II. Recombination in Sexually Propagated Higher Plants

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1. Introduction

Recent reviews in this series have focused on sexual and asexual recombination with particular relevance for plant breeding. Particular emphasis has been put on interspecific hybridization and cell culture technology (Friedt and Wenzel 1985) and on asexual recombinant technology, respectively (Friedt and Brune 1987). Besides, an extensive review on mechanisms of meiotic recombination has been provided by Friebe (1985), where recent molecular models as well as cytological and enzymological aspects of meiotic synapsis of homologous chromosomes are discussed. In addition, mechanisms controlling meiotic recombination and its influence upon the genetic structure of populations are summarized.

Furthermore, ten review articles on genetic recombination, grouped in meiotic, mitotic, and bacterial processes were compiled by Wilson (1985). More recently, additional, extensive studies on chromosome pairing and synaptonemal complex formation in hexaploid wheat and wheat-rye hybrids were carried out by Holm (1988a, b, c) and by Wang and Holm (1988).

Therefore, molecular processes of recombination as well as synaptonemal complex, chromosome pairing, and chiasma formation will not be considered in this chapter. Instead, an overview on linkage analysis and gene localization as well as recent results on interspecific and intergeneric hybridization will be presented. Genetic maps have recently received much attention by plant breeders since they are considered as a helpful breeding tool (Tanksley and Rick 1980; Soller and Beckmann 1983; Helentjaris et al. 1985). Although the limits of "wide crosses" for direct application have certainly been recognized, the value of interspecific and intergeneric hybrids as a potential source of new genetic variability is now appreciated even in practical plant breeding.

2. Cytogenetic Methods for Gene Localization

a) New Aneuploids for Gene Localization

α) Monosomics and Mechanisms of Monosomic Formation

Monosomics are a unique and still very useful tool for determining the chromosomal location of specific genes. Newly established monosomics of different species are summarized in Table 1.

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Table 1. Monosomics and addition lines

Species	Cultivar/genotype/source	Reference(s)
Avena byzantina	cv. Kanota	Morikawa (1985)
Zea mays	r-x1 deficiency	Simcox and Weber (1985)
Brassica napus	*Diplotaxis muralis*	Fan and Tai (1985)
Beta vulgaris	*B. procumbens*	van Geyt et al. (1988)

The r-x1 deficiency on chromosome 10 of maize produces large numbers of monosomics (Simcox and Weber 1985) since r-x1 conditions nondisjunction during embryo sac development. Variation in kernel size associated with r-x1 are found to be correlated with aneuploidy, both monosomy and trisomy, in the embryo (Lin and Coe 1986).

In self-pollinated progenies of two monosomic types of *B. napus*, Chang et al. (1987) found that transmission of the monosomic chromosome was very high. The absence of one chromosome increased the frequency of multivalents.

β) Trisomics and Telotrisomics

More or less complete series of trisomics and/or telotrisomics were recently reported for various species (Table 2).

In rye plants, telotrisomics for the short arm of chromosome 1R and pairing preferences were observed (Benavente and Orellana 1986). The long arm of chromosome 1R seems to play an important role in the pairing preference of the short one (Benavente and Orellana 1985).

b) Gene Localization with Aneuploids

α) Monosomic and Telosomic Analysis in Wheat

Genetic analyses of heading date and spikelet number were carried out in common wheat *(Triticum aestivum)* multispikelet line "Noa" by using the monosomic series of the normal line "Mara". High spikelet number is controlled by a recessive major gene on chromosome 2D; a slight reduction in spikelet number is induced by another recessive gene on chromosome 7A. Late heading date was found to be controlled by two recessive genes, located on chromosomes 2D and 6B, respectively (Millet 1987). Hoogendoorn (1985) worked with a reciprocal F_1 monosomic analysis in wheat to associate chromosomes with differences in days to ear emergence, number of leaves, and number of spikelets.

Genetic analyses using the "Chinese Spring" monosomic series showed genes and respective chromosomes which influence the expression of yellow berry, a grain disorder in bread wheat. Dhaliwal et al. (1986) demonstrated that two major dominant genes on chromosomes 1A and 7A and four modifiers on 4A, 4B, 6A, and 6D influence the expression of yellow berry.

Table 2. Trisomics and telotrisomic lines

Species	Type (origin)	References
Rye	Primary trisomics (cv. "Esto")	Schlegel et al. (1986) Melz et al. (1988)
	Monotelotrisomics	Melz and Schlegel (1985)
	Monotelodisomics	Melz and Winkel (1986)
	Different telotrisomics (cv. "Heines Hellkorn")	Zeller et al. (1987)
Barley	Primary trisomics	Shahla and Tsuchiya (1985)
	Telotrisomics	Furuta and Tsuchiya (1987)
	Primary trisomics (*Hordeum bulbosum*)	Thomas and Pickering (1988)
	Compensating trisomic chr. 4	Furuta and Tsuchiya (1986)
	Segmental tetrasomics chr. 5	Sheedy and Ramage (1985)
	Acrotrisomic chr. $5S^{SL}$	Shahla and Tsuchiya (1986)
	Double trisomics (mutation)	Prasad et al. (1985)
Pearl millet	Primary trisomics	Vari and Bhowal (1986, 1987) Rao et al. (1988a, b)
	Interchange trisomics	Singh et al. (1988)
	Tertiary trisomics	Kumar et al. (1985)
Beets	Primary trisomics	Romagosa et al. (1986, 1987)
Red clover	Primary trisomics	Taylor and Chen (1988) Taylor and Wiseman (1987)
Common bean	Primary trisomics (interchange heterozygote)	Ashraf and Bassett (1987)
Pea	Tertiary trisomics	Mercykutty and Kumar (1985)
	Interchange trisomics	Kumar et al. (1987a)
Soybean	Primary trisomics	Gwyn et al. (1985)

Monosomic analysis of F_2 populations derived from crosses between the monosomics of "Chinese Spring" and line "492" with a stunting gene revealed that chromosomes 4B and 5B of "492" each carry major genes for height reduction (Christopher et al. 1985).

Reciprocal monosomic analysis was used by Sutka and Kovacs (1985) to determine that frost resistance of wheat is under the control of genes on chromosome 5A. Furthermore, a gene for resistance to *Puccinia recondita* has been located on the long arm of chromosome 1B of common wheat using monotelosomics, monoisomics, and monosomics (Dyck et al. 1987).

A recessive, hemizygous-ineffective gene for resistance to *Puccinia graminis tritici* was located on chromosome 6AS using various "Chinese Spring" aneuploids (Singh and McIntosh 1986, 1987). Wheat lines with a transferred segment of *Agropyron elongatum* chromatin carry a gene for resistance to leaf rust. Using telosomes, it was demonstrated that the *Agropyron* chromatin is located on the long arm of wheat chromosome 7A (Eizenga 1987).

Ditelocentric accessions of "Chinese Spring" were analyzed electrophoretically for peptidase and amino peptidase activity. The structural genes encoding these isozymes were shown to be located on the long arms of chromosomes 6A and 6B (Golenberg 1986).

Additons of complete and telocentric chromosomes of *Elytrigia elongata* "Nevski" to *T. aestivum* "Chinese Spring" were used to assign genes coding for seed storage proteins to chromosome arms in the *E. elongata* genome. Genes coding for prolamins equivalent to wheat gliadins were found on chromosome arms 1ES and 6Ep (Dvorak et al. 1986).

By using monosomics and telodisomics in durum wheat, it could be shown that gene(s) on chromosome arm 7Ap prevent the production of diploid (2n) egg cells. Chromosome arm 7Dp probably contains a second gene that is capable of preventing the production of triploid plants (Joppa et al. 1987).

Singh and Joshi (1986) were able to locate genes for chlorophyll synthesis on specific chromosome arms in *Triticum aestivum*, using monosomics and ditelocentrics.

β) Trisomic Analysis in Barley and Rye

A review on gene analysis and linkage studies including trisomic analysis has recently been prepared by Tsuchiya (1987). Genetic experiments of Shahla and Tsuchiya (1986) demonstrated the usefulness of acrotrisomics in physical gene mapping by locating genes on specific chromosome segments. Six acrotrisomic lines were used by Tsuchiya et al. (1987) for genetic analysis with 28 genes mapped on the respective chromosomes. Results provide information on the approximate break points in each of the chromosome arms and the approximate physical positions of some relevant genes. Furthermore, telotrisomic analysis, conventional three-point tests, and acrotrisomic analysis were applied for linkage studies of barley chromosome 1 (Shahla and Tsuchiya 1987).

Trisomic analysis was also carried out with a spontaneous fragile stem and leaf mutant found in "Kobinkatagi 4" and the mutant gene was found to be located on chromosome 1 (Hayashi and Moriya 1985).

Table 3. Chromosomal location of 19 genes in diploid rye determined by trisomic and telotrisomic analyses (Table and references from Schlegel et al. 1986)

Gene symbol	Character affected	Chromosomal location	Reference
an1a	Anthocyaninless	7R	Melz (unpubl.)
an1b	Anthocyaninless	2R	Melz (unpubl.)
An3	Anthocyanin	2R	Melz (unpubl.)
An4	Anthocyanin	3R	Sturm et al. (1981)
br	Brittle	5R	Melz (unpubl.)
ct1	Compactum-1	7R	Melz et al. (1984)
ct2	Compactum-2	3Rq	Sturm and Müller (1982)
Dw1	Dwarf-1	3R	Sturm (1978)
Dw2	Dwarf-2	7R	Melz et al. (1984)
Ha1	Hairy-1	3R	Melz (unpubl.)
Ha2	Hairy-2	5Rq	Melz et al. (1984)
Ha3	Hairy-3	6R	Melz (unpubl.)
Per1	Peroxidase-1	1Rq	Lindner et al. (1984)
Sf1	Self-fertile-1	1R	Melz (unpubl.)
Sf2	Self-fertile-2	3R	Melz (unpubl.)
Sf3	Self-fertile-3	5R	Romanova (1982)
Sf4	Self-fertile-4	6R	Melz (unpubl.)
Sp	Spring type	3R	Melz (unpubl.)
wa	Waxless	7R	Melz (unpubl.)

Table 4. Results of monosomic, trisomic, telosomic, and marker analyses reported for different species

Species	Phenotype	Gene symbol	Chromosome (arm)	Reference
Wheat	Reduced height	Rht8	2D	Worland et al. (1988a)
	Reduced (dwarf)	Rht12	5A	Sutka and Kovacs (1987)
	Male sterility	Ms3	5As	Maan et al. (1987)
	Red auricle	Ra	2D	Knott and Zeven (1987)
Barley	Hordein polypeptide	Hor4	5s	Shewry et al. (1988)
	Mildew resistance	Jml-h	6	Hayashi and Heta (1985)
	BaYMV resistance	ym	3	Kaiser and Friedt (1989)
Rice	Green leafhopper resistance	Glh6	5	Tomar and Tomar (1987)
Maize	Benzoaxinless	bx	4	Simcox and Weber (1985)
Soybean	β-amylase mobility	Sp1	1	Griffin and Palmer (1987a)
Solanum	Topiary	tp	3	Wagenvoort (1988)

Extentive genetic studies based on appropriate trisomics and telotrisomics in rye resulted in the localization of 19 genes including their linkage relationships (reviewed by Schlegel et al. 1986; cf. Table 3).

Further examples of gen localization with comparable cytogenetic methods are given in Table 4.

c) Gene Localization with Structural Chromosomal Variants

α) Translocation Tester Sets

Chromosomes of the Wageningen translocation tester set of rye could be identified by examining their hybrids with the series of "Imperial" rye additions to "Chinese Spring" wheat: 1R=VII, 2R=III, 3R=II, 4R=IV, 5R=VI, 6R=V, 7R=I (Sybenga et al. 1985).

A translocation mapping procedure was used to map centromere distances for the genes controlling endosperm proteins on the short arms of chromosomes 1A, 1B, and 1D of wheat (Singh and Shepherd 1988a). The same procedure was used to map the Glu-1 genes controlling high-molecular-weight (HMW) glutenin subunits on the long arms of group 1 wheat chromosomes (Singh and Shepherd 1988b).

Translocations between A- and B-chromosomes were utilized in *Zea mays* to assign regions affecting the fatty acid composition of embryo oil to chromosome arms. A region affecting palmitic, stearic, oleic, and linoleic acids was identified on the long arm of chromosome 4, whereas another region affecting palmitic and stearic acid was identified on the long arm of chromosome 10 (Shadley and Weber 1986).

Gorz et al. (1987) used a set of 11 reciprocal translocations in "Combine 7978" grain sorghum, involving each of the ten chromosome pairs in at least two of the translocations, to determine which chromosomes carry genes conditioning the dhurrin (p-hydroxy-(S)-mandelonitrile-β-D-glucoside) content of sorghum seedlings. Results suggest the presence of one or more genes encoding the dhurrin content on at least five of the ten chromosomes.

β) Deletion

By using a spontaneous deletion in *Triticum aestivum* Kota and Dvorak (1986) were able to map a chromosome pairing gene and 5S rRNA genes on chromosome arm 5Bp.

d) Gene Localization with Alien Additions and Substitutions

α) Addition Lines

Subunits of tetrameric α-amylase inhibitors of *Hordeum chilense* have been located on chromosomes $4H^{ch}$ and $7H^{ch}$ based on the analysis of *H. chilense – Triticum turgidum* addition lines (Sanchez-Monge et al. 1987).

The chromosomal locations of the structural genes for secalin storage proteins in *Secale cereale* and *S. montanum* were determined by electrophoresis of grain proteins from wheat-rye addition and substitution lines. Shewry et al. (1985, 1986) demonstrated that the genes for all of the high-molecular-weight secalins are present on chromosome 1RL, and for all the ω-secalins and at least some of the γ-secalins with a relative molecular mass (M_r) of 40 000 on chromosome 1RS of both species. In contrast, the genes for the γ-secalins (M_r 75 000) are located on $2R^cS$ of *S. cereale* but $6R^m$ of *S. montanum.*

Studies of esterase isozyme phenotypes of wheat-rye additions "Imperial", "King II", and "Dakold" led to the following results: dimeric esterases are controlled by one locus located on chromosome 3R of rye. Five loci involved in the production of monomeric esterases have been located on chromosome 6R, particularly 6RL of "King II" (Salinas and Benito 1985b).

Further, malate dehydrogenase isozyme genes in wheat-rye addition lines were located on chromosomes 1R and 3R of rye (Salinas and Benito 1985a).

β) Substitution Lines

Reciprocal substitutions between the hard red winter wheat cvs. "Wichita" and "Cheyenne"associated were used to identify additive and interactive effects of individual chromosomes on nine traits associated with lodging (Al-Qaudhy et al. 1988). Chromosomes that carry genes for heading date were identified by the same procedure (Zemetra et al. 1986). The same sets were also used by Zemetra et al. (1987) to identify chromosomes carrying genes for glutenin protein, flour mixing time, and mixing tolerance.

Using disomic wheat substitution lines in which each of the D-genome chromosomes replaces the respective homoeologous A- or B-genome chromosomes, Gorham et al. (1987) showed the gene(s) determining K/Na ratios in wheat plants grown in the presence of salt to be located on the long arm of chromosome 4D. By using substitutions for chromosome 2D, some genes affecting characters like height, day-length intensity, hybrid dwarfism, and yellow-rust resistance could be positioned in the genetic map (Worland and Law 1986).

3. Genetic Marker Analyses

a) Morphological Markers and Resistance Genes

Morphological markers have been used for linkage analyses for a long time, for example, in tomato, maize, and barley. Several novel mutants of barley cv. "Morex" promise to provide suitable genetic markers. In an attempt to assign them to chromosomes, Ramage and Eckhoff (1985) crossed some of them with a tester set of male sterile genes that are closely linked to the centromers of the seven chromosomes. The linkage block of genes *hs* for hairy sheath and *yh* for yellow head character was determined on chromosome 4 using genetic markers (Hayashi and Takahashi 1986).

Locating genes for male sterility is often difficult. However, Franckowiak (1987) demonstrated that male-sterility genes in barley can be located by using a multiple marker stock.

Röbbelen and Heun (1985) selected a wide range of different mutants for barley powdery mildew (*Erysiphe graminis* f.sp. *hordei*) reaction and assigned induced genes to allelic groups. The mutated gene of B1101 could be identified as the ml-o gene and the mutated gene of N182 exhibited linkage to four marker genes on chromosome 4 and is located in or near the Ml-g locus. The E61- and the E202-gene, respectively, are independent of the ml-o and the N192 locus.

In wheat, Howes (1986) was able to demonstrate linkage between the *Lr 10* gene conditioning resistance of leaf rust, two endosperm proteins, and hairy glumes (*Hg*). Furthermore, linkage relationships between gliadin proteins and glume color were found in durum wheat by Leisle et al. (1985).

A gene for resistance to eyespot (*Pseudocercosporella herpotrichoides*) was located on chromosome 7D of bread wheat by Worland et al. (1988a). Simultaneously, Delibes et al. (1988) showed by using biochemical markers that eyespot resistance of wheat line H-93-70 is associated with a different chromosome than the resistance factor from cv. "Roazon" on chromosome 7D.

Biochemical and morphological markers were used to study linkage relationships in soybean (Kiang and Chiang 1985), where pubescence color locus *t* and the β-amylase locus *Am3* were found to be linked. Linkage assays were run by Rennie et al. (1987) with soybean lines differing in resistance to *Phytophthora megasperma* (*Rps*) and isozyme alleles in an attempt to identify markers for *Rps* loci; no linkages were detected for the 18 Rps-isozyme pairs tested.

In addition to qualitative traits, linkage analysis was also carried out for quantitative traits in tomato by means of genetic markers (Weller 1987; Weller et al. 1988).

b) Biochemical Markers for Linkage Analysis

α) Cereals and Grasses

The chromosomal locations of 59 structural genes for barley proteins have been compiled by Nielsen and Hejgaard (1987). Furthermore, the authors present a linkage map of isozyme and protein loci on chromosomes 3, 4, and 6 (Fig. 1).

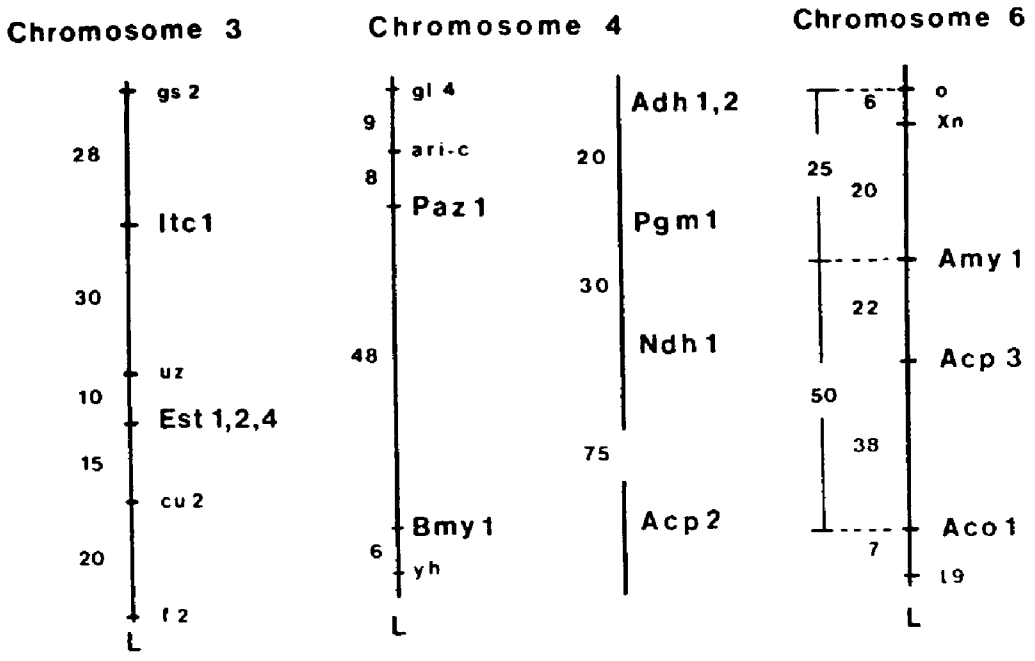

Fig. 1. Mapping of isozyme and protein loci on barley chromosomes 3, 4, and 6 (Nielsen and Hejgaard 1987)

A comparison of Est-5 grain esterase phenotypes identified homoeologous Est-5 loci on chromosome 3H of *Hordeum vulgare*, $3H^{ch}$ of *H. chilense*, $3S^{b}$ of *Aegilops bicornis*, $3S^{l}$ of *Ae. sharonensis* and *Ae. longissima* as well as on 6R of *Secale cereale* and $6R^{m}$ of *S. montanum* (Ainsworth et al. 1986).

Zymogram analysis was used to identifiy *Aegilops umbellulata* chromosomes that carry structural genes for particular isozymes (Benito et al. 1987); i.e., chromosome A: 6-phosphogluconate dehydrogenase; chromosome B: glucose phosphate isomerase and phosphoglucose mutase; chromosome D: leaf peroxidase; chromosome E: endosperm peroxidase, acid phosphatases, and leaf esterases; chromosome F: embryo plus scutellum peroxidases; chromosome G: endosperm alkaline phosphatase, leaf alkaline phosphatases, and leaf esterases.

Leaf peroxidases provide a useful biochemical genetic marker system for group 2 chromosomes in the Triticinae. Structural genes for these isozymes have been located on chromosome arms 2BS, 2DS, and probably 2AS of wheat, 2RS of rye, and on chromosome 2H of barley (Bosch et al. 1986).

Structural genes for leaf dimeric phosphatases have been located on wheat chromosome arms 7BL and 7DL and provide very useful genetic markers (Sanchez et al. 1988).

Two systems of monomeric aconitase isozymes, designated Aco-1 and Aco-2, were found in *Triticum aestivum* and in five diploid Triticeae species and their chromosomal location was identified: the gene loci Aco-A1, Aco-B1, and Aco-D1 are located in *T. aestivum* (cv. "Chinese Spring") chromosome arms 6Aq, 6Bq, and 6Dp, respectively, and the gene loci Aco-A2, Aco-B2, and Aco-D2 on 5Aq, 5Bq, and 5Dq, respectively (Chenicek and Hart 1987).

Chromosome locations of some isozyme structural genes were examined in different rye cultivars by Salinas and Benito (1985c). One locus for phosphoglucomutase isozymes is located on chromosome 4R, whereas another locus controlling the phosphoglucose isomerase isozymes is located on chromosome 1R, and three loci controlling the glutamate transaminase isozymes have

been placed on chromosomes 7R, 6R, and 3R. Close linkage between a peroxidase isozyme locus *(Prx7)* and one of the two incompatibility loci in rye has been reported by Wricke and Wehling (1985).

The genes controlling the D-group of low-molecular-weight (LMW) glutenin subunits have been located on the short arm of chromosome 1D by recombination mapping (Payne et al. 1986). Comparable chromosome mapping of the high-molecular-weight (HMW) subunits of glutenin and gliadin gene loci of *Triticum tauschii* revealed that the genes are conserved in the D-genome "homologue" (chromosome 1D) of *T. aestivum* (Lagudah and Halloran 1988).

Genetic control of maize *(Zea mays)* major zein polypeptides was studied by isoelectric focusing in agarose by Wilson et al. (1989). Markers sugary-1 (chromosome 4), yellow-8, and waxy 7-9 translocation (chromosome 7) were used to identify chromosome locations: nine zeins were found to be in one linkage group on chromosome 4, and four zeins are located in one linkage group on chromosome 7; other zeins are described, too.

β) Other Species

Recombination frequencies between three protein loci on linkage group 9 in soybean were determinated by Kiang (1987). The examined loci are acid phosphatase (Ap), leucine aminopeptidase (Lap1), and trypsin inhibitor (Ti), and the order of the three loci was found to be Ap-Ti-Lap1.

Linkage studies in soybean with four aconitase (Aco-1, Aco2, Aco-3, Aco-4) and one endopeptidase (Enp) were carried out by Griffin and Palmer (1987b) in order to facilitate their use as genetic markers. Their results allow one to assign Aco-3 to linkage group 1; the other four loci segregated independently from all loci tested. A second leucine aminopeptidase, controlled by locus Lap2, was found by Kiang and Chiang (1987a) in soybean. Linkage tests indicate that the Lap2 locus segregates independently of the Am3, Lap1, and W1 loci.

Close linkages of glutamate oxaloacetate transaminase isoenzyme GOT-1 with the incompatibility S-locus as well as the isocitrate dehydrogenase locus 1DH-1 were found by Manganaris and Alston (1987) in apple. Further analyses suggested linkage relationship of GOT-1 and GOT-2 with leucine aminopeptidase genes: GOT-2 linked with LAP-2 and GOT-4 linked with LAP-1 (Manganaris and Alston 1988).

Linkage analysis for 18 enzyme loci in *Pinus rigida* led to estimations of recombination frequencies between enzyme loci Mdh3/Pgm2 and Pep1/mdh4; tighter linkage was ruled out for nearly all gene pairs examined (Malley et al. 1986).

Segregation of isozyme markers in watermelon was studied by Navot and Zamir (1986) who were able to identifiy four linkage groups. Examination of isozymes as genetic markers in bananas and plantains carried out by Jarret and Litz (1986) led to the result that isozymes of glutamate oxaloacetate transaminase were most useful for discriminating among clones of a particular genomic group.

Gene-centromere map distances for ten isozyme loci in *Solanum* were obtained by application of half-tetrad analysis to the segregating tetraploid progenies of 4x × 2x interspecific crosses (Douches and Quiros 1987).

Table 5. Biochemical markers and their chromosome locations

Species	Isozymes	Loci	Chromosome	Reference(s)
Horedeum chilense	Esterase	Est-$H^{ch}1$	$6H^{ch}$	Fernandez and Jouve (1987a)
	Glutamate oxalacetate transaminase	Got-$H^{ch}2$	$6H^{ch}$	
	Glutamate oxalacetate transaminase	Got-$H^{ch}3$	$3H^{ch}$	
	Phosphoglucomutase	Pgm-$H^{ch}1$	$4H^{ch}$	
	Malate dehydrogenase	Mdh-$H^{ch}1$	$1H^{ch}$	Fernandez and Jouve (1987b)
	Phosphogluconate dehydrogenase	pgd-$H^{ch}2$	$1H^{ch}$	
Hordeum vulgare	Esterase	Est1/Est4	3/3	Nielsen (1985)
	Nitrate reductase deficient	nar1/nar2	6/7	Melzer et al. (1988)
Secale cereale	ω-secalin	Sec1	1RS	Lawrence and Appels (1986)
	HMW-secalin	Sec3	1RL	
	Glucose-phosphate isomerase	Gpi-R1	1RS	
	Phosphogluconate dehydrogenase	Pgd2	1RS	
	Alkaine phosphatase	Alph1	1RL	Figueiras et al. (1987)
	Alkaine phosphatase	Alph2	7RS	
	Alkaine phosphatase	Alph3	1RL	
	Alkaine phosphatase	Alph4	7RS	
	Alkaine phosphatase	Alph5	7RS	
Oryza sativa	Alcohol dehydrogenase	Adh-1	11	Ranjhan et al. (1988)
	Esterase	Est-8	7	
Phosphogluco-	isomerase	Pgi-1	4	
	Shikimate dehydrogenase	Sdh-1	6	
Glyc. max	Alcohol dehydrogenase	Adh-1	8	Kiang and Chiang (1987b)
Allium fistulosum	Alcohol dehydrogenase	Adh-1	5	Peffley and Currah (1988)
	Phosphoglucomutase	Pgm-1	4	

Further results of chromosomal locations of isozymes in different species are summarized in Table 5; comparable chromosome assignments of structural genes for barley *(Hordeum vulgare)* proteins have recently been compiled by Nielsen and Hejgaard (1987).

c) RFLPs as Molecular Markers

In practice, it is often difficult or impossible to identify large numbers of morphological or isozyme markers segregating in a relevant cross. However, recent advances in molecular biology have provided a new type of genetic marker, restric-

tion fragment length polymorphisms (RFLPs), which usually occur in large numbers sufficient to build up detailed genetic maps (Soller and Beckmann 1983). Primary advantages of RFLPs and isozymes over morphological markers are codominant expression and absence of pleiotropic effects (Havey and Muehlbauer 1989). In addition, RFLPs have the advantage of developmental stability (Beckmann and Soller 1983). Like isozyme and morphological markers, RFLPs have recently been used in plant breeding programs to map quantitative trait loci (QTLs) (Edwards et al. 1987; Stuber et al. 1987; Weller et al. 1988).

The principle of inheritance of an RFLP is schematically presented in Fig. 2.

Utilizing RFLPs as genetic markers, linkage maps were constructed for both maize and tomato by Helentjaris et al.(1986). The map for maize (Fig. 3) consists of several hundreds of RFLP loci that cover all ten chromosomes (Helentjaris 1987a). This map has been correlated with the genetic linkage map for morphological and isoenzyme markers derived from cytological data and linkage analyses (Helentjaris 1987b; Heltentjaris et al. 1988). The polymorphism in maize is apparently larger than that currently known for any other organism. Mapping of RFLP markers in maize can be accelerated by the use of B-A translocation stocks (Evola et al. 1986).

Wright et al. (1987) give a list of 28 cloned maize loci and their chromosome arms assigned by RFLP mapping. Using RFLP markers, *Css* (constitutive sucrose synthase 2) was mapped 32 ± 4 cM from *Sh1* (sucrose synthase 1) and 11 ± 2 cM from *Wx1* (waxy 1) on chromosome 9 (Behrendsen et al. 1987). Southern blot analysis of DNA from monosomic maize plants derived from an r-x1 stock, coupled with RFLP mapping, led to the same results (McCarty et al. 1986).

Recombinant inbred lines of maize have been developed by Burr et al. (1988) for the rapid mapping of molecular probes to chromosome location. A genetic map based largely on isozymes and RFLPs has been produced that covers virtually the entire maize genome. In order to map a new gene, an investigator has only to determine its allelic distribution among the recominant inbred lines and then compare it by computer with the distributions of all previously mapped loci.

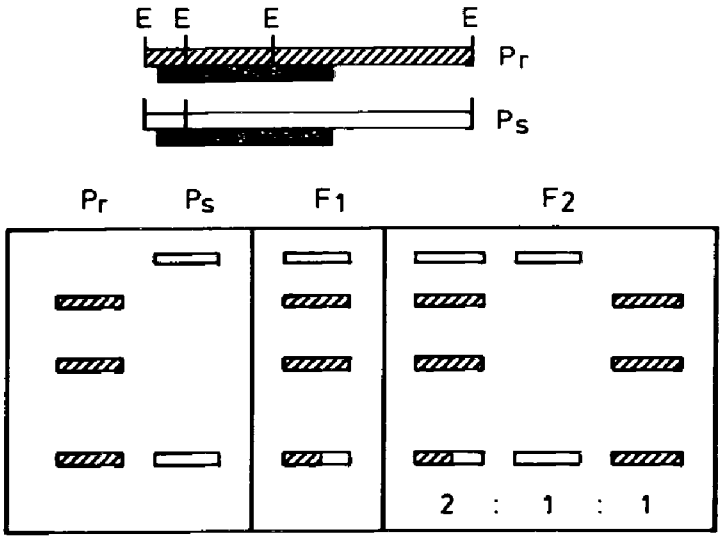

Fig. 2. Schematic diagram of the heredity of RFLPs (after Graner 1988). Above, Segments of homologous chromosomes of two cross parents (*Pr* = resistant; *Ps* = susceptible) are shown with restriction sites *(E)* and binding site of cDNA probe *(hatched)*; below, RFLP for parents, F_1 and F_2, is shown after electrophoretic separation of the probe and subsequent hybridization with the respective cDNA

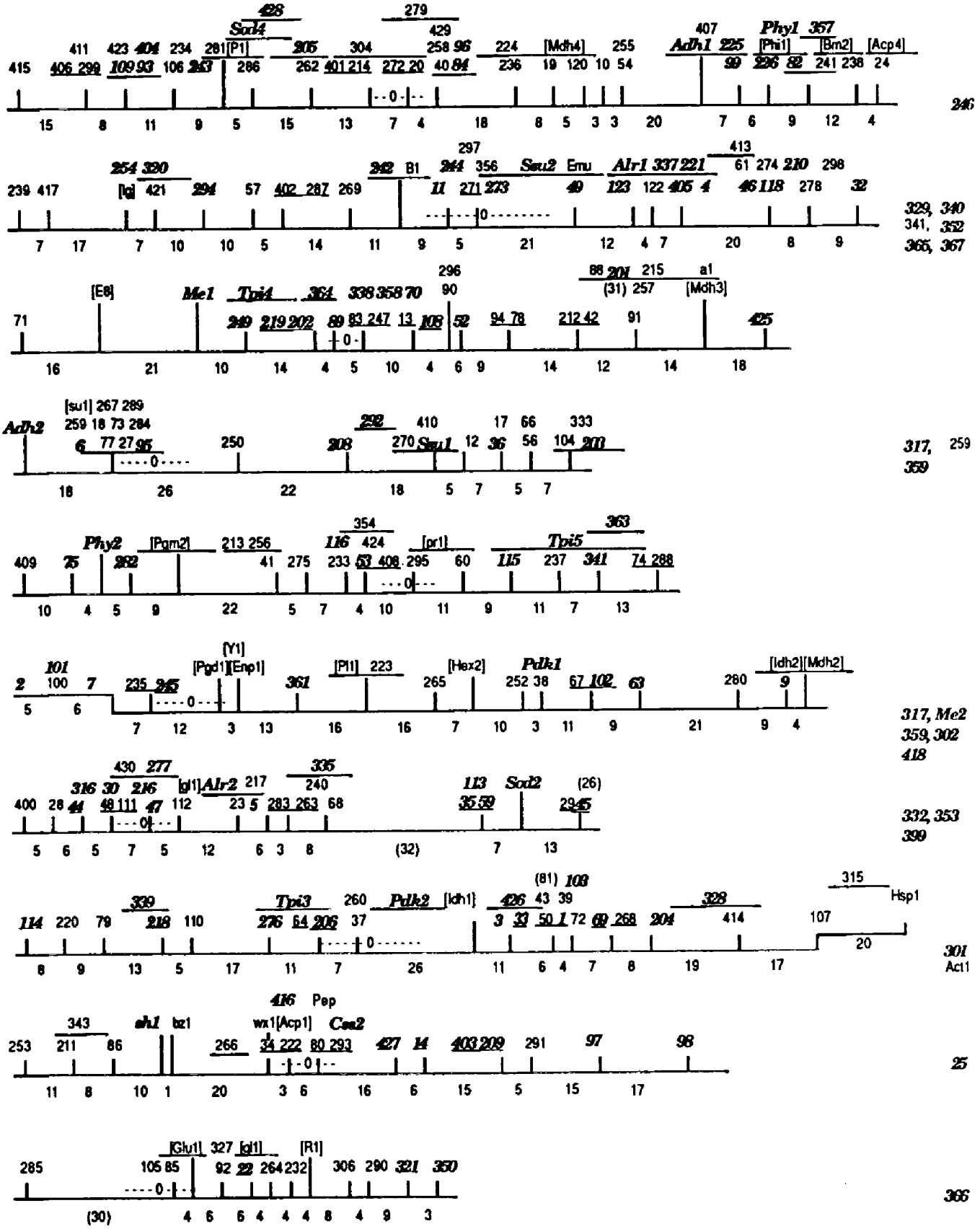

Fig. 3. Maize RFLP linkage map (Helentjaris et al. 1988)

A linkage map in tomato has been developed by using isozyme and random cDNA clones derived from mRNA; allelic differences in cDNA markers were based on RFLPs (Bernatzky and Tanksley 1986). Through earlier breeding efforts, portions of the genome of the wild species *Lycopersicon chmielewski* have been introgressed into the cultivated tomato *(L. esculentum)*. These introgressed chromosome segments have been reported to increase soluble solids (SS) in fruit of certain tomato varieties. Analysis of variance of SS content for different RFLP genotypic classes indicated that RFLP alleles at one of the loci were linked to genes controlling SS content (Osborn et al. 1987). Tanksley and Hewitt (1988) tested the association between RFLP and isozyme markers and genes controlling SS and other characters in the material described above. Three introgressed chromosomal segments from *L. chmielewskii* map to the center and the end of chromosome 7 and to the telomere of chromosome 10, respectively. Foreign genes from alien wild species are usually introduced into the cultivated one by backcross breeding procedures. Depending on the number of backcrosses applied, the introgressed genes will be flanked by unwanted segments of DNA derived from the donor parent ("linkage drag"). For example, the Tm-2 gene of *L. peruvianum* conferring resistance to tobacco mosaic virus was introduced in several tomato cultivars by repeated backcrossing. The sizes of introgressed segments flanking the Tm-2 locus have been measured by using a high density RFLP map; the smallest introgressed segment was estimated to be 4 cM in length, while the longest measures more than 51 cM, i.e., the entire short arm of chromosome 9 (Young and Tanksley 1989). The authors conclude that, by monitoring recombination around interesting introgressed genes with RFLP markers, the amount of linkage drag can be rapidly reduced so that the efficiency of backcross breeding procedures can be dramatically improved (Young and Tanksley 1989).

The tomato gene encoding the type II chlorophyll a/b-binding polypeptide of photosystem I (Cab-7) is located at the end of chromosome 10, at a distance of 1.3 ± 1.3 cM from the RFLP marker TG122 (Pichersky et al. 1988).

Bonierbale et al. (1988) report the construction of a genetic linkage map of potato chromosomes based on genomic and cDNA clones from tomato. Nearly all of the tomato probes tested hybridized to potato DNA, and in most cases the copy number of the clones used was the same in both species. Furthermore, all clones mapped to the respective linkage group in both species. For nine chromosomes, the order of loci appears to be identical in the two species.

In lentil *(Lens culinaris)* Havey and Muehlbauer (1989) constructed a linkage map comprising 333 cM by using 20 RFLP, 8 isozyme, and 6 morphological markers segregating in the interspecific cross *L. culinaris* × *L. orientalis*. It was concluded that 50% of the lentil genome could be linked within 10 cM of the 34 markers and that the map was sufficient to be used for QTL mapping (Havey and Muehlbauer 1989).

The high degree of polymorphism found even among closely related *Brassica* accessions indicates that RFPL analysis will be a very useful tool in genetic analyses of the *Brassica* genus. The development of RFLP linkage maps is now in progress (e.g., Figdore et al. 1988).

A detailed genetic map of lettuce *(Lactuca sativa)* was constructed using 53 genetic markers including 41 RFLP loci (Landry et al. 1987). In soybean *(Glycine max)* twenty-seven RFLP markers were analyzed for linkage and 11 of them could be assigned to 4 linkage groups (Apuya et al. 1988).

Strategies for RFLP analysis in barley were first introduced by Blake (1987). Recently, a β-amylase cDNA clone isolated from barley has been used to locate β-amylase encoding sequences on wheat, rye, and *Aegilops umbellulata* chromosomes by hybridization to restriction endonuclease digested DNA. Structural genes were identified on homoeologous groups 2, 4, and 5 (Sharp et al. 1988). Among several *Aegilops squarrosa* accessions investigated by Kamumorgan (1988), extensive RFLP was revealed using nine cDNA clones. In wheat-barley addition

lines, one cDNA clone each was assigned to chromosome groups 1, 2, and 4, three clones each were assigned to groups 3 and 7 and six clones were assigned to group 5 chromosomes. Genes corresponding to the respective cDNA clones were subsequently located on individual chromosome arms.

An RFLP genetic map has now also been constructed for rice chromosomes, which show a significant amount of RFLP variation (McCouch et al. 1988).

d) Construction and Completion of Genetic Linkage Maps

In addition to the genetic maps mentioned above, comparable surveys have also been given for other species. For example, an extensive overview on barley genes and genetic maps of the seven barley chromosomes has been provided by Sogaard and Wettstein-Knowles (1987). Additionally, a detailed linkage map of barley chromosome 4 based on all available and applicable recombination data has been presented by Jensen (1987).

The first attempt to present a map of the cotton *(Gosypium hirsutum)* genome with reference points on all but one of the chromosomes was made by Menzel et al. (1985). The recombination map was constructed based on chiasma frequencies in chromosome regions defined by the breakpoints of 58 reciprocal chromosome translocations. Positions and total lengths of arms as well as distances of genes from the centromeres were mapped. Subsequently, the maps of chromosome 15 (Menzel and Richmond 1986) and chromosome 16 of cotton have been revised (Menzel et al. 1987).

4. New Approaches to Interspecific Hybridization

a) Recently Established Sexual Interspecific Hybrids

In addition to numerous existing interspecific hybrids, a large number of new combinations have been reported recently. For example, diploid hybrids of *Hordeum chilense* with *H. vulgare, H. bulbosum,* and *Secale cereale* are described together with the amphidiploid *H. chilense* × *H. vulgare* (Thomas and Pickering 1985). Other hybrids of *Hordeum procerum* were readily produced with *H. parodii* (7.9%) and *Elymus virginicus* (14.3%) by Gupta and Fedak (1986a).

Zea diploperennis, a newly discovered species of the tribe Maydeae, was characterized using interspecific crosses to *Z. perennis* (Molina 1985). Triploid interspecific hybrids between *Sorghastrum nutans* (2n=40) and *S. pellitum* (2n=20) were produced by Read and Maika (1987).

Interspecific hybridizations among *Vicia narbonensis* and its related species were successful, whereas the crosses *Vicia narbonensis* × *V. faba* and *V. narbonenbsis* x *V. bithymica* were unsuccessful (Yamamoto 1986). Interspecific hybridization between cultivated broad bean *(Vicia faba)* and other *Vicia* species generally leads to limited development of hybrid tissue due to aborted embryos. It is suggested that in *Vicia* DNA content may be a better guide to postfertilization, interspecific compatibility than current views on taxonomic relationships (Ramsay and Pickersgill 1986).

Successful crossing was recently reported between *Lupinus atlanticus* (2n=38) and *L. cosentinii* (2n=32), using lines of both species selected for crossability followed by selection of relatively fertile progenies (Roy and Gladstones 1985). Therefore, Roy and Gladstones (1988) suggested that hybrid sterility in *Lupinus* may be overcome, if special, selected lines are used for crossing. It is also expected that some of the interspecific recombinants could act as genetic bridges.

In legumes, successful crosses were also obtained between *Glycine max* and wild perennial *Glycine* species (Newell et al. 1987). Further, a new interspecific *Lathyrus hybrid (L. hirsutus* × *L. odoratus)* has been produced (Khawaja 1988).

Genetic information conferring nonshattering of siliques has been introgressed in rape seed following interspecific hybridization between *Brassica napus* and *B. juncea* (Prakash and Chopra 1988).

In *Helianthus*, Georgieva-Todorova (1988) was able to produce a few hybrid plants between the cultivated sunflower *(H. annuus)* and *H. decapetalus*, a tetraploid species. A number of new hybrids have very recently been produced by Kräuter and Friedt (1989), where *H. annuus* has been successfully crossed with *H. angustifolius, H. argophyllus* (n=17), *H. bolanderi* (n=17), *H. debilis* (n=17), *H. decapetalus* (n=17,34), *H. laetiflorus, H. nuttallii* ssp. (n=17), *H. originalis, H. strumosus* (n=34,51), and *H. tuberosus* (n=51). Hybrid plants have been regenerated via embryo rescue (see below). Various interspecific combinations obtained by Skoric et al. (1988) have already been promoted to the second backcross generation (BC_2) and are expected to be very useful for sunflower improvement.

A highly sterile tetraploid (2n=36) interspecific hybrid was obtained involving three species belonging to three different sections of *Beta* (Oleo et al. 1986).

Reciprocal interspecific crosses involving *Zinnia angustifolia* clones and *Z. elegans* lines showed that in both species sporophytic self-incompatibility systems are present (Boyle and Stimart 1986). Further interspecific crosses between *Z. angustifolia* and *Z. elegans* were performed to investigate postzygotic barriers and to determine the influence of parental genotype on embryonic and vegetative development of interspecific hybrids. It was shown that *Z. angustifolia* influences variation in postzygotic development by multiple gene action (Boyle et al. 1987).

b) Application of Embryo Rescue in Vitro

In many interspecific cross combinations, seeds are not readily obtained due to postzygotic incompatibility. In these cases, embryo-, ovule-, or ovary-culture techniques can help to recover sexual progeny (hybrids) as, for example, in the case of *Helianthus* interspecific hybrids mentioned above (Kräuter and Friedt 1989). A total of 19 different interspecific hybrid combinations could be raised through "embryo rescue" in vitro, i.e., by extracting immature embryos from the ovule and culturing them on solid media. In detail, the following success rates were obtained:

Cross combinations:	46
– without success	15 (33.0%)
– successful	31 (67.0%)
In vitro culture of embryos:	384
– globular stage	9 (2.4%)
– young heart stage	214 (55.7%)
– differentiated stage	162 (41.9%)
Regenerated plants (rate)	163 (42.0%)

Ovule-embryo culture was also used to produce the first interspecific hybrids between cultivated alfalfa *(Medicago sativa)* and *M. rupestris* via embryo rescue (McCoy 1985). This technique was also essential for recovering interspecific hybrids between alfalfa and several perennial *Medicago* species; hybrids were confirmed by their peroxidase phenotypes (McCoy and Smith 1986).

Interspecific hybrid embryos of *Phaseolus vulgaris* × *P. lunatus* could be identified by slower growth rates in vitro. The *P. vulgaris* maternal genotype affected both the number and size of 15-day-old interspecific embryos (Leonard et al. 1987).

Sterile interspecific hybrids have been obtained in an otherwise incompatible cross between *Brassica juncea* × *B. hirta* through in vitro culture of hybrid ovules and ovaries (Mohapatra and Bajaj 1987).

An interspecific hybrid between *Lycopersicon esculentum* and *L. peruvianum* has been raised by embryo rescue, which was used to confirm a new S-allelic specificity in *L. peruvianum*, which is not associated with a detectable change in an S-associated protein (Maheswaran et al. 1986).

c) Cytogenetics

α) Poaceae

A better understanding of the cytogenetics of wild species aids in the utilization of exotic germplasm to improve cultivated species. Therefore, double cross hybrids involving wild *Pennisetum* species were examined cytogenetically to study the potential of germplasm transfer from wild species to pearl millet (Dujardin and Hanna 1984; Hanna and Dujardin 1986).

Several hybrids between the cultivated rice *Oryza sativa* and *O. glaberrima* and their backcrosses to *O. sativa* were studied by Bouharmont et al. (1985). Genetic imbalance was shown to be the main cause of hybrid sterility in these cases.

In other F_1 hybrids regenerated from *Oryza sativa* × *O. latifolia* and *O. glumaepatula* x *O. latifolia* crosses meiotic chromosome pairing was examined. The high number of bivalents observed in hybrids of these divergent parents indicates that a genetic system for pairing control may be present in the genus *Oryza* (Nowick 1986).

Bothmer et al. (1986a) reported on meiotic pairing behaivor of 39 new interspecific combinations between diploid *Hordeum* species. On the basis of their data, four "basic genomes" are probably present in the genus *Hordeum*. Further, Bothmer et al. (1986b) studied the development and meiosis of three interspecific hybrids between cultivated barley *(H. vulgare)* and *H. secalinum, H. tetraploidum,* and *H. parodii,* respectively.

The use of micronuclei frequency (MF) per microspore quartet has been proposed to indicate the relative reduction in chromosome homology among interspecific at *(Avena)* hybrids. It was shown that coherence of the characters studied was not associated consistently with differences in MF (Luby et al. 1985). Examinations of chromosome pairing affinities of some interspecific hybrids involving the perennial oat species *Avena macrostachya* indicated that the chromosomes of this parent undergo preferential pairing (Leggett 1985). Chromosomal stability in the backcross progenies of pentaploid hybrids between *Avena sativa* and *A. maroccana* was reported to be satisfactory with two backcrosses (Zadoo et al. 1988).

Evans and Davies (1985) demonstrated that suppression of heterogenic pairing in a series of tetraploid hybrids of *Lolium temulentum* × *L. perenne* is achieved by a

genetic system involving the A- as well as the B-chromosome system. Chromosome pairing in hybrids between diploid species of *Festuca* was described by Morgan et al. (1986). As a rule, it can be summarized that the larger the difference between the DNA content of the parental species, the more pronounced the failure of chromosome pairing in the F_1 hybrids.

β) Other Species

Intra- and intersectional interspecific hybrids mostly involving *Nicotiana umbratica* (section *Suaveolentes*) were morphologically and cytologically studied by Gangadevi et al. (1987). F_1 hybrids (2n=35) of the interspecific cross *N. knightiana* (n=12) × *N. umbertica* (n=23) showed mostly univalents during meiosis and were therefore completely sterile (Gangadevi et al. 1985).

In meiosis of F_1 hybrids between *Coffea arabica* and tetraploid *C. canephora*, irregularities and uneven distribution of chromosomes appeared, which could be improved by backcrossing with *C. arabica* (Owuor 1985).

Similarly, irregular meiosis and subsequent partial sterility were obtained in the interspecific hybrids *Capsicum annuum* var. *"cerasiformis"* × *C. chinense* var. "mishme" and *C. annuum* var. *"cerasiformis"* × *C. baccatum* var. *"pendulum"* (Kumar et al. 1987b).

Chromosome pairing and the number of univalents, as well as pollen viability in F_1 hybrids between diploid guayule (*Parthenium argentatum*) is striking, although there are many morphological differences between the parents (Hashemi et al. 1986).

Observations of chromosome pairing in autotetraploids of diploid wild species of *Arachis* indicated good prospects of utilizing autotetraploids as genetic bridges in transferring desired traits to groundnut (Singh 1986). Genomic balance in interspecific hybrids of diploid and tetraploid *Solanum* is critical due to both embryo and endosperm development (Smith and Desborough 1986).

Barrier(s) to interspecific hybridization between cultivated chickpea, *Cicer arietinum* and eight other annual wild species, were investigated by Ahmad et al. (1988) and are believed to be due to factor(s) operating after fertilization.

d) Improvement of Resistances

Helianthus debilis ssp *debilis* (2n=34) was found to be highly resistant to sunflower powdery mildew (*Erysiphe cichoracearum*) and was used to transfer resistance to the cultivated sunflower, *Helianthus annuus* (2n=34) (Jan and Chandler 1985).

In sugarbeet (*Beta vulgaris*) Jung and Wricke (1987) were able to successfully incorporate a chromosome fragment from *B. procumbens* which provides resistance to the beet cyst nematode (*Heterodera schachtii*). However, meiotic stability of progeny plants was shown to be very low (Brandes et al. 1987) so that stable sexual transmission of nematode resistance remains doubtful.

Efforts to introduce Dutch elm disease resistance into the American elm through breeding with Asian elms has been hampered by sexual incompatibility, which was shown to be induced by pollen inhibition on the stigmatic surface through an inhibitory substance (β-1,3 glucose polymer) (Bob et al. 1986).

Sterile interspecific hybrids of *Zinnia elegans* and *Z. angustifolia* were examined to determine the mode of inheritance to *Erysiphe cichoracearum*. Resistance appears to be complexly inherited

and it is speculated that the genes conferring resistance in the florets are acting independently of those controlling leaf resistance. Most of the resistance genes are derived from *Z. angustifolia* (Terry-Lewandowski and Stimart 1985).

5. Intergeneric Hybridization

a) Crosses to Create Novel Intergeneric Hybrids

α) Triticum × Other Species

It is well established that dominant alleles of the Kr1 and Kr2 genes reduce crossability of hexaploid wheat with many alien species by affecting pollen tube growth. However, wheat genotypes "Highbury" and "Chinese Spring" homozygous recessive for the two genes, kr1 and kr2, were crossable with "Seneca 60" maize. Fertilization occurred and hybrid zygotes with one complete haploid chromosome set from each parent zygotes with one complete haploid chromosome set from each parent was formed; however, endosperm development failed. All three wheat × maize combinations were karyotypically unstable and rapidly eliminated maize chromosomes to produce haploid wheat embryos (Laurie and Bennett 1986, 1987).

Crosses were also made between "Chinese Spring" and the diploid grain sorghum "S9B". Sixty-nine of 100 florets fixed 48 h after pollination contained an embryo, an endosperm, or both, a remarkably high frequency in view of the taxonomic distance between the cross parents (Laurie and Bennett 1988).

The diploid and tetraploid wheats possess an additional genetic system that inhibits development and viability of F_1 hybrid seeds resulting from pollination with rye. From the results obtained by crossing the "Chinese Spring" monosomic series to a diploid rye composite, it was concluded that the breakdown of this barrier in hexaploid wheat is determined by polygenes, but may also involve gene dosage effects (Marais and Westhuizen 1987). However, this postzygotic barrier to endosperm and embryo development, which also operates in crosses between durum wheat (genome AABB) and rye (RR), could not be suppressed by any specific chromosome of the D-genome using a set of D-genome disomic substitutions (Pienaar and Marais 1986).

"Hybrid necrosis" in triticale (× *Triticosecale*) is caused by gene interaction between its wheat and rye genomes, where a recessive gene in rye and a dominant gene in wheat are effective (Jung and Lelley 1985).

β) Other Species

An update on intergeneric hybrids in *Hordeum* and some examples of recent accomplishments in crosses with *Triticum, Agropyron,* and *Secale* were provided by Fedak (1987). For interspecific and intergeneric hybridizations involving the genus *Hordeum*, Gupta and Fedak (1987c) proposed the use of mutants or hybrid combinations stimulating allosyndetic meiotic chromosome pairing, since this will not cause undesirable translocations or deletions.

Table 6. Recently established intergeneric hybrids

Triticum aestivum × *Elytrigia repens*	Fedak et al. (1986)
Triticum aestivum × *Elymus caninus*	Sharma and Baenziger (1986)
Triticum aestivum × *Thinopyrum scirpeum* (4 ×)	Gupta and Fedak (1986d)
Triticum aestivum × *T. junceum* (6 ×)	Gupta and Fedak (1986d)
Triticum durum × *Haynalida villosa*	Stefani (1986)
Elymus canadensis × *T. aestivum*	Mujeeb-Kazi and Bernard (1985)
Secale cereale × *Thinopyrum intermedium*	Fedak and Armstrong (1986)
Secale montanum × *Pseudoroegneria spicata*	Wang (1987a)
Secale montanum × *Agropyron mongolicum*	Wang (1987a)
Hordeum parodii × *Agropyron caninum*	Gupta and Fedak (1985b)
Hordeum californicum × *Secale cereale*	Gupta and Fedak (1987b)
Hordeum chilense × *Secale cereale*	Pohler and Schrader (1986)
Agropyron cristatum × *Pseudoroegneria libanotica*	Wang (1986)
Critesion violaceum × *Psathyrostachys juncea*	Wang (1986)
Cajanus cajan × *Atyloisa* sp.	Pundir and Singh (1985)
Cajanus cajan × *Atylosia acutifolia*	Dundas et al. (1987)
Cajanus cajan × *Atylosia pluriflora*	Dundas et al. (1987)
Raphanus sativus × *Brassica nigra*	Matsuzawa and Sarashima (1986)

Fujigaki and Tozu (1987) attemped to produce new hybrids from several combinations between *Hordeum* and *Secale* species and succeeded through young hybrid caryopsis culture of *H. vulgare* × *S. africanum.*

Pollination of *Zea mays* by *Sorghum bicolor* has not as yet led to hybrid embryos (Heslop-Harrison et al. 1985). Correspondingly, no evcidence of hybridization between maize and sorghum or millet could be obtained by Bernard and Jewell (1985), whereas in crosses involving maize and *Tripsacum* many true hybrids were isolated.

With the aid of embryo rescue, both a monoploid and several hybrids were obtained from the cross *Thinopyrum elongatum* × *Agropyron mongolicum.* The monoploid was a result of gradual elimination of *A. mongolicum* chromosomes in the hybrid. All plants died, because the genomes carry complementary genes for hybrid necrosis (Wang 1987b).

Male sterility was investigated in backcross populations from hybrids between *Diplotaxis muralis* and *Brassica napus* using the former as the female parent. Cytological examinations indicated that an extra chromosome which was derived from *Diplotaxis muralis* appears to be the sole cause of male sterility in these backcross populations (Fan et al. 1985).

Further examples of recently established intergeneric hybrids are summarized in Table 6.

b) Chromosome Pairing, Recombination and Hybrid Performance

In triticale (× *Triticosecale*) it has been demonstrated that primary lines have more univalents and less chiasmata per pollen mother cell (p.m.c.) than the corresponding wheat and rye parents together (Jung et al. 1985).

The ph1b mutant in bread wheat has specifically been used to induce homoeologous pairing and recombination between the chromosome arm 1RL of rye and wheat chromosomes. Koebner and Shepherd (1985) presented the first substantiated genetic evidence for homoeologous recombination between wheat and rye chromosomes.

To study the inheritance of genetic variation in rye affecting homoeologous chromosome pairing in triticale, chiasmata frequencies were analyzed in hybrid plants derived from wheat × rye F_1 ("Petkus" × "Prolific"; "Prolific × "Puma") crosses. It was concluded that the genetic system differs in these cultivars and also in comparison to *Aegilops speltoides* (Gupta and Fedak 1986b).

In triticale breeding the importance of backcross hybrids with the parental species is increasing. Some advantages could be observed using wheat, whereas crosses to *Secale* did not show much success. For example, Skiebe and Schreiber (1986) examined the possibilities of genetic recombination in secondary 6x-*Triticale* derived from backcrosses to rye, but they did not yield substantial breeding progress. Another analysis of meiosis in triticale × rye F_1 hybrids at three ploidy levels led to the conclusion that an increase in the proportion of wheat chromosomes in the hybrids had a slight suppresion effect on homologous as well as homoeologous pairing of rye chromosomes. In contrast, an increase of the rye complement promoted homoeologous pairing between wheat chromosomes (Gupta and Priyadarshan 1987).

The meiotic behavior of three hexaploid *triticale* × *Triticum aestivum* hybrids carrying different doses of ph1 mutant alleles was also investigated by Jouve and Giorgi (1986). D-genome chromosomes were increasingly promoted to pair with their A- and B-genome homoelogoues in the absence of ph1 gene. However, wheat-rye associations were not enhanced when one or two ph1 alleles were present.

In another approach, Gupta and Fedak (1987a) determined the inheritance of rye genes which induce high chiasma frequency in hybrids with wheat. It is expected that by intermating segregating rye plants it should be possible to accumulate genes and eventually to isolate homozygous lines inducing high pairing in hybrids with wheat.

Examinations of meiotic pairing in different hybrids between tetraploid triticale and related species showed that the haploid complement of these triticales consists of seven rye chromosomes and seven wheat chromosomes. A comparison of different hybrid combinations indicated that the involvement of D-genome chromosomes in homoeologous pairing is quite limited. In contrast, a quite high pairing frequency exists between some R-chromosomes and their A- and B-homoeologues (Bernard and Bernard 1985).

Further, meiotic pairing in *Triticum turgidum* cv. "Ma" (4 ×) was compared with ciasma frequency in its hybrids with several triticale strains, "Chinese Spring" wheat and its addition lines for "Imperial" rye chromosomes 4R and 6R. All combinations showed depression of chiasma frequency where the rye addition line 4R showed the strongest effects in hybrids (Gupta and Fedak 1986c).

Studies of F_1 hybrids between aneuploids (ditelosomics) of "Chinese Spring" and *Aegilops variabilis, Ae. longissima,* and *Secale cereale* support the finding that the short arms of chromosomes 2A, 2B, and 2D carry pairing promoters, while the long arms of 2D and possibly of 2A and 2B carry minor suppressors. Promoters are more potent than suppressors and the overall effect of group-2 chromosomes results in promotion of pairing (Ceoloni et al. 1986).

Studies of chromosome pairing at meiosis of F_1 hybrids of *Triticum aestivum* and hexaploid *Agropyron junceum* showed that chromosomes of the J_1 and J_2 genomes of *Agropyron* paired in the F_1 hybrid in spite of the presence of the Ph1 gene of common wheat which normally suppresses homoeologous pairing (Charpentier et al. 1986).

Allosyndetic recombination was induced between chromosome 1U of *Aegilops umbellulata* and wheat chromosomes by producing plants monosomic for this alien chromosome and homozygous for the mutant ph1b allele, which permits homoeologous chromosome pairing (Koebner and Shepherd 1987). Interactions between wheat, rye, and *Aegilops ventricosa* chromo-

somes on homologous and homoeologous pairing were studied by Cunado et al. (1986). The frequencies of all types of homoeologous pairing were very constant in all hybrids analyzed and independent of the number of genomes which were present in the hybrids.

Diploid intergeneric hybrids of the perennial species *Secale montanum* (R-genome) and *Pseudoroegneria spicata* (P-genome) with *Agropyron mongolicum* (S-genome) were produced by Wang (1987a). Meiotic pairing of hybrids indicated that chromosome homology between S- and P-genomes is higher than either the S and R or the P and R. Both S × R and P × R hybrids represent new genomic combinations.

Meiosis was studied in hybrids between *Aegilops crassa* and six *Secale* species. Examination of chiasmata frequency provides further evidence that a meiotic pairing control system is operating in *Ae. crassa*. *Secale* genotypes suppressed the function of this system in a manner which was inversely related to their total DNA and heterochromatin content, respectively (Gupta and Fedak 1985a).

A total of seven intergeneric hybrids were produced by intercrossing six *Secale* strains onto five species of *Hordeum* including three ploidy levels. With the exception of infrequent heteromorphic bivalents there was no pairing between chromosomes of the two genera which indicates that there is no homology between the parental genomes (Gupta and Fedak 1985c).

A low frequency of rod bivalents indicating little homology was also observed at meiotic metaphase I in the F_1 hybrid between *Hordeum pubiflorum* (2×) and *Secale africanum* (2×) by Fedak (1985a). However, in F_1 hybrids between *Hordeum geniculatum* and *Secale cereale* an unexpected high frequency of homoeologous pairing occurred in comparison to the wild barley parent (Staat et al. 1985).

Also, *Agropyron intermedium* var. *trichophorum* was crossed onto *Hordeum vulgare*. Meiotic chromosome pairing indicated no homology between parental genomes and was characterized by aneuploid meiocytes with chromosome instability (Fedak 1985b). Two other diploid *Hordeum* species, *H. californicum* and *H. brevisubulatum*, were used successfully to produce hybrids with *Agropyron caninum* (2n=4x=28). It could not be ascertained whether the difference in bivalent formation of the two hybrids was due to a difference in the degree of homology or difference in meiotic control mechanisms (Gupta and Fedak 1985d).

Hybrids were obtained by pollinating *Hordeum vulgare* cv. "Betzes" with *Agropyron caninum* (4×) and *A. dasystachyum* (4×). Chromosome pairing at meiosis was very low and thus provided no indication of homoeology between parental genomes (Fedak 1985c). Further intergeneric hybrids between *Hordeum californicum* and *Triticum aestivum* cv. "Chinese Spring" were produced by Gupta and Fedak (1985e). Again, low bivalent frequency indicates no homology between parental genomes.

Shepherd and Islam (1987) examined whether wheat and barley chromosomes can be induced to pair with each other at meiosis in the absence of the normal suppressor effect of chromosome 5B. In a similar approach, *Triticum aestivum* "Chinese Spring" mutant ph1b lacking the major homoeologous pairing prevention gene was pollinated with *Hordeum vulgare* line "Tuleen 346", a triple interchange homozygote with all chromosomes distinct from one another. Although homoeologous chromosome pairing occurred in the hybrids, no evidence of interspecific chromosome pairing was observed (Sethi et al. 1986).

Intergeneric hybrids were obtained between *Hordeum parodii* (6×) and three cultivars of triticale. The differences in chiasma frequencies in the different hybrid combinations were attributed to a meiotic pairing control mechanism in *H. parodii* whose function was affected primarily by the rye chromosome constitution of the triticale cultivars and to a lesser extent by the heterochromatin content of rye chromosomes (Gupta and Fedak 1986e).

In new intergeneric hybrids between *Raphanus sativus* and *Brassica nigra* Matsuzawa and Sarashima (1986) observed more frequent autosyndetic than allosyndetic pairing at MI.

c) Chromosome or Gene Transfer Between Genera

Many wheat lines derived from wheat × rye hybrids (triticale) have already shown introgression of rye genes into these lines. In one line a short segment of rye chromosome 2R has been detected more recently (Fominaya et al. 1986). A different translocation between wheat chromosome 1A and rye chromosome 1R has now been confirmed in the wheat variety "Amigo" by Schlegel and Kynast (1987).

Friebe et al. (1987) were able to transfer the 1BL/1RS wheat-rye translocation from hexaploid bread wheat to tetraploid durum wheat. Thus, disease resistance genes located on the short arm of rye chromosome 1R can now also be used for the improvement of durum wheat. *Aegilops ventricosa* has proved to be a very valuable source of disease resistance for wheat: chromosome segments carrying genes for resistances to powdery mildew (*Erysiphe graminis* f.sp. *tritici*; Delibes et al. 1987) and eyespot (*Pseudocerocosporella herpotrichoides*; Delibes et al. 1988; Worland et al. 1988b) have been successfully transferred to hexapolid wheat.

A translocation between a common wheat chromosome and chromosome 6 of *Elytrigia pontica* confers resistance to feeding by *Eriophyes tulipae*, the mite vector of wheat streak mosaic virus and the wheat spot mosaic agent (Whelan et al. 1986).

Crosses between 8 × *Triticale* and *Triticum aestivum* were used by Löbnitz et al. (1986) to produce wheat-rye introgression lines. Results indicate that genetic information of rye had been incorporated in *T. aestivum* through substitution or translocation. The number of D-genome chromosome pairs substituted for A- and (or) B-genome chromosomes in hexaploid triticale averages 2.1 substitutions per line. Most frequent were substitutions for chromosomes 3D and 6D, followed by 1D (Lukaszewski et al. 1987).

6. Conclusions

From the literature review presented above, the following conclusions with regard to the relative importance of the different aspects discussed can be drawn.

1. Recently the construction of *genetic linkage maps* which long remained to be an interesting art for "pure" genetics became a very interesting tool even for applied plant breeders. This is mainly due to the fact that morphological markers, which have been available for a long time, are now subsidized by isozyme and RFLP markers. The latter two classes of genetic markers offer a much greater potential for genetic analyses than the traditional class, since they are often large in number, they are expressed codominantly without any pleiotropic effects, and they are independent of environmental and/or developmental effects. RFLPs can now be considered not only for identification of simply inherited (mono- or oligogenic) characters but also for mapping of quantivative characters (quantitative trait loci, QTLs). For the future, it can be expected that the response of selection for quantitative traits, like yield or stress/pest tolerances, can be predicted and monitored in

segregating (recombined) generations in the course of a plant breeding program. Accordingly, plant breeding programs could be run much more efficiently than up till now.

2. Wide crossing with the aim of broadening genetic variation in a crop species, which also used to be a "playground for cytogeneticists", can now be considered as a very helpful tool for plant breeding. This is particularly recognized today, after intraspecific limitation of genetic variation for disease and pest resistance became obvious in our major crop plants, e.g., the cereals. Basic material derived from *interspecific and intergeneric recombination*, which can now be obtained in numerous combinations through sophisticated in vitro techniques, will be a very helpful source of variation, particularly for resistance breeding.

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