomes plus a single known rye addition chromosome. It was shown that antipodal cells of each of the seven rye addition chromosomes contained a single obvious rye body, with the exception of addition chromosome V, which contained two rye bodies. In this way it was established that each rye chromosome bore a single large rye body, with the exception of chromosome V, which bore two. Furthermore, observations in rye addition line plants showed that each rye body was located at, or very near, the telomere of one chromosome arm. On chromosome V, however, one rye body was apparently located at the end of either chromosome arm.

5 Antipodal cells were examined from each of the available ditelocentric addition lines of King II rye chromosomes to Holdfast wheat. Unfortunately, ditelocentric addition lines were available for only one arm of chromosomes V, VI, and VII. Results obtained (Table 2) for six out of the seven rye chromosomes agree with those obtained for whole addition chromosome lines. Thus, rye bodies are located on the short arm of chromosomes I, II, and IV but not on the long arm. Presumably rye bodies are located on the short arm but not the long arm of chromosome VII, and on the long arm but not the short arm of chromosome VI, and one on each arm of chromosome V. The results obtained for telocentrics of the supposed α and β arms of chromosome III were unexpected, since both apparently carried a single rye body. The significance of this result will remain unclear until further tests have been carried out on further ditelocentric lines for both arms of this chromosome.

TABLE 2. Distribution of rye bodies in ditelocentric addition lines of King II rye chromosomes to Holdfast wheat.

Chromosome no.[a]	Long arm[b]		Short arm[b]	
	Genotype	No. rye bodies	Genotype	No. rye bodies
I	(C3)	None	(C17)	1
II	(A24)	None	(H1/6/23)	1
III	(T3)	1	(H2/11)	1
IV	(G25/30)	None	(G25/17)	1
V	(24B/48)	1	–[a]	–
VI	–[a]	–	(H3/4)	None
VII	(H1/16/L)	None	–[a]	–

[a]The numbers of rye chromosomes are those given by Riley (1960).

[b]Chromosomes III and V have telocentrics that are not distinguishable as long or short. For these two chromosomes the α arm is arbitrarily placed with the long-arm telocentrics of the remaining chromosomes.

Use of Giemsa Stain

Giemsa staining techniques have been developed recently that reveal characteristic banding patterns in plant and animal chromosomes (Pardue and Gall 1970; Schweizer 1973) and that, therefore, are useful for karyotype analysis. It seemed reasonable to investigate whether the presence of the chromatin that forms the rye bodies in polynemic chromosomes of antipodal cells could be demonstrated in diploid somatic cells using the Giemsa techniques mentioned above. Although only preliminary results are available it seems useful to mention them here.

Using root-tip meristem cells treated with a Giemsa staining technique (modified from Vosa and Marchi 1972) the following results have been obtained: (*1*) no Giemsa bands were detected at the telomeres of any chromosome in hexaploid wheat (Chinese Spring) chromosomes; however, dark-staining Giemsa bands were found in diploid rye (Petkus Spring) chromosomes; (*2*) all the Giemsa bands seen in rye chromosomes were located at the telomeres; and (*3*) most rye chromosomes had a Giemsa band at only one telomere; however, up to four chromosomes per cell were observed that had Giemsa bands at both telomeres.

Further experiments are being conducted to determine the distribution of Giemsa bands within the rye karyotype using addition lines of King II rye chromosomes to Holdfast wheat. It seems possible from the preliminary results that the distribution of Giemsa bands in rye diploid somatic chromosomes may be the same as the distribution of rye bodies in polynemic rye antipodal cell chromosomes.

The presence of distinct rye bodies on one or both telomeres of each rye chromosome but not of any *T. aestivum* wheat chromosome may offer a simple screening method for determining the presence or absence of whole rye chromosomes in triticale and other genotypes and also perhaps for counting the number of rye chromosomes. Furthermore, the presence of two rye bodies on chromosome V may allow this chromosome to be distinguished from other rye chromosomes.

Each floret in triticale contains about 20 or 30 antipodal cells and these are available for investigation for at least 48 h starting from anther dehiscence. Compared with first metaphase of meiosis, which lasts less than 2 h at 20°C (Bennett and Smith 1972), antipodal cell nuclei are more readily available for study.

Basis of Genome Incompatibility

It has already been noted that the DNA content of the diploid rye genome is much greater (by about 34%) than the largest diploid genome in hexaploid or tetraploid wheat. Furthermore, the rye chromosomes have a higher mean DNA content than wheat chromosomes. It has also been shown that the distinctive chromatin that forms the rye bodies may constitute about 32% of the total rye genome. It is possible that much of the extra DNA possessed by rye compared to diploid wheat is contained in the rye bodies located at eight or nine of the 14 telomeres in the haploid rye complement.

Comparison of cell cycle studies in wheat and rye shows that the mean percentage of the cell cycle taken by DNA synthesis (*S*) is about one-third longer in rye than in wheat (Bennett, unpublished data). It has been shown (Lima-de-Faria and Jaworska 1972) first, that in diploid rye the duration of *S* is proportional to chromosome length, and second, that the last third of the *S* phase involves DNA synthesis occurring only at the telomeres in what is probably heterochromatin (Lima-de-Faria and Jaworska 1972; Darlington and Hague 1966). Ayonoadu and Rees (1973) recently suggested that only one telomere on each chromosome in rye is heterochromatic.

The distribution of cytologically distinct chromatin forming rye bodies is apparently identical with that of late-replicating heterochromatic DNA segments in rye chromosomes. Wheat chromosomes bear neither rye bodies nor obvious heterochromatic segments at their telomeres. It is suggested, therefore, that genome incompatibility in triticale, manifested both in meiocytes and coenocytic endosperm, is caused by the presence of a large segment of late-replicating heterochromatin at the telomeres of rye chromosomes but not of the much smaller chromosomes of wheat.

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