Theor Appl Genet (1986) 72:721–734

Review

Rye cytology, cytogenetics and genetics – Current status

R. Schlegel [1], G. Melz [2] and D. Mettin [1]

[1] Zentralinstitut für Genetik und Kulturpflanzenforschung, Akademie der Wissenschaften der DDR, DDR-4325 Gatersleben, German Democratic Republic
[2] Institut für Pflanzenzüchtung, Akademie der Landwirtschaftswissenschaften der DDR, DDR-2601 Gülzow-Güstrow, German Democratic Republic

Received August 10, 1985; Accepted April 20, 1986
Communicated by P. L. Pfahler

Table of contents

1 Summary. Progress in rye karyology is reviewed with respect to chromosome structure, recognition and chromosome nomenclature. Considerable contributions have been brought about by molecular techniques which have even revealed nucleotide sequences of some of the ribosomal DNA. DNA sequence organization correlates with the distribution of major Giemsa C-band regions as well as with N-bands and the binding sites of fluorescent dyes. The several banding patterns permit the classification of rye chromosomes. The increased data and widespread application of banding analysis require a consistent system of chromosome and/or band designation. Therefore, a standard band nomenclature is proposed with reference to the recommendations of the 'Paris Conference on Standardization in Human Cytogenetics'. In addition, advances in genetics are summarized and discussed. Based on the original accepted standard karyogram and banding patterns of the rye chromosomes, meanwhile, 120 genes determining several characters have been associated with individual chromosomes and/or chromosome arms, including linkage studies for about 19 arrangements. Most results were obtained using wheat-rye addition lines as well as test crosses with defined translocations. Moreover, genetical studies based on appropriate trisomic and telotrisomic material resulted in the localization of 19 genes, including their linkage relationships.

Key words: Nuclear cytology – C-banding – Chromosome nomenclature – Gene localization – Trisomics – Rye

2 Introduction

The development and utilization of new techniques in genetic analysis, karyotype identification and chromosome manipulation, and the elucidation of homoeologous relationships in the *Triticinae* have greatly contributed to our present understanding of the cytogenetics of rye.

Our knowledge of rye genetics, for a long period far behind other diploid crops, is progressing and gradually becoming useful for breeding. While Jain (1960) in his review article stated that the genetics of rye had not received so much attention and that simple markers were hardly available, genetic and cytological markers for all seven rye chromosomes are now available.

The following presentation aims at summarizing the hitherto known data on molecular genome structure, chromosome recognition and symbolization, and includes a proposal for a uniform nomenclature. They will be supplemented by the present status of gene

analysis, gene localization and linkage relationships which were carried out using rye aneuploids, translocations as well as wheat-rye substitutions or additions.

3 Genome characterization of rye

3.1 Molecular structure of the genome

The 1*C* DNA content of the rye genome is 9.5 pg (Bennett and Smith 1976). Using the data for mean rye chromosome length published by Gustafson and Bennett (1976), the 1*C* DNA content of individual rye chromosomes should range from about 1.2 to 1.4 pg considering that chromosome length and DNA content are directly proportional. Only 10–20% of the genome can be assigned, biochemically, to the major part of the genome which belongs to the repeated sequence category (Ranjekar et al. 1974; Smith and Flavell 1977). The kinetic analysis of genome organization has revealed that repeated sequences are, in general, interspersed among unrepeated sequences. The discovery of a very rapidly reannealing class of DNA sequence provided useful information about specific regions of the genome. In rye this class of DNA constitutes 4–10% of the genome and although it is believed to be composed largely of sequences capable of renaturation, this class also contains long tandem arrays of simple, repeated sequences (Appels 1982; Appels et al. 1978). Ranjekar et al. (1974) were the first to demonstrate several boyant density components in a fraction of DNA renaturing with a density of 0–0.1 (10–12% of the genome). However, the predominant component was a well-defined species at 1.702 g/cc in a CsCl-gradient. Smith and Flavell (1977) considered this class of DNA to consist mainly of palindromic sequences which are distributed in clusters throughout at least 30% of the genome. DNA, with a mean fragment length of 500 bp, was fractionated by Appels et al. (1978) to allow recovery of a very rapidly renaturing fraction (C_0t 0–0.2). This DNA was shown to contain several families of highly repeated sequence DNA. Two of them were purified which resulted in a fraction renaturing to a density of 1.701 g/cc and comprised 0.1% of the total genome, and the other polypyrimidin tract DNA which comprised 0.1% of the genome.

Further hybridization studies between wheat, rye, barley, and oat DNAs have shown that 22% of rye DNA are species-specific repeated sequences (Rimpau et al. 1978) that have probably arisen by the amplification of single copy DNA since species divergence (Flavell 1982). Bedbrock et al. (1980); Appels (1982); Appels et al. (1978); Appels and Morgan (1984) and Hutchinson et al. (1980) have described the physical properties, sequence divergence and chromosomal distribution of altogether twelve different DNA sequences highly specific in detecting rye chromosome segments. These are located predominantly within blocks of constitutive telomeric heterochromatin of the seven rye chromosomes.

In addition, the nucleotide sequence of a major repeat family was reported for the first time (Appels et al. 1981). The –3 to 646 bp sequence cloned in *pSc* 7235 was established using a standard procedure of 8 restriction enzyme fragments. It contains 21 tracts of pyrimidines 5–10 residues long and the sequences

5′ AACATTTTTTGAA 3′ and 5′ AAATTTGA 3′
3′ TTGTAAAAAACTT 5′ 3′ TTTAAACT 5′

are repeated twice and three times, respectively.

3.2 Chromosome banding and chromosome structure

The distribution of very rapidly renaturing sequences correlates with the distribution of the major C-band regions (Appels et al. 1981; Gerlach and Peacock 1980; Jones and Flavell 1982). Nevertheless, the nature of the contribution of DNA composition to C-banding is still uncertain. The use of molecules with a defined base specifity of binding, combined with counterstaining with a compound of complementary base specifity, does not reveal the terminal heterochromatic regions of rye chromosomes (Schweizer 1979). This lack of a distinctive base composition of the heterochromatic regions compared to the remaining genome is consistent with the fact that the very rapidly renaturing sequences fail to be resolved as boyant density satellites in various types of cesium salt gradients (Appels 1983).

The rDNA region, however, is revealed by base-specific fluorescent compounds with a well-defined genomic structure, as the 5S RNA genes which are located in the nucleolus organizer region (NOR) of rye chromosome 1R. The mitotic chromosomes were stained with chromomycin A and counterstained with distamycin A and DAPI. The NORs exhibited very bright fluorescent bands (Schweizer 1979). By using chromomycin A only narrow quenched regions appear (Fig. 1). Corresponding DNA can be isolated as a boyant density satellite in actinomycin-D/CsCl and can also be partly sequenced as GGATGCGATACCATC-AGCACTAAAGCACCGGATCCATCAGAACTCCG-AAGTTAAGCGTGCTTGGGCGAGAGTAGTACTA-GGATGGGTGACCTCCTGGGAAGTCCTCGTGTT-GCATCCT (Appels 1982).

Hoechst 33258 and DAPI are the only fluorescent compounds to date which preferentially stain rye heterochromatin (Sarma and Natarajan 1973; Schlegel and Gill 1984, unpublished; Fig. 2). These dyes appear to have a greater requirement with respect to the sequence of DNA to which it will bind. The sequencing of a major heterochromatic sequence has shown a predominance of three and more adjacent A-T pairs

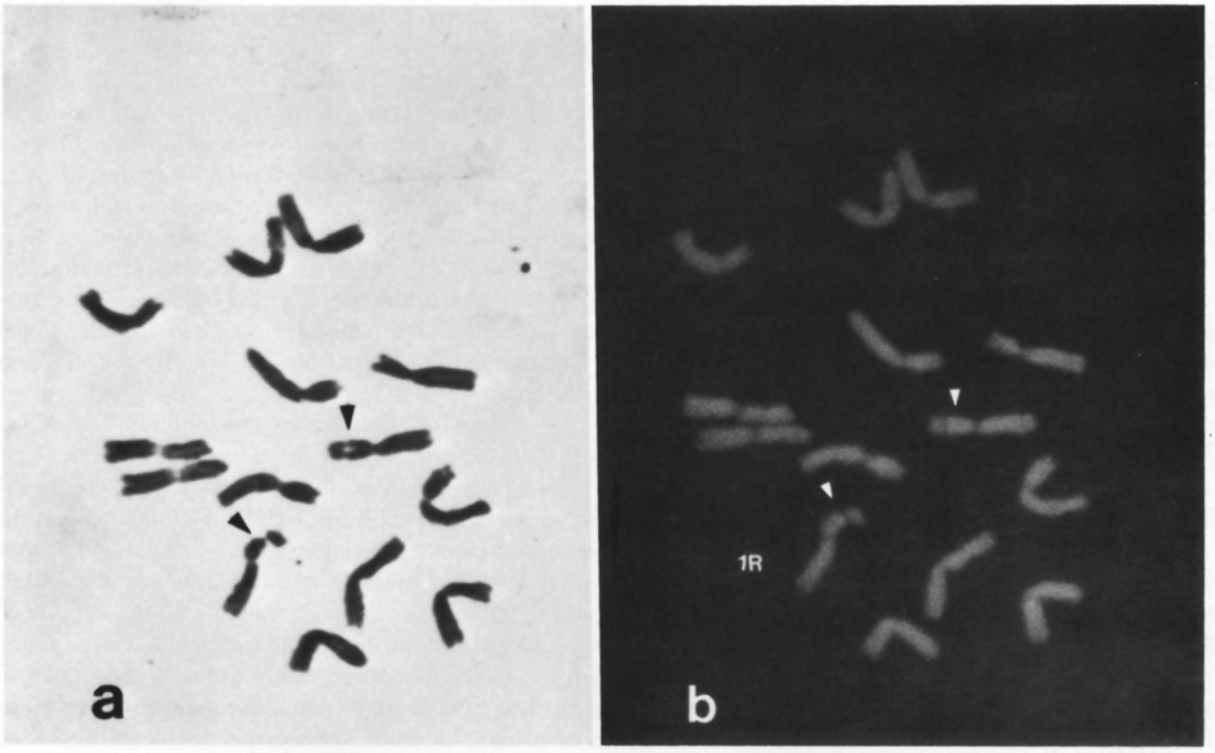

Fig. 1. Sequential staining of somatic rye chromosomes by aceto-carmin (**a**) and the G-C specific fluorescent dye chromomycin A (**b**)

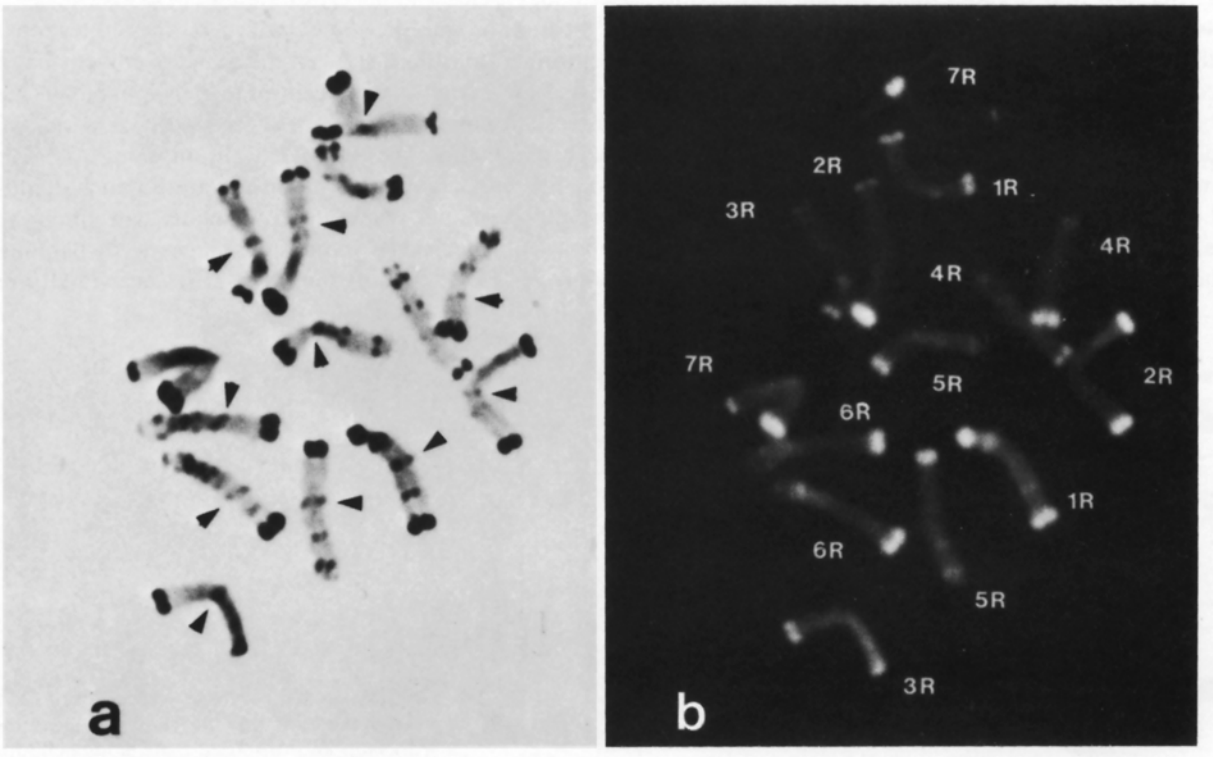

Fig. 2. Sequential staining of somatic rye chromosomes by Giemsa C-banding (**a**) and the A-T specific fluorescent dye 4′-6-diamidino-2-phenylindole, DAPI (**b**)

which could account for the reason why Hoechst 33258 and DAPI preferentially stain these regions.

Observations on sequential C- and N-banding (Schlegel and Gill 1984) revealed the heterogeneity of heterochromatin. Because prominent N-bands occupy positions where faint C-bands will often be observed and where all other minor and major C-bands disappear, it indicates at least two classes of heterochromatin in rye chromosomes. Thus, the observed heterochromatic regions marked by the N-bands, as well as C-bands, can be described as C- and N-banding positive (C^+N^+), while the remaining are C-banding positive and N-banding negative (C^+N^-). Dennis et al. (1980) and Gerlach and Peacock (1980) have noted the correspondence of N-bands and satellite DNA (GAA)m (GAG)n locations in barley and wheat. It is highly probable that site locations of (GAA)m(GAG)n satellite DNA correspond to N-bands observed in rye and are located on rye chromosome 2R, 3R, and 6R. If this is correct, it is significant to note that in cereal species so far examined, N-bands only reveal (GAA)m(GAG)n sequence DNA. On the other hand, C-bands reveal additional heterochromatin that does not contain (GAA)m(GAG)n sequence DNA.

3.3 Chromosome banding and identification of rye chromosomes

During the past four decades quite a number of publications have been devoted to the description and classification of rye chromosomes. These attempts originated for karyological reasons and the results were used to identify linkage groups. Accordingly, the various workers tried to establish a uniform chromosome nomenclature system. However, all of the conventional procedures used do not account perfectly for the normal variation of chromosome morphology in rye populations.

A first comparative banding analysis proved to be a valuable tool with which to recognize rye chromosomes in more detail. So, it seemed possible to relate the hitherto known systems of chromosome designation to the homoeology classification via comparative chromosome morphology and heterochromatin pattern (Schlegel and Mettin 1982). The 'Chinese Spring-Imperial' wheat-rye addition series, thus, has been proposed as a standard series of rye chromosomes. It was confirmed during the '1st International Workshop on Rye Chromosome Nomenclature and Homoeology Relationships' (Sybenga 1983) and reaffirmed in 1985 during the '2nd Workshop'.

The C-banding patterns of the individual chromosomes of the series have been carefully determined (Fig. 3). Derived from these patterns a generalized karyogram was established which includes 'common' Giemsa C-bands occurring in the majority of genotypes analysed so far, and all additional bands for which accurate references were presented.

Since 1982 no further evidence for other prominent minor C-bands have been found in the literature. Only by introduction of the N-banding procedure were three chromosomes additionally marked (Schlegel and Gill 1984). Chromosome 2R showed a small band near the centromere in the long arm.

Chromosome 3R, which, along with 1R, is one of the smallest chromosomes, showed a band in the short arm that is closer to the centromere than in 2R.

Chromosome 6R, characterized by the subterminal centromere position, showed the most prominent band in the long arm near the centromere. The bands in the three chromosome pairs are always seen as a dot on each chromatid. The unbanded chromosomes are 1R, 4R, 5R, and 7R. It is of interest to note that N-bands occupy positions where faint C-bands can often be observed. The results imply advantages to N-banding analysis. First, all of the N-bands discovered are

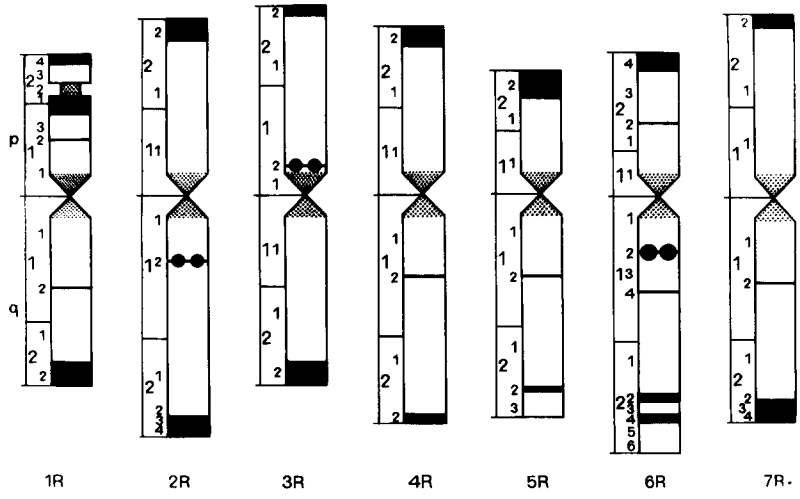

Fig. 3. Standard karyogram according to the recommendation of the Rye cytogenetics Workshop and proposed band nomenclature of rye chromosomes (*black dots* mark N-bands)

located in regions of chromosome arms which are not covered by heavy C-bands. Thus, they can be used as additional markers for those chromosomal regions. Of special importance is the consistent labelling of the long arm of chromosome 2R and the short arm of chromosome 3R which sometimes cannot be distinguished from one another by C-banding. Clearly, as a complementary technique to C-banding and because of comparatively simple handling, N-banding would be very useful for the rapid identification of chromosome 2R, 3R, and 6R and/or 2R*q*, 3R*p*, and 6R*q*.

3.4 Rye trisomics and telotrisomics as a new standard tester material

There are several ways of identifying rye chromosomes. Cytologically, they can be characterized through chromosome measurements or banding analysis of complete genomes, by individual chromosome additions and by substitutions into the alien wheat background, by reciprocal translocations or trisomics and telotrisomics, and, at least, genetically, by expression of chromosomal genes.

More or less complete series of primary trisomics in rye were developed by Kamanoi and Jenkins (1962); Balkandschiewa and Mettin (1974); Zeller et al. (1977); Pilch (1978) and Sturm (1978).

The chromosome symbolization introduced by Heneen (1962) has been adopted by most of those authors with slight modifications. The morphological markers of primary trisomics were used to discriminate the extra chromosomes which were measured in Feulgen and Giemsa stained somatic metaphases. There is a fairly sufficient morphological similarity between the corresponding trisomics (see Schlegel and Mettin 1982). This gives some reason to suppose the identity of the additional chromosomes of the trisomics compared. The phenotypes of aneuploids were verified as good chromosomal markers facilitating their cytological and genetical handling.

However, because of the very low male transmission of the extra chromosome, test crosses to prove chromosomal identity have never been performed, although crosses between the trisomics of the variety 'Esto' and Sybenga's translocations as well as the wheat-rye additions ('Chinese Spring' – 'Imperial') and the telotrisomics are now in progress (Melz and Schlegel 1985).

Since in recent cytological and genetical studies the pale grained variety 'Esto' has been increasingly used, its karyological features were determined in more detail.

In earlier studies on C-banding (Schlegel and Mettin 1982) most of the rye cytogeneticists used arbitrary chosen designations or standard nomenclature to designate the chromosomes, but until now no attempt was made to develop a nomenclature for describing the bands. It is anticipated that with increased application of banding techniques in rye cytogenetic analysis, an urgent need for a standard chromosome band nomenclature will arise. Similar efforts are being attempted also in wheat (Gill and Schlegel, in preparation). Because of the widespread banding polymorphism in many cultivars, the band proposal for a nomenclature is based on the chromosomes of the variety 'Imperial' added, individually, to the hexaploid wheat variety 'Chinese Spring'.

The designation of chromosome arms and bands follows the recommendations of the Paris Conference on Standardization in Human Cytogenetics (Rowley 1974). Under the proposed rules of nomenclature, each chromosome short arm is designated as '*p*' and the long arm as '*q*', respectively. Each *p* and *q* arm is subdivided into regions based on chromosome landmarks (see Fig. 3).

Comparing the standard C- and N-banding patterns of 'Imperial' rye chromosomes present in addition lines with the patterns of the variety 'Esto' introduced as the basic material for trisomics and telotrisomics (see below), several differences can be observed. In addition to small morphological deviations, bands 1R*p*24, 1R*q*24, 2R*p*22, 5R*p*22, and 6R*p*24 are more prominent in 'Esto' than in 'Imperial' while bands 1R*p*12, 2R*q*12, 2R*q*22, 3R*q*22, 5R*q*12, and 6R*p*22 are completely missing. Additional bands, however, have been found on chromosome 1R, 4R, and 6R which are designated 1R*q*21.1, 4R*q*21.1, and 6R*q*21.1, respectively. The karyogram of 'Esto' was established on the basis of chromosome arm and band measurements of C-banded chromosomes and adjusted to the standard karyogram of 'Imperial' rye (Schlegel and Melz, unpubl., Fig. 4).

This tester material gained increased interest because several disadvantages of single rye chromosome additions and/or substitutions (Miller 1984) or reduced vigour through inbreeding (Smirnov and Sosnichina 1984) and modified genome structure in reciprocal translocation lines (Sybenga et al. 1985) can be widely overcome. Trisomic and telotrisomic plants can be utilized as normal outbreeding rye because the dosage effect of the individual chromosomes allows their identification.

The presence of certain extra chromosomes in the tester set of the variety 'Esto' were also confirmed by cytological traits as well as by C- and N-banding analysis (Schlegel and Sturm 1982; Melz and Schlegel 1985). The karyological results are given in Fig. 4. In addition to the differences in growth habit and individual chromosome morphology of the trisomics, the pale kernel character of the particular rye determined by recessive alleles would be of additional advantage in test crossing experiments.

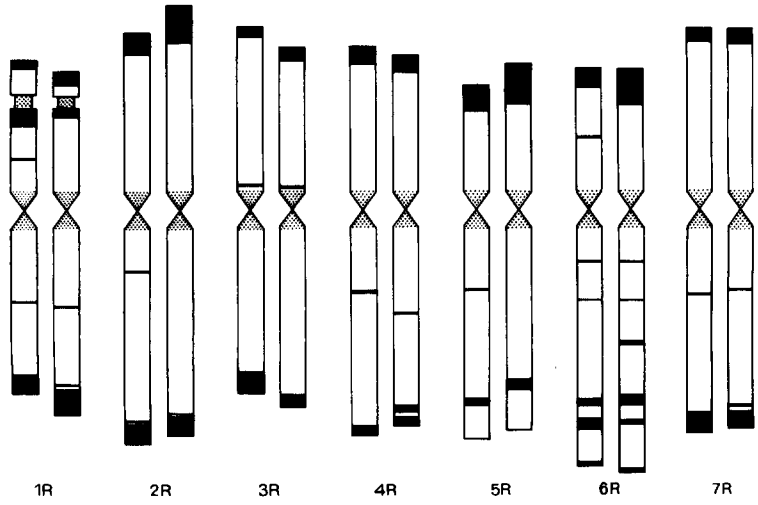

Fig. 4. Comparison of standard karyogram (*left*) and the karyogram of the variety 'Esto' (*right*)

Sturm (1978) has been the first to utilize trisomics for genetical linkage studies. A dominant gene *Dw1* (former *Hl*) of a short straw mutant was localized on chromosome 3R using trisomic analysis by adjusting the procedure after Hermsen (1970). Since that time more than 19 genes have been located in most of the rye chromosomes (Sturm and Engel 1980; Sturm et al. 1981; Sturm and Mueller 1982; Lindner et al. 1984; Melz et al. 1984). Moreover, a telotrisomic stock has been established (Sturm and Melz 1982; Melz and Schlegel 1985) which allows even gene mapping on chromosome arms.

4 Genetic analysis and gene localization on rye chromosomes

Progress in rye genetics has remained, for several reasons, far behind other diploid crops such as maize, barley or pea. However, the advances in molecular analysis, in classification of the chromosomes and the development of aneuploid stocks as well as translocation testers which have been described in the previous sections have greatly contributed to the establishment of gene-chromosome associations. Depending on the different approaches and methods applied, the present situation is characterized by the availability of quite a lot of genetic data based on a wide range of genotypes or cultivars.

As compared to the older compendia of inheritance studies given by Roemer (1939); Laube and Quadt (1959); Jain (1960) and Schlegel and Mettin (1982), there is especially a remarkable improvement in the genetics of simple inherited characters with regard to linkage results.

4.1 Ribosomal genes

The ribosomal RNA gene region of rye is located on chromosome 1R, which is characterized by large chromosomeres in pachytene from which a nucleolus originates, while in mitotic chromosomes a secondary constriction with a proximal C-band indicates the same region. In rye, a significant fraction of the rDNA is located in the C-band proximal to the secondary constriction.

It is thus likely that the large chromosomeres observed at the base of the nucleolus (Lima-de-Faria 1952) contain rDNA. The DNA structure of this region has been well defined. The repeating unit of rDNA is 9.0–10.0 kb in length (Appels 1983).

The 5S rDNA of chromosome 1R is located in tandem arrays distal to the rDNA region although it is not clearly associated with a heterochromatic band.

4.2 Localization of genes by primary trisomics

Since 1982 four basic contributions did stimulate, significantly, the classification of rye chromosomes and their gene localization. They can be summarized as follows: First, a generalized karyogram was accepted related to the individual rye chromosomes of wheat-rye additions (Sybenga 1983). Secondly, the translocation tester set developed by Sybenga and co-workers (Sybenga et al. 1985) was involved in test crosses with the standard wheat-rye addition series to verify the identity of the translocated chromosomes:

Standard nomenclature:	1R	2R	3R	4R	5R	6R	7R
Tester set chromosomes:	VII	III	II	IV	VI	V	I

Third, the previously established series of primary trisomics of the variety 'Esto' was characterized by chromosome banding and genetical markers (Schlegel and Melz, unpubl.). The identity was confirmed as

shown below:

Standard nomenclature:	1R	2R	3R	4R	5R	6R	7R
Primary trisomics:	G	C	B	D	E	F	A

Fourth, the chromosomes 1R, 2R, 3R, 5R, and 6R show close homoeology to groups 1, 2, 3, 5, and 6 of wheat, respectively, considering ability to compensate adequately when substituted for a single homoeologous wheat group. Chromosome 4R and 7R, however, show reciprocal homoeology to groups 4 and 7.

Although there are indications of partial homeology to more than one group for most of the chromosomes, they can easily be assigned to a single homoeology group. Apparent homoeology with more than one group may indicate translocation differences or residual duplications of genetical material which has arisen during the course of cereal evolution (Miller 1984). Moreover, according to a former recommendation (Sybenga 1983) a modified system of gene symbolization was confirmed during the 2nd Rye Cytogenetics Workshop (Svalöv, Sweden 1985). Two-letter to multiple-letter (biochemical markers) gene symbols are used which refer to the main phenotypic features. For several markers, an identification to genes described in related studies is proven or may be considered plausible.

Based on these principles the results of trisomic analysis have been associated with chromosome nomenclature and previous genetical findings, as can be taken from Table 1. Furthermore, the genetic correspondence of genes *Hp* (hairy peduncle), *Ha2* (hairy), *Hs* (hairy sheath) and *Ha1* (hairy) as well as *ct* (compactum) and *cp* (compactum), as listed earlier by Schlegel and Mettin (1982), has been now proven by Melz (1985, unpubl.) in test crosses and linkage studies. It is, therefore, proposed to replace the gene symbols *Hp* and *Hs* by *Ha2* and *Ha1*, respectively, and *cp* by *ct*. The *Hl* gene named by Kobyljanski (1972) and localized by Sturm (1978) on chromosome B (3R) was also reconsidered as *Dw1* (dwarf). The changed description from 7R to 3R on which the genes are located (Schlegel and Mettin 1982) is in accordance with the nomenclature recommended previously (Sybenga 1982).

Smirnov and Sosnichina (1984) described ten linkages which do not fit with either the results of de Vries and Sybenga (1984) or Melz et al. (1984) very well. Therefore, the results have been checked once more by Melz (1985, unpubl.). He showed that some of single segregations were disturbed, for example between the genes *ct2* and *el*. Thus, the gene *el* can not be located on chromosome 3R but on the chromosome 2R because of its close linkage to the gene *mo*. This was confirmed by de Vries and Sybenga (1984). The presumed linkage between spring growth habit *Sp* and the hairy peduncle and hairy sheath characters (*Ha1*, Surikov and Romanova 1978) has been confirmed with the localization of both *Sp* and *Ha1* on chromosome 3R (Melz, unpublished).

Nevertheless, there are still some differences for other genes. Although the genes *ct2* (de Vries and

Table 1. Compiled list of the chromosomal location of 19 genes in diploid rye determined by trisomic and telotrisomic analysis

Gene symbol	Name	Phenotypical characteristics	Source[a]	Chromosomal location	Authors
an1a	Anthocyaninless	No anthocyanin expression in plants	IPZ	7R	Melz, unpubl.
an1b	Anthocyaninless	No anthocyanin expression in plants	IPZ	2R	Melz, unpubl.
An3	Anthocyanin	Anthocyanin expression in seeds	IPZ	2R	Melz, unpubl.
An4	Anthocyanin	Purple seeds	IHAR	3R	Sturm et al. 1981
br	Brittle	Brittle stem	IPZ	5R	Melz, unpubl.
ct1	Compactum-1	Short straw mutant (Guelzow kurz)	IPZ	7R	Melz et al. 1984
ct2	Compactum-2	Short straw mutant (Moskovski karlik)	VIR	3R*q*	Sturm and Mueller 1982
Dw1	Dwarf-1	Dominant short straw mutant (EM1)	VIR	3R	Sturm 1978
Dw2	Dwarf-2	Dominant short straw mutant (K 10028)	VIR	7R	Melz et al. 1984
Ha1	Hairy-1	Hairy peduncle and sheat	IHAR	3R	Melz, unpubl.
Ha2	Hairy-2	Hairy peduncle	IPZ	5R*q*	Melz et al. 1984
Ha3	Hairy-3	Hairy peduncle	IHAR	6R	Melz, unpubl.
Per1	Peroxidase-1	Leaf peroxidase-1	IPZ	1R*p*	Lindner et al. 1984
Sf1	Self-fertile-1	Self-fertility	IHAR	1R	Melz, unpubl.
Sf2	Self-fertile-2	Self-fertility	IHAR	3R	Melz, unpubl.
Sf3	Self-fertile-3	Self-fertility	IHAR	5R	Romanova 1982
Sf4	Self-fertile-4	Self-fertility	IHAR	6R	Melz, unpubl.
Sp	Spring type	Spring type growth habit	IPZ	3R	Melz, unpubl.
wa	Waxless	Waxless stem and leafs	IPZ	7R	Melz, unpubl.

[a] IPZ = Institut f. Pflanzenzüchtung Guelzow, DDR; IHAR = Institut Hod. Akl. Ros. Krakow, Poland; VIR = Vsesoj. Institut Ras. Leningrad, USSR

Sybenga 1984) and *ct2(4)* (Melz, unpubl.) should be from the same origin, *ct2* was localized on chromosome 5R*q* (de Vries and Sybenga 1984) while the present results indicate 3R as the critical chromosome. A direct test for allelism of *ct2* and *ct2(4)* confirmed the identity of the genes. In addition, telotrisomic analysis concerning chromosome arm 3R*q* resulted in a critical segregation ratio (Melz, unpubl.). The short arm telocentric, moreover, was determined by a highly diagnostical N-band (Schlegel and Gill 1984). Contrary to de Vries and Sybenga (1984) it was shown that translocation line 240 rather than line 501 was linked to the *ct2* locus, though in both of the lines the alleged 5R*q* chromosome arm should be involved. From the results of de Vries and Sybenga (1984) it would be more plausible to conclude that chromosome 3R carries the *ct2* locus since the translocation line 240 even includes chromosome 3R (3R–5R*q*). Thus, it can be safely assumed that *ct2* is located on chromosome arm 3R*q*.

Recently, Ruebenbauer et al. (1983) found gene *rg* (reduced glumes), whose identity to *ct2* and *ct2(4)* has also been confirmed by test crosses (Melz, unpubl.). It is proposed, therefore, to symbolize the genes *rg, ct2,* and *ct2(4)* as *ct2* (see Tables 1, 2, 3). Since linkage between the genes *ct2, gr,* and *wil* has been already confirmed by de Vries and Sybenga (1984), *wil* and *gr* have to be located also on chromosome 3R which is in contrast to the authors' assumption. Moreover, it is very likely that *wil* (de Vries and Sybenga 1984) is identical with *Sp* (Melz, unpubl.). So, it would be logical to further designate the gene as *Sp* instead of *wil* since winter rye has the greater importance than spring material. The symbol *Sp* will be used, therefore, in the proposed catalogue (see below). The gene *br* (brittle stem), however, has been located on chromosome 5R. Thus, it can be suggested that a translocation is involved in the difference mentioned above.

Somewhat more conflicting seems to be the localization of the gene *an1* (anthocyaninless), first described by Koller and Zeller (1976) and Zeller and Koller (1981) on chromosome arm 4R*q*, while the data of Melz, unpubl. confirmed the findings of de Vries and Sybenga (1984) that this particular gene is associated to 7R. Notwithstanding this correspondence, Sybenga and

Table 2. Compiled list of chromosomal locations of genes in rye

Chromosome/arm	Gene	Phenotypical effects	References
1R*p*	*Sec1*	Secalin-1 (gliadin, prolamin)	Paneva and Konarev 1978; Shewry et al. 1985, Shepherd and Jennings 1971
1R*p*	*Gpi1*	Glucose phosphate isomerase	Chojecki and Gale 1983; Figueiras et al. 1985
1R*p*	*LPer1*	Leaf peroxidase	Höhler et al. 1979; Lindner et al. 1985; May et al. 1973
1R*p*	*Lr1*[a]	Leaf rust resistance, 26	Bartos and Bares 1971; Zeller 1972
1R*p*	*Sr1*[a]	Stem rust resistance, 31	Bartos and Bares 1971; Zeller 1972
1R*p*	*Pm1*[a]	Powdery mildew resistance, 8	Bartos and Bares 1971, Zeller 1972
1R*p*	*Wsm*[a]	Wheat streak mosaic virus res.	Martin et al. 1976
1R*p*	*Yr1*[a]	Stripe rust resistance, 9	Bartos and Bares 1971; Zeller 1972
1R*q*	*Mdh2a*	Malate dehydrogenase	Figueiras et al. 1985; Salinas and Benito 1985
1R*q*	*Sec3*	Secalin-3 (glutenin)	Bernard et al. 1977; Sing and Shepherd 1984
1R*q*	*Thi*	Thionin production	Sanchez-Monge et al. 1979
1R	*Ci1*	Chymotrypsin/subtilisin inhib.	Hejgaard et al. 1984
1R	*Ci2*	Chymotrypsin/subtilisin inhib.	Hejgaard et al. 1984
1R	*Gbr*[a]	Green bug resistance	Martin et al. 1976
1R	*Sf1*	Self-fertility-1	Melz, unpubl.
2R*p*	*LPer1 – 4*	Leaf peroxidase	Figueiras et al. 1985; Salinas and Benito 1984
2R*p*	*Mdh1*	Malate dehydrogenase	Figueiras et al. 1985; Salinas and Benito 1985
2R*p*	*Rfc1*	Male sterility restorer	Hossain and Driscoll 1983
2R*q*	*Gdh1*	Glutamate dehydrogenase	Salinas and Benito 1983
2R*q*	*Pgd2*	6-phosphogluconate dehydrogen.	Figueiras et al. 1985; Salinas and Benito 1983
2R*q*	*Pm2*[a]	Powdery mildew resistance, 7	Driscoll and Jensen 1963; Lind 1982; Riley and Macer 1966
2R*q*	*Yr2*[a]	Stripe rust resistance	Riley and Macer 1966
2R	*Sec2*	Secalin	Shewry et al. 1985
2R	*Ssp1*	Salt soluble protein	Fra-Mon et al. 1984
2R	*LEst2*	Leaf esterase	Schmidt et al. 1984

Table 2 (continued)

Chromosome/arm	Gene	Phenotypical effects	References
2R	*Glu*	beta-glucosidase	May and Appels 1978
2R	*Asi*	alpha-amylase/subtilisin inhib.	Hejgaard et al. 1984
2R	*el*	Absent ligula	Smirnov and Sosnichina 1984
2R	*Sup*	Superoxide dismutase	Jaaska 1982
2R	*Tyr*	Tyrosinase	Zeven 1972
2R	*Lr2*[a]	Leaf rust resistance, 25	Driscoll and Jensen 1963
2R	*dw2*	Recessive dwarf mutant	De Vries and Sybenga 1984
2R	*mo*	Monstrous growth habit	De Vries and Sybenga 1984
2R	*An3*	Anthocyanin	Melz, unpubl.
2R	*an1b*	Anthocyaninless	Sturm et al. 1981; Melz unpubl.
2R	*Ps*	Purple seed color	De Vries and Sybenga 1984
3R*p*	*Sec4*	Secalin-4 (prolamin)	Owen and Larter 1983
3R*p*	*Sr2*[a]	Stem rust resistance, 27	Luid and Watson 1976; Stewart et al. 1968
3R*p*	*Pm3*[a]	Powdery mildew resistance	Lind 1982; Riley and Macer 1966
3R*q*	*Aat1*	Aspartat aminotransferase	Schmidt et al. 1984; Tang and Hart 1975
3R*q*	*Got3*	Glutamate oxaloaceatate trans.	Figueiras et al. 1985; Tang and Hart 1975
3R*q*	*Mdh2b*	Malate dehydrogenase	Figueiras et al. 1985; Salinas and Benito 1985
3R*q*	*ct2*	Short straw mutant	(De Vries and Sybenga 1984); Melz 1985, unpubl.; Sturm and Mueller 1982
3R*q*	*gr*	Grassy habit	(De Vries and Sybenga 1984)
3R*q*	*Sp1*	Spring growth habit	(De Vries and Sybenga 1984); Melz 1985, unpubl.
3R	*Alt2*	Aluminiumtolerance	Aniol and Gustofson 1984
3R	*Est1*	Esterase	Barber et al. 1969
3R	*Tpi1*	Triosephosphate isomerase	Hart and Tuleen 1983; Pieto and Hart 1985
3R	*Tia*	Major endosperm trypsin inhib.	Hejgaard et al. 1984; Tanner and Reinbergs 1982
3R	*An4*	Anthocyanin (purple seed)	Melz 1985, unpubl.
3R	*An5*	Anthocyanin (red leaf base)	Melz 1985, unpubl.; Smirnov and Sosnichina 1984
3R	*Dw1*	Dominant dwarf mutant, EM1	Sturm 1978; Sturm and Engel 1980
3R	*dw3*	Recessive dwarf mutant	De Vries and Sybenga 1984
3R	*Ha1*	Hairy peduncle and sheath	Melz 1985, unpubl.; Surikov and Romanova 1978
3R	*Sf2*	Self-fertility	Melz 1985, unpubl.
3R	*Cpp*	Chromosome pairing promotion	Miller 1984
4R*p*	*Adh1*	Alcohol dehydrogenase	Artyomova 1982; Irani and Bhatia 1972; Tang and Hart 1975
4R*p*	*Pgm1*	Phosphoglucose mutase	Figueiras et al. 1985
4R*p*	*Rfc2*	Male sterility restorer	Hossain and Driscoll 1983
4R*p*	*Nca*	Neocentric activity	Viinikka 1985
4R*q*	*EPer1*	Endosperm peroxidase	Salinas and Benito 1984b
4R*q*	*Pgd1a*	6-phosphogluconate dehydrogen.	Hsam et al. 1982; Rao and Rao 1980; Salinas and Benito 1983
4R*q*	*Est10*	Esterase-10	Wehling et al. 1985
4R*q*	*an1a*	Anthocyaninless	Zeller and Koller 1981
4R*q*	*lg*	Light green leaf habit	De Vries and Sybenga 1984
4R*q*	*Pc*	Purble culm	Miller 1984
4R	*Alt3*	Aluminium tolerance	Aniol and Gustafson 1984
4R	*Lap2*	Leucine aminopeptidase	Tang and Hart 1975
4R	*Ssp2*	Salt soluble protein	Fra-Mon et al. 1984
4R	*Pm6*[a]	Powdery mildew resistance	Lind 1982
5R*p*	*Gpd4*	Glucose-6-phosphate dehydrogen.	Figueiras et al. 1985; Salinas and Benito 1983
5R*p*	*Skd*	Shikimate dehydrogenase	Koebner and Shephard 1982
5R*p*	*br*	Brittle stem	De Vries and Sybenga 1984; Melz 1985, unpubl.

(continued overleaf)

Table 2 (continued

Chromosome/arm	Gene	Phenotypical effects	References
5R*p*	*ti*	Tigrina	De Vries and Sybenga 1984
5R*q*	*Aadh1*	Aromatic alcohol dehydrogenase	Schmidt et al. 1984
5R*q*	*β-Amy1*	beta-amylase	Artyomova 1982; Bernard et al. 1977
5Rq	*Est2*	Leaf esterase	Artyomova 1982; Schmidt et al. 1984
5R*q*	*Cps*	Chromosome pairing supressor	Riley et al. 1973
5R*q*	*Ce*	Copper efficiency	Graham 1978; Graham 1979
5R*q*	*Ha1*	Hairy leaf sheath	Miller 1984
5R*q*	*Ha2*	Hairy peduncle	Chang 1975; Melz et al. 1984
5R*q*	*Pm4*[a]	Powdery mildew resistance	Lind 1982; Riley and Macer 1966
5R	*Adh2*	Alcohol dehydrogenase	Hart and Tuleen 1983
5R	*α-Amy3*	alpha-amylase	Salinas et al. 1985
5R	*Tpi2*	Triosephosphate isomerase	Hart and Tuleen 1983
5R	*Aco2*	Aconitase	Chenicek 1984
5R	*fv*	Flavovirens	Schilko and Kedrov-Zichman 1982
5R	*Lys*	Lysin	Evans and Scoles 1980
5R	*Sf3*	Self-fertility	Melz 1985, unpubl.; Romanova 1982
5R	*wa2*	Waxless stem	Nalepa 1983
6R*p*	*Lap1*	Leucine aminopeptidase	Tang and Hart 1975
6R*p*	*Alt1*	Aluminium tolerance	Aniol and Gustafson 1984
6R*p*	*wh*	White plant habit	De Vries and Sybenga 1984
6R*p*	*Co*	Corroded plant habit	Miller 1984
6R*q*	*Aadh2*	Aromatic alcohol dehydrogen.	Schmidt et al. 1984
6R*q*	*Aat2*	Asparatat aminotransferase	Schmidt et al. 1984; Tang and Hart 1975
6R*q*	*EEst2*	Endosperm esterase	Artyomova 1982; Schmidt et al. 1984
6R*q*	*Got2*	Glutamate oxaloacetate trans.	Hart 1978; Tang and Hart 1975
6R*q*	*Pgd1b*	6-phosphogluconate dehydrog.	Rao and Rao 1980; Salinas and Benito 1983
6R*q*	*SPer1–2*	Empryo and scutellum perox.	Salinas and Benito 1984 b
6R*q*	*Reg*	Red grain	Miller 1984
6R*q*	*Rog*	Round grain	Miller 1984
6R*q*	*Yr3*	Yellow rust, 3	Miller 1984
6R	*Adh3*	Alcohol dehydrogenase	Hart and Tuleen 1983
6R*q*	*α-Amy1*	alpha-amylase	Miller 1984
6R	*Amp1*	Aminopeptidase	Hart and Tuleen 1983
6R	*Ha3*	Hairy peduncle	Melz 1985, unpubl.
6R	*Pm5*[a]	Powdery mildew resistance	Lind 1982
6R	*Pro*	Prolin	Evans and Scoles 1980
6R	*Sf4*	Self-fertility	Melz 1985, unpubl.
7R*p*	*Acph*	Acid phosphatase	Figueiras et al. 1985; Hart 1978; Tang and Hart 1975
7R*p*	*Alk3*	Alkine phosphatase	Figueiras et al. 1985; Salinas and Benito 1984 a
7R*p*	*EPer2–4*	Endosperm peroxidase	Salinas and Benito 1984
7R*p*	*Sec5*	Secalin (prolamin)	Owen and Larter 1983
7R*q*	*α-Amy2*	alpha-amylase	Miller 1984
7R*q*	*Got1*	Glutamate oxaloacetate trans.	Tang and Hart 1975
7R*q*	*ct1*	Short straw mutant	De Vries and Sybenga 1984; Melz, unpubl.
7R*q*	*an1a*	Anthocyaninless	De Vries and Sybenga 1984; Melz, unpubl.
7R	*Ep1*	Endopeptidase	Hart and Tuleen 1983
7R	*an2*	Anthocyaninless leaf base	Surikov 1971
7R	*Dw1*	Dominant dwarf mutant	Melz et al. 1984; Melz, unpubl.
7R	*wa1*	Waxless leaf and stem	Melz, unpubl.

[a] Resistance against wheat diseases and pests
( ) Re-considered localization after de Vries and Sybenga (1984)

Table 3. Linkage relationships between rye genes

Linkage	Chromosome	Recombination frequency (%)	Reference
wa1-Dw2	7R	32.6	Melz 1985, unpubl.
wa1-ct1	7R	40.0	Melz 1985, unpubl.
Ps-mo	2R	29.7/26.1	De Vries and Sybenga 1984; Smirnov and Sosnichina 1984
Ps-dw2	2R	2.2	De Vries and Sybenga 1984
mo-dw2	2R	31.0	De Vries and Sybenga 1984
mo-el	2R	31.5	Smirnov and Sosnichina 1984
Pgd2-Mdh1	2R	16.0	Figueiras et al. 1985
Per3-Per4	2R	26.0	Figueiras et al. 1985
Mdh2-Got3	3R	21.0	Figueiras et al. 1985
ct2-Dw1	R3	27.0	Melz 1985, unpubl.
An5-Dw1	3R	25.9	Smirnov and Sosnichina 1984
An5-ct2	3R	42.0	Smirnov and Sosnichina 1984
Ha1-Sp1	3R	32.3	Surikov and Romanova 1978
Sp1-ct2	3R	11.7	De Vries and Sybenga 1984
Ha2-wa2	5R	18.8	Nalepa 1983
an1a-an2	7R	5.7	Surikov 1971
an1a-ct1	7R*q*	0	De Vries and Sybenga 1984
centromere-*Ha2*	5R*q*	46.8	Chang 1975
centromere-*Sec3*	1R*q*	4.6	Singh and Shepherd 1984

Mastenbroek (1980) located *an1* on the long arm of chromosome 7R based on calculation of recombination interference.

Finally, linkage studies, including the arrangements *wa-Dw2, wa-ct1,* and *ct2-Dw1* showed recombination frequencies of 32.6%, 40.0%, and 27.0%, respectively (Melz, unpubl.).

4.3 The up-dated catalogue of localized genes in rye

An up-dated catalogue of gene-chromosome associations, gene symbolization and linkage relationships was prepared. Considering the recommendations of nomenclature accepted at the 2nd Rye Workshop, an earlier proposal (Schlegel and Mettin 1982) was revised as well as completed by current data.

Referring to individual symbolizations by different workers modifications were proposed and discussed to avoid further confusion. The gene symbols used follow the recommended rules for gene nomenclature in rye that were accepted in 1982. These rules specify that two or more non-allelic genes having phenotypically similar effects should be designated by a common basic symbol. When the two or more genes belong to a paralogous set in biochemical markers, the basic symbol is followed by a locus designation taking the form of the accepted genome symbol and a set number represented by an Arabic numeral. The hyphen between gene symbol and locus designation as proposed in 1982 should be revised following the international trend. Since the present contribution deals with rye genes only the genome symbol has been neglected. Due to the missing paralogy with wheat genes, non-allelic genes having phenotypically similar effects are designated in sequential series by an Arabic numerical immediately following the gene symbol, e.g. *Adh3.* Chromosome arms are designated already in this report in accordance with the above mentioned *p* and *q* symbolization. While in the first list of gene symbols the biochemical markers glutenin, prolamin, and gliadin were listed separately these now have been commonly designated as Secalin (*Sec*) with respect to the proposal of Shewry et al. (1985).

5 References

Aniol A, Gustafson JP (1984) Chromosome location of genes controlling aluminium tolerance in wheat, rye and triticale. Can J Genet Cytol 26:701–706

Appels R (1982) The molecular cytology of wheat-rye hybrids. Rev Cytol 80:93–132

Appels R (1983) Chromosome structure in cereals: the analysis of regions containing repeated sequence DNA and its application to the detection of alien chromosomes introduced into wheat. In: Kosuge T, Meredith CP, Hollaender A (eds) Genetic engineering in plants. Plenum Press, New York, pp 229–256

Appels R, Moran LB (1984) Molecular analysis of alien chromatin introduced into wheat. In: Gustafson JP (ed) Proc 16th Stadler Genet Symp, Gene manipulation in plant improvement. Columbia, pp 529–558

Appels R, Driscoll C, Peacock WJ (1978) Heterochromatin and highly repeated DNA sequences in rye (*Secale cereale*). Chromosoma 70:67–89

Appels R, Dennis ES, Smyth DR, Peacock WJ (1981) Two repeated DNA sequences from the heterochromatic regions of rye (*Secale cereale*) chromosomes. Chromosoma 84:265–277

Artyomova NV (1982) Chromosomal control of alcohol dehydrogenase, esterase and beta-amylase isoenzymes in different rye cultivars. Genetika, Moscow 18:661–668

Balkandschiewa J, Mettin D (1974) Morphologie und Zytologie der primären Trisome des Winterroggens 'Danae'. Arch Züchtungsforsch 4:19–28

Barber HN, Driscoll CJ, Long PM, Vickery RS (1969) Gene similarity of the *Triticinae* and the study of segmental interchanges. Nature 22:897–898

Bartos P, Bares I (1971) Leaf and stem rust resistance of hexaploid wheat cultivare 'Salzmuender Bartweizen' and 'Weique'. Euphytica 20:435–440

Bedbrock JR, Jones J, O'Dell M, Thompson RD, Flavell RB (1980) A molecular describtion of telomeric heterochromatin in *Secale* species. Cell 19:545–560

Bennett MD, Smith JB (1976) Nuclear DNA amounts on angiosperms. Philos Trans R Soc London 274:227–274

Bernard M, Autran JC, Joudrier P (1977) Possibilites d'identification de certaine chromosomes de seigle a l'aide de marqueurs biochemiques. Ann Amelior Plant 27:355–362

Chang TD (1975) Mapping of the gene for hairy peduncle (*Hp*) on rye chromosome 5R. Can J Genet Cytol 17: 127–128

Chenicek KJ (1984) Evidence for the genetic control and subcellular location of aconitase isozymes in Triticeae species. MSc Thesis, Texas A&M University, College Station (abstr)

Chojecki AJS, Gale MD (1983) Genetic control of glucose phosphate isomerase in wheat and related species. Heredity 49:337–347

Dennis ES, Gerlach WL, Peacock WJ (1980) Identical polypyrimidine-polypurine satellite DNAs in wheat and barley. Heredity 44:349–366

De Vries JN, Sybenga J (1984) Chromosomal location of 17 monogenetically inherited morphological markers in rye (*Secale cereale* L) using the translocation tester set. Z Pflanzenzücht 92:117–139

Driscoll CJ, Jensen NF (1963) A genetic method for detecting induced intergeneric translocation. Genetics 48:459–468

Evans LE, Scoles DJ (1980) Cytogenetics, plant breeding and agronomy. In: Roz proisvodstvo chimia i technologia. Moskva, pp 16–36

Figueiras AM, Gonzalez-Jean M, Salinas J, Benito C (1985) Association of isozymic alleles with a reciprocal translocation in cultivated by (*Secale cereale* L.). Genetics 109:177–193

Flavell RB (1982) Sequence amplification, deletion and rearrangements: major source of variation during species divergence. In: Dover GA, Flavell RB (eds) Genome evolution. Academic Press, London, pp 301–323

Fra-Mon P, Salcedo G, Aragoncillo C, Garcia-Olmedo G (1984) Chromosome assignment of genes controlling salt-soluble proteins (albumins and globulines) in wheat and related species. Theor Appl Genet 69:167–173

Gerlach WC, Peacock WJ (1980) Chromosomal location of highly repeated DNA sequences in wheat. Heredity 44: 269–276

Graham RD (1978) Tolerance of triticale, wheat and rye to copper deficiency. Nature 271:542–543

Graham RD, Pearce DT (1979) The sensitivity of hexaploid and octoploid triticale and their parent species to copper deficiency. Aust J Agric Res 30:791–799

Gustafson JP, Bennett MD (1976) Preferential selection for wheat-rye substitutions in 42-chromosome triticale. Crop Sci 16:688–693

Hart GE (1978) Chromosomal arm locations of Adh-R2 and an acid phosphatase structural gene in Imperial rye. Cereal Res Commun 6:123–135

Hart GE, Tuleen NA (1983) Introduction and characterization of alien genetic material. In: Tanksley SD, Orton TJ (eds) Isozymes in plant genetics and breeding. Elsevier Publications, Amsterdam, pp 103–120

Heneen WK (1962) Chromosome morphology in inbred rye. Hereditas 48:182–200

Hejgaard J, Bjorn SE, Nielson G (1984) Rye chromosome carrying structural genes for the major grain protease inhibitors. Hereditas 101:257–259

Hermsen JG (1970) Basic information for the use of primary trisomics in genetic and breeding research. Euphytica 19:125–140

Höhler B, Schlegel R, Blüthner WD (1979) Das Muster von Peroxidase-Isoenzymen in 1R (1B) Weizen-Roggen-Substitutions- bzw. Translokationslinien. Biochem Physiol Pflanz 174:838–843

Hossain MA, Driscoll CJ (1983) Fertility compensation of Cornerstone male sterility of wheat by rye. Genetics 104:181–187

Hsam SLK, Zeller FJ, Huber W (1982) Genetic control of 6-phospho-gluconate dehydrogenase (6-PGD) isozymes in cultivated wheat and rye. Theor Appl Genet 62:317–321

Hutchinson J, Chapman V, Miller TE (1980) Chromosome pairing at meiosis in hybrids between *Aegilops* and *Secale* species; a study by in situ hybridization using cloned DNA. Heredity 45:245–254

Irani BN, Bhatia CR (1972) Chromosome location of alcohol dehydrogenase gene(s) in rye using wheat-rye addition lines. Genetica 43:195–220

Jaaska V (1982) Isoenzymes of superoxide dismutase in wheats and their relatives: alloenzyme variation. Biochem Physiol Pflanz 177:747–755

Jain SK (1960) Cytogenetics of rye (*Secale* ssp). Bibliogr Genet 19:1–86

Jones JDG, Flavell RB (1982) The structure, amount and chromosomal localization of defined repeated DNA sequences in species of the genus *Secale*. Chromosoma 86:613–641

Kamanoi M, Jenkins BC (1962) Trisomics in common rye, *S. cereale*. Seiken Ziho 13:145–152

Kobyljanski VD (1972) On the genetics of the dominant factor of short-strawed rye (russ). Genetika 8:12–17

Koebner RMD, Shephard KW (1982) Shikimate dehydrogenase – a biochemical marker for group 5 chromosomes in the *Triticinae*. Genet Res 41:209–213

Koller OL, Zeller FJ (1976) The homoeologous relationships of rye chromosome 4R and 7R with wheat chromosomes. Genet Res 28:177–188

Laube W, Quadt F (1959) Roggen (*Secale cereale*). In: Handbuch der Pflanzenzüchtung, Bd 3, 2 Aufl. Parey, Berlin Hamburg, pp 5–25

Lima-de-Faria A (1952) Chromomere analysis of the chromosome complement of rye. Chromosoma 5:1–68

Lind V (1982) Analysis of the resistance of wheat-rye addition lines to powdery mildew of wheat (*Erysiphe graminis F* sp *tritici*). Tagungsber Akad Landwirtschaftswiss DDR 198: 509–520

Lindner A, Melz G, Mueller HW, Buschbeck R (1984) Genetic analysis of rye (*Secale cereale* L). 2. Leaf Peroxidase isoenzymes in trisomic and telotrisomics of chromosome 1R. Genet. Pol 25:345–348

Luid NH, Watson IA (1976) Strains of *Puccinia graminis* virulent on wheat plants carrying gene *Sr27* derived from 'Imperial' rye. Phytopathology 66:664–666

Martin TJ, Harvey TL, Livers RW (1976) Resistance to wheat streak mosaic virus and its vectors, *Aceria tulipae*. Phytopathology 66:346–349

May CE, Appels R (1978) Chromosome 2R substitution and translocation lines in hexaploid wheat. Cereal Res Commun 6:231–234

May CE, Vickery SS, Driscoll CJ (1973) Gene control in hexaploid wheat. Sears ER, Sears LMS (eds) Proc 4th Int Wheat Genet Symp. University of Missouri, Columbia, pp 843–849

Melz G, Schlegel R (1985) Identification of seven telotrisomics of rye (*Secale cereale* L). Euphytica 35:361–366

Melz G, Neumann H, Müller H, Sturm W (1984) Genetical analysis of rye (*Secale cereale* L). 1. Results of gene localization on rye chromosomes using primarty trisomics. Genet Pol 25:111–115

Miller TE (1984) The homoeologous relationships between the chromosomes of rye and wheat. Current status. Can J Genet Cytol 26:578–589

Nalepa S (1983) A genetical investigation of hexaploid triticale III. The inheritance of some characters in hexaploid triticale and linkage between them. Hodowla Rosl Aklim Nasienn 27:39–50

Owen MRL, Larter EN (1983) The effect of telomeric heterochromatin on prolamin (secalin) synthesis in inbred *Secale cereale* L. Agron Abstr: 74–75

Paneva TI, Konarev VG (1978) The control of gliadins in rye cultivars (russ). Dokl Vses Akad Skh Nauk 4:12–14

Pieto ME, Hart GE (1985) The genetic control of triosephosphatase isomerase of hexaploid wheat and other *Triticeae* species. Genet Res 45:127–142

Pilch J (1978) Cytological and morphological characteristics of primary trisomics in rye. Genet Pol 19:137–152

Ranjekar PK, Lafontaine JG, Pallotta D (1974) Characterization of repetitive DNA in rye (*Secale cereale*). Chromosoma 48:427–440

Rao IN, Rao PVM (1980) Evidence for duplicate genes coding for 6-phosphogluconate dehydrogenase in rye. Genet Res 35:309–312

Riley R, Macer RFC (1966) The chromosomal distribution of the genetic resistance of rye to wheat pathogens. Can J Genet Cytol 8:640–653

Riley R, Chapman V, Miller TE (1973) The determination of meiotic chromosome pairing. In: Sears ER, Sears LMS (eds) Proc 4th Int Wheat Genet Symp. University of Missouri, Columbia; pp 731–738

Rimpau J, Smith DB, Flavell RB (1978) Sequence organization analysis of the wheat and rye genomes by interspecies DNA/DNA hybridization. J Mol Biol 123:327–359

Roemer R (1939) Roggen (*Secale cereale*). In: Handbuch der Pflanzenzüchtung, Bd 2, 1 Aufl. Parey, Berlin, pp 1–23

Romanova NP (1982) Ispolsovanie medoda opredelenija zeplenija faktorov samonesovmestimosti morfologitscheskimi markerami u rzi (russ). Sesd Vsesoj Obsch Genetikov i Selek, Kishinev 4:142

Rowley JD (1974) Identification of human chromosomes. In: Yunis JJ (ed) Human Chromosome Methodology. Acad Press, New York, pp 17–46

Ruebenbauer T, Kubara-Szpunar L, Pajak K (1983) An interesting mutation of pleiotropic character induced by fast neutrons in rye (*Secale cereale* L). Genet Pol 24:319–325

Salinas J, Benito C (1983) Chromosomal location of genes controlling 6-phosphogluconate dehydrogenase, glucose-6-phosphate dehydrogenase and glutamate dehydrogenase isozymes in cultivated rye. Euphytica 32:783–790

Salinas J, Benito C (1984a) Phosphate isozymes in rye. Characterization, genetic control and chromosomal location. Z Pflanzenzücht 93:115–137

Salinas J, Benito C (1984b) Chromosomal location of peroxidase structural genes in rye (*Secale cereale* L). Z Pflanzenzücht 93:291–309

Salinas J, Benito C (1985) Chromosomal location of malate dehydrogenase structural genes in rye (*Secale cereale* L). Z Pflanzenzücht 94:208–217

Salinas J, Figueiras MT, Gonzalez-Jean MT, Benito C (1985) Chromosomal location of isozyme markers in wheat-barley addition lines. Theor Appl Genet 70:192–198

Sanchez-Monge R, Delibes A, Hernandez-Lucas C, Carbonero P, Garcia-Olmedo F (1979) Homoeologous chromosomal location of genes encoding thionins in wheat and rye. Theor Appl Genet 54:61–63

Sarma NP, Natarajan AT (1973) Identification of heterochromatic regions in the chromosomes of rye. Hereditas 74:233–238

Schilko TS, Kedrov-Zichman OO (1982) The linkage group of the pseudonormal trisomic of winter rye (russ). Sesd Vsesoj Obsch Genetikov i Selek, Kishinev 4:267

Schlegel R, Gill BS (1984) N-banding analysis of rye chromosomes and the relationship between N-banded and C-banded heterochromatin. Can J Genet Cytol 26:765–769

Schlegel R, Mettin D (1982) The present status of chromosome recognition and gene localization in rye, *Secale cereale* L. Proc Eucarpia Meeting in Rye Breeding and Research. Tagungsber Akad Landwirtschaftswiss DDR 198:131–152

Schlegel R, Sturm W (1982) Das meiotische Paarungsverhalten der primären Trisome des Roggens (*Secale cereale* L). Proc Eucarpia Meeting in Rye Breeding and Research. Tagungsber Akad Landwirtschaftswiss DDR 198:225–247

Schmidt JC, Seliger P, Schlegel R (1984) Isoenzyme als biochemische Markerfaktoren für Roggenchromosomen. Biochem Physiol Pflanz 179:197–210

Schweizer D (1979) Fluorescent chromosome banding in plants: mechanisms, and implications for chromosome structure. In: Proc 4th John Innes Symp, pp 61–72

Shewry PR, Bradberry D, Franklin J, White RP (1985) The chromosomal locations and linkage relationships of structural genes for the prolamine storage proteins (selacins) of rye. Theor Appl Genet 69:63–71

Shepherd KW, Jennings AG (1971) Genetic control of rye endosperm protein. Experientia 27:88–98

Singh NK, Shepherd KW (1984) Mapping of the genes controlling high-molecular-weight glutelin subunits of rye on the long arm of chromosome 1R. Genet Res 44:117–123

Smirnov WG, Sosnichina SP (1984) Genetika rzi. Leningrad, pp 1–156

Smith DB, Flavell RB (1977) Nucleotide sequence organization in the rye genome. Biochim Biophys Acta 474: 82–97

Stewart DM, Gillmare EC, Ausemus ER (1968) Resistance to Puccinia graminis derived from *Secale cereale* incorporated into *Triticum aestivum*. Phytopathology 58:508–511

Sturm W (1978) Identifizierung von Trisomen der Sorte 'Esto' und Trisomen-Analyse des Gens *Hl* für Kurzstrohigkeit bei *Secale cereale* L. PhD Thesis Akademie der Landwirtschaftswissenschaften der DDR, pp 1–180

Sturm W, Engel KH (1980) Trisomenanalyse des Allels HL für Kurzstrohigkeit bei *Secale cereale* L. Arch Züchtungsforsch 10:31–35

Sturm W, Müller H (1982) Localization of the recessive gene of the Moscow dwarf mutant short straw character in *Secale cereale* L (russ). Citol i Genet, Kiev 16:13–17

Sturm W, Neumann H, Melz G (1981) Trisomenanalyse für das Merkmal Anthocyanfärbung bei *Secale cereale* L. Arch Züchtungsforsch 11:49–53

Surikov IM (1971) Inheritance of two chlorophyll aberrations in rye (russ). Tr Prikl Bot Genet Sel 46:122–130

Surikov IM, Romanova NP (1978) A contribution to factoral genetics of rye, *Secale cereale* L. 1. Inheritance of differences in such characters as pubescence of leaf sheath and winter or spring habit of growth (russ). Genetika 14: 396–405

Sybenga J (1983) Rye chromosome nomenclature and homoeology relationships. Workshop Report. Z Pflanzenzücht 90:297–304

Sybenga J, Mastenbroek I (1980) Combined genetic and cytological analysis of positive and negative interference in an interchange heterozygote of rye (*Secale cereale* L). Heredity 44:83–92

Sybenga J, van Eden J, van der Meijs QG, Roeterding BW (1985) Identification of the chromosomes of the rye translocation tester set. Theor Appl Genet 69:313–316

Tang KS, Hart GE (1975) Use of isoenzymes as chromosome markers in wheat-rye addition lines and in triticales. Genet Res 26:187–201

Tanner DG, Reinbergs E (1982) Genetic analysis of the trypsin inhibitor activity of triticale and rye. Z Pflanzenzücht 88: 177–185

Viinikka Y (1985) Identification of the chromosomes showing neocentric activity in rye. Theor Appl Genet 70:66–77

Wehling P, Schmidt-Stohn G, Wricke G (1985) Chromosomal location of esterase, peroxidase, and phosphoglucomutase isozyme structural genes in cultivated rye. Theor Appl Genet 70:377–382

Zeller FJ (1972) Cytogenetics of some rust resistant wheat cultivars. In: Prtoc Europ Mediterr Cereal Rusts Conf. Praha, pp 297–301

Zeller FJ, Koller CL (1981) Identification of a 4A/7R and a 7B/4R wheat-rye chromosome translocation. Theor Appl Genet 59:33–37

Zeller FJ, Kimber G, Gill BS (1977) The identification of rye trisomics by translocations and Giemsa staining. Chromosoma 62:279–289

Zeven AC (1972) Identification of chromosome carrying a locus for a gene conditioning the production of tyrosinase. Wheat Inf Serv 35:3–8