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1. Introduction

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2. Genetic control and substrate specificity of recombination in bacteria

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Recombination in bacteria plays an important role in repair of damaged DNA and segregation of viable chromosomes during cell division. The conjugal process of genetic exchange in *Escherichia coli* provides a useful model of recombination which has been used widely to investigate the molecular mechanisms leading to the formation of recombinants. Recombination in this system depends normally on RecA protein and RecBCD enzyme. RecA is indispensable and catalyses pairing and strand exchange between homologous DNA molecules. RecBCD is a DNA helicase and exonuclease that acts on duplex ends and is thought to provide single-stranded DNA for RecA. In the absence of RecBCD, recombinants can be formed by alternative mechanisms that rely on the products of the *recFJNOQ* and *ruv* genes, some of which are inducible as part of the SOS response to DNA damage. Most of these genes have been cloned and their products identified. A review of recent studies suggests that these alternative mechanisms may also make a significant contribution to genetic exchange in the presence of RecBCD by making use of different DNA substrates. The possibility that the course of recombination in general is dictated by the nature of the available DNA substrates will be discussed.

3. The enzymes of genetic recombination; protein-DNA interactions at the molecular level

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The enzymatic process of genetic recombination involves the breakage and reunion of homologous DNA molecules to produce new linkage relationships between genes or parts of genes. In bacteria, this process takes place in a concerted reaction that can be subdivided into three stages; (1) *Synapsis*, in which homologous DNA sequences are brought together, (2) *Strand exchange*, in which strands from each parent unite to form a heteroduplex joint, and (3) *Resolution*, in which single strand crossovers are cut, enabling separation of the recombinant DNA molecules which now contain part of each parental DNA duplex.

Studies of purified *E. coli* RecA protein *in vitro* have shown that RecA plays a dual role in recombination. In addition to its enzymatic function in the catalysis of homologous pairing and strand exchange, RecA protein was found to form a nulceoprotein scaffold on DNA within which the exchange reactions occur. A molecular model for genetic recombination based on the enzymatic properties of RecA protein will be presented.

In recent studies, cell-free extracts from *S. cerevisiae* have been fractionated to reveal a nuclease that cleaves synthetic Holliday junctions in DNA. Using supercoiled plasmids that extrude cruciform junctions, or X-junctions contained within a small DNA fragment, we have shown that cleavage occurs at or close to the site of the crossover. Consistent with the notion that this enzyme is specific for Holliday junctions in DNA, the nuclease shows little or no activity on single stranded or relaxed circular duplex DNA. The similarities between the yeast nuclease and T4 endonuclease VII will be discussed.

4. Biochemical mechanism of meiotic recombination

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Four features of the biochemical program of meiosis (as observed primarily in *Lilium*) may be described: (1) Four stage-related intervals of DNA replication occurring at premeiotic S-phase, zygotene, pachytene, and at some time between diplotene and metaphase I. (2) Each of the prophase replications involves a distinctive group of DNA sequences, each of which has a unique meiotic function. (3) Regulation of these events is assignable to certain meiosis-specific proteins and RNAs. (4) A group of meiosis-specific proteins essential to the catalysis of synapsis and/or recombination is prominent during prophase but not during the premeiotic S-phase.

Replication of no more than 0·2 per cent of the genome is suppressed by an "L-protein" during premieotic S-phase. The suppressed component ("zygDNA") consists of widely distributed 5–10 kbp segments that replicate (incompletely) at zygotene as L-protein level declines. The protein effects a single site-specific nick when bound to the DNA. The nick is presumed to permit formation of single-strand tails and thus to provide for homologous DNA alignment. Some of the zygDNA segments are transcribed during synapsis; the "zygRNA" is unique to meiosis and to the zygotene interval. The newly replicated zygDNA strands are flanked by short gaps at each of the segments: replication is completed at diplotene or later.

During pachytene only repair replication occurs. A meiosis-specific endonuclease initiates the process by nicking DNA belonging to many families of moderately repeated sequences (PDNA). The sites and timing of the nicking are governed by a replacement of the histones in the PDNA regions by a non-histone protein and by a nuclear RNA ("PsnRNA") that is homologous to PDNA and that binds selectively at the non-histone protein.

At least four meiosis-specific proteins are synthesized during early meiotic prophase: an unwinding protein that forms single strand tails at nicks or gaps in DNA; a reassociation protein that catalyzes single-strand reassociation; a RecA-like protein; and an incompletely characterized protein that effects recombination between complementary mutant plasmids *in vitro*. All four proteins are maximally active during the zygotene-pachytene intervals.

5. Gene conversion, recombination nodules and the initiation of meiotic synapsis

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In virtually all organisms, reciprocal recombination is an essential feature of meiosis. Exchange events accomplished during prophase I become the chiasmata of metaphase I; and in most organisms, chiasmata are essential for proper disjunction of homologous chromosomes at anaphase I. Nondisjunction at the first meiotic division occurs if crossing-over fails, leading to aneuploid gametes and a reduction in effective progeny number. There is therefore immediate strong selection for maintenance of a meiotic system that will insure at least one reciprocal recombination event per pair of homologues.

However, simple gene conversion (recombinational transfer of a stretch of information between chromosomes without an accompanying exchange) does not yield chiasmata, yet simple gene conversion is a meiotic recombinational feature for all organisms examined to date. Why does gene conversion persist? There are three general kinds of answers: (1) gene conversion is an unavoidable byproduct of the molecular events that produce reciprocal recombinants; (2) gene conversion is itself selected by virtue of long-range evolutionary benefits, or (3) simple gene conversion performs a unique, essential role during meiosis. I will present and defend the hypothesis that simple gene conversion events are an integral part of the recognition of homology during the initiation of synapsis.

6. The evolution of recombination

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What selective forces were responsible for the evolution of the genes that mediate recombination? The traditional answer has been in terms of the evolutionary advantages of new gene combinations. However, the discovery that the same enzymes are involved in recombination and in DNA

repair has led to the idea that there may be a more immediate advantage for the relevant genes. Several theories of this kind will be described and criticised. The relative importance of direct and indirect selection for recombination genes will be discussed, in both prokaryotes and eukaryotes.

7. The control of recombination in allopolyploids

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Recombination between genes in the different genomes of natural allopolyploids is prevented by the action of genes which completely suppress the chiasmate association of homoeologues chromosomes at meiosis. Typical examples are polyploids of *Triticum*, *Avena*, *Festuca*, *Gossypium* and *Nicotiana*.

No such control exists in most artificial interspecific polyploids based on diploids and consequently recombination between genes on homoeologous chromosomes can readily occur. However, diploid genotypes of both *Lolium perenne* and *L. multiflorum* have been found which can modify the association of chromosomes at meiosis in interspecific hybrids at both the diploid and tetraploid level. The genetic factors responsible for this are located on both the A chromosome complement and on supernumary B chromosomes. An attempt has been made to determine the number of genes involved and their locations on the chromosomes.

Analysis of meiosis in intergeneric hybrids between these diploid genotypes and the natural allohexaploid *Festuca arundinacea* shows that the "pairing control" genes from the diploid *Lolium* interact with the diploidizing gene(s) from the Fescue to produce a range of pairing patterns at first metaphase of meiosis.

8. Chromosome pairing in allopolyploids

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Several years ago it was discovered that exclusive bivalent formation at metaphase I of meiosis in achiasmate autopolyploid *Bombyx* females was not the result of strict two-by-two pairing of homologues during meiotic prophase, but rather was the product of transformation into bivalents of illegitimate multiple pairing configurations formed during zygotene. Furthermore, it was suggested that the correction process was impeded in chiasmate *Bombyx* males by crossing over within the multivalents. This led to speculation that classic allopolyploid organisms may form bivalents in the same way and may have developed genetic control mechanisms to restrict crossing over to strictly homologous chromosomes. The allohexaploid bread wheat, *Triticum aestivum*, contains three homoeologous genomes, yet regularly forms 21 homologous bivalents at metaphase I. Three-dimensional reconstruction and whole-mount spreading of synaptonemal complexes has, indeed, shown that non-homologous chromosomes regularly form multivalents during zygotene in wheat and that these are transformed to homologous bivalents at pachytene. The correction system is largely under the influence of the Ph locus, which may delay crossing over until the correction process is complete. Allopolyploid Lolium hybrids also form multivalents at zygotene, which are corrected to bivalents at pachytene only in the presence of "diploidising genes" and accessory B chromosomes. These pairing determinants operate, therefore, in a similar way to the Ph locus of wheat, but probably act more on the siting of crossovers than on the timing of crossing over itself.

9. Recombination in plant breeding

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A great deal of "lip-service" has been given to the importance of altering the position and frequency of recombination to release or conserve variation through the breakage or retention of linkage groups. In reality, however, little of this interest has filtered through into crop breeding. The greatest influence on the release of variation through homologous recombination is still achieved by maximising heterozygosity through inter-mating. This is despite increasing evidence of localisation in recombination amongst crop plants. In cereals regions of chromosomes with high and low levels of recombination have been

observed, but whether these are correlated with the presence and absence of coding genes is not known. If not, then some of the observed failures in fixing heterosis in plants might be explained.

By far the greatest application of directed recombination has been made in the induction of chromosome pairing and recombination between homoeologues. Such interventions occur in allopolyploids and exploit, in some cases, the genetical regulation of chromosome pairing and recombination and in others, physical and chemical agents to bring about chromosome breakage and re-union. The results of this type of manipulation are being used widely in breeding today.

Directed recombination resulting from plant transformation and molecular genetic engineering may lead to the exploitation of genetic variation outside the normal genetic confines of a crop species. It remains to be seen whether such variation will be useful.

10.

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11. Legumes, *Rhizobium* and their interaction: what are we missing?

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Although both host and bacterial genetics, as they pertain to the legume-*Rhizobium* symbiosis, have reached attention for many years, only during the past years have these studies gained impetus. This has been due to the advent of the techniques of molecular biology, to the necessity to improve nitrogen fixation by existing associations, and to the exciting prospect of introducing the ability to fix nitrogen, by symbiosis, to those plant families currently unable to do so.

Prior to the mid-1970s little was known of the genetics of rhizobia. Today we know of the location, and in many cases the structure, of numerous genes required for nodulation, including those responsible for host specificity and for nitrogen fixation. Not surprisingly, much less is known of their regulation and their gene products, but the recent identification of flavones and flavone-type compounds in root exudates, and their ability to regulate the expression of certain nodulation (*nod*) genes, in association with *nodD*, provides the first real marriage of genetics and physiology. The search for bacterial factors involved in infection, nodule initiation and nodule development is intensifying and should yield the information necessary to understand the precise role of the rhizobia in symbiosis.

Numerous host genes in clovers, peas and other legumes have been documented and their gross effects described, but without any understanding of their physiological base. Through the identification of nodule specific proteins, termed nodulins, and the isolation of some of the genes involved, progress towards understanding the precise role of the host in the establishment of nodules is being achieved. The leghemoglobin genes, a gene responsible for a protein in the peribacteroid membrane, and genes involved in the metabolism of fixed N, have been described and cloned. Their regulation is another matter, but obviously the invading bacteria play a major role. It is the study of host genetics, perhaps even more so than the study of bacterial genetics, that will provide the base for extending symbiotic diazotrophy beyond existing limits. However, the two cannot be considered in isolation. Equally fascinating, but undoubtedly involving a very different range of plant functions, is the quest to transfer nitrogen-fixing ability, *per se*, to plants.

Using conventional genetic approaches, significant advances have been achieved in breeding plants with improved symbiotic capacity. Similar studies with rhizobia have been disappointing, but this could be improved when the most appropriate goals have been established.

12. Molecular genetics of the symbiotic genes of *Rhizobium*

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The ability of bacteria of the genus *Rhizobium* to nodulate legumes and to fix nitrogen within the nodules depends on their possession of particular "symbiotic" genes which specify these phenotypes. Such genes have been studied in considerable detail in several *Rhizobium* species and one of the features to emerge is that many symbiotic genes are expressed only when the *Rhizobium* bacteria are near, or in, the host plant. Thus, the genes that specify the enzyme complex nitrogenase are, in

most *Rhizobium* strains, expressed only in mature bacteroids in the nodule. Recently, it has been found that most of the genes that specify the early stages of infection and the host-range specificity of a *Rhizobium* strain are not transcribed in cells grown in normal growth media but when exposed to compounds in the exudate obtained from legume roots, these nod genes are transcribed at high levels, this induction being dependent on the regulatory *nodD* gene. The activating molecules were identified as being certain flavones (*e.g.*, apigenin) or flavonones (*e.g.*, eriodictyol). Other phenolic compounds synthesized by plants inhibited this activation; these antagonistic molecules included flavanols, isoflavonoids and acetophenones. Further details of this complex system of induction and antagonism of *nod* gene transcription will be presented.

Other recent studies have shown that the expression of *Rhizobium* genes requires for the synthesis of the exopolysaccharide (EPS) polymer is also different in the free-living and the bacteroid state and that genes which affect EPS synthesis have profound effects on symbiotic nitrogen fixation. The relationship between the genes that affect the expression or function of genes required for EPS production and those which are involved with the control of other genes that are directly involved in nitrogen fixation will be discussed.

13. Relationships of *nif*, *ntr* and *gln* genes in free-living nitrogen fixing bacteria to those in *Rhizobia*

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More than 20 genes involved in nitrogen fixation (*nif*), general regulation of nitrogen metabolism (*ntr*), or assimilation of $NH4^{+}$ by glutamine synthetase (*gln*) have been best studied in the free-living diazotrophs *Klebsiella pneumoniae* and *Azotobacter vinelandii*. A number of these have been now identified in various species of *Rhizobium*, either by DNA hybridisation experiments or by complementation of *K. pneumoniae* mutants. Recent results on the characterization of a number of these genes, including *nifA*, *glnA* and *glnB* in Rhizobium, Azotobacter and Klebsiella will be presented and discussed.

14. Instability in *Rhizobium leguminosarum* strains carrying two symbiotic plasmids

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Rhizobium leguminosarum biovars *trifolii*, *phaseoli* and *viceae* for N_2 fixing root nodules in symbiotic association with leguminous plants, the biovars being defined according to the host plant genera which they nodulate. The host range of these rhizobia is determined by the symbiotic plasmid in each strain, which carries information required for nodule formation and symbiotic N_2 fixation. Rhizobia isolated from root nodules in the field normally carry only one symbiotic plasmid and can nodulate only one of the groups of host plants. However, plasmids can be transferred between strains forming hybrids able to nodulate two different groups. These hybrids usually inherit both plasmids stably during laboratory culture but when isolated from nodules formed on one of the host plant groups are often found to have undergone plasmid rearrangements or deletions and to have lost the ability to nodulate the other group. The cause of this incompatibility during the symbiotic association is not clear. We have investigated the problem by transferring a plasmid determining the nodulation of peas, pRLIJI, into a range of *R. leguminosarum* bv. *trifolii* strains that normally nodulate clover plants, and analysing the progeny of the hybrid strains isolated from pea or clover root nodules. The results confirm the "functional incompatibility" of two symbiotic plasmids in the same *Rhizobium* strain, but indicate that the degree of this incompatibility depends on both the *Rhizobium* strain, but indicate that the degree of this incompatibility depends on both the *Rhizobium* strain and the host plant.

15. The genetic diversity of *Rhizobium leguminosarum* populations

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The genome of *Rhizobium leguminosarum* consists of a chromosome and a number of large plasmids, including the Sym plasmid which carries a region of genes involved in the symbiosis with legumes.

Both chromosomal and plasmid-borne genes show a great deal of natural variation, and a study of this variation can tell us about geographical spread, adaptation, and gene exchange within the species, as well as about the evolution of Sym plasmids and their genes.

Studies of enzyme electrophoretic variants have shown that *R. leguminosarum* strains fall into a number of distinct chromosomal lineages, and that some of these lineages are found in more than one of the three biovars (*viceae*, *trifolii* and *phaseoli*) that make up the species (Young, J. P. W., *J. Gen. Microbiol. 131*, 2399, 1985). Within a legume crop these lineages are very well mixed to the extent that the nodules on a single plant may include almost all the diverse types (Young, J. P. W., Demetriou, L. and Apte, R. G., *Appl. Envir. Microbiol. 53* (2), 1987 in press). Many of these lineages are widespread in Britain, and most populations that have been sampled have had a similar high level of genetic diversity, but the very acid soil of some hill pastures seems to support only a very restricted range of strains (Harrison, S. P., Young, J. P. W. and Jones, D. G., unpublished).

When cloned symbiotic genes are used as probes to restriction enzyme digests of DNA from natural isolates, it is apparent that there are many restriction fragment length polymorphisms on Sym plasmids. Indeed, Sym plasmids, even of one biovar, appear to be even more diverse than chromosomes. There is a non-random association between plasmid and chromosomal genotypes, and some chromosome lineages have much greater plasmid diversity than others. Nevertheless, indistinguishable plasmids are sometimes found from geographically separate sites, implying that strain mobility may be considerable, and from separate lineages at one site, implying that some plasmid transfer occurs.

16. Host genes in *Pisum sativum* L. controlling nodulation and N_2-fixation

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Wild and primitive lines of peas, occurring naturally in the Middle East and central Asia are incompatible with *Rhizobium* strains, isolated from the cultivated pea in Europe (Lie, T. A. *Ann. Biol., 88*, 462, 1978). We make use of this incompatibility, which is expressed as a defect in nodulation or N_2-fixation as a marker for genetic analysis of symbiotic genes (Lie, T. A., *Plant Soil, 82*, 415, 1984).

Two genes were found which confer "general resistance" and "specific resistance" to European *Rhizobium* strains. A third gene was detected which controls temperature-sensitive (t_s) nodulation. A number of genes were found in several plant lines, modifying N_2-fixation. The genetic analysis is complicated due to the presence of genes controlling nodule number. In one case a "maternal" effect was observed (Lie, T. A. and Timmermans, P. C. J. M. *Plant Soil, 75*, 449, 1983).

Fully compatible *Rhizobium* strains for the above-mentioned pea lines can be isolated from soils of the region where these plants grow naturally. There is some interest to make use of these resistance genes for the design of crop plants which are resistant to the natural soil population of *Rhizobium* and susceptible to the introduced inoculant strain. However, one should be aware of the possibility of competition between compatible and incompatible *Rhizobium* strains. We showed that a non-nodulating European *Rhizobium* strain can suppress nodulation of a Middle East strain completely, when applied together to a pea line from Afghanistan (Winarno, R. and Lie, T. A. *Plant Soil, 51*, 135, 1979).

17. A breeding programme to improve nitrogen fixation in white clover

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Clover and *Rhizobium* populations generally exhibit quantitative variation in nitrogen fixation. The symbionts also tend to interact rather than react together and frequently show unpredictable perturbations in performance as environments change. As a result, symbiotic genes and gene combinations of economic significance have generally proved intractible to analysis.

Problems of an essentially similar nature are frequently encountered in general plant breeding programmes but in this case there are proven practical procedures for dealing with difficulties such as genotype-environment interactions and low heritabilities of quantitative traits. In view of this it seems probable that modifications to established

breeding procedures so as to encompass the additional level of variability which the *Rhizobium* genotype imposes on the plant phenotype may lead to rapid and more reliable methods of exploiting symbiotic variability. Results are presented from an experimental breeding programme which show that, with suitable selection criteria and appropriate progeny testing, substantial advances in fixation and dry matter yield can be achieved.

18.

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19. The biometrical genetical basis of heterosis

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An early success of biometrical genetics was the development of theoretical, experimental and analytical procedures for investigating the genetical basis of heterosis. Plant breeding data generated and analysed by these procedures supported the conclusion that dominant genes dispersed between the parents of a cross rather than super- or over-dominance is the cause of heterosis.

Subsequent refinements of biometrical genetical theory, the introduction of more sophisticated experimental designs and the availability of more extensive and higher quality plant breeding data, have merely served to strengthen this conclusion. The breadth and consistency of the supporting evidence, which ranges from investigations of the nature of the gene action in heterotic F_1 hybrids, as revealed by analyses of basic generations, diallels and F_2 triple test crosses, to the direct demonstration of inbred lines extracted from them with predictable superiority to the heterotic F_1's for mean performance and environmental sensitivity, will be reviewed.

The genetical basis of heterosis imposes no limitation on the use of either highly homozygous or highly heterozygous material to improve performance. The choice may, therefore, rest on other considerations, biological, technical or economic. However, as dominance is rarely complete or unidirectional, the greater speed with which F_1 hybrids can be produced must be balanced against the greater superiority of the best inbred lines which are potentially extractable from them.

20. Heterozygosity and heterosis in autopolyploids

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In diploids, maximum hybrid vigour is achieved in the single cross of inbred parents. In autotetraploids, on the other hand, hybrid vigour is progressive and does not reach a maximum until the double cross or even later generation. Progressive heterosis in autotetraploids is correlated with the progressive increase in heterozygosity from single crosses to double crosses. However, it is not known whether the gene action involved in the maximum heterozygosity (heterosis) phenomenon is due to the interaction of multiple alleles at a locus, or is due to favourable dominant alleles on linked chromosome segments. A research strategy will be reported that separates the two types of gene action involved in yield improvement.

Results thus far indicate that favourable alleles with additive effects are more important than interactions of multiple alleles in tetraploid alfalfa. Population improvement by accumulation of favourable alleles prior to making single and double crosses enhances the levels of progressive heterosis.

21. Heterosis: its prediction and utilisation in plant breeding

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To discuss the utilisation of heterosis in plant breeding it is necessary to consider its genetic basis. The cross fertilised plants in which the phenomenon of heterosis is very important, such as maize, it appears that a great part can be explained by the mutation load. However in both autogamous or allogamous plants it is difficult to exclude a role of "Marginal" superdominance which could justify hybrid variety production.

To know in a relatively short time if it will be better to develop lines or hybrids it is necessary to

know the parameters (mean and variance) of the distribution of all varieties of a given type which can be derived from the breeding population. Some results are given in maize showing that the variance among lines is very much greater than the variance among crosses. Arguments for the partial fixation of heterosis are given.

To develop lines or hybrids, a general strategy is given. Its main axis is population improvement which has to be adapted to the type of varieties to be developed. It is shown that according to the situation the type of varieties to develop can change with time: single cross can be more justified at the beginning and lines can be justified later if all heterosis were fixable. To develop hybrids the best scheme is reciprocal recurrent selection with half sib progenies following by pedigree reciprocal selection initiated by full-sib progeny tests. With this strategy there is no problem of the prediction of hybrid performances. However, it seems possible to develop some predictors of heterosis or of specific combining ability between two lines using some criteria of genetic distances. Preliminary results with distances computed from the behaviour of lines in a two-tester top cross design appears very stimulating.

22. Exploitation of heterosis in wheat breeding

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In the 1970s hybrid wheats were produced experimentally using a cytoplasmic system and a single gene mutant for male sterility. The system proved unsuitable for commercial use in the UK. The possibilities for hybrid wheats have now opened up with the development of chemical hybridising agents (CHA) by several companies. Hybrid wheats have been entered into National List Trials and could be introduced within a few years.

Crossing blocks treated with CHA have confirmed large differences between breeding lines in pollen release and in female receptivity, to the extent that many varieties are unsuitable as either male or female parent. It is, however, clear that the technical problems in producing hybrid seed can be overcome. F_1 yields are commonly 10–12 per cent above the higher yielding parent, with indications that heterosis reduces with increasing yield of the parents. Heterosis for yield is mainly expressed as increased 1000 grain weight and grain quality requirements can be readily met in suitable crosses. To reduce seed costs consideration is also being given to F_2 as the farm crop. In the expectation that heterosis can be mostly fixed in pure lines, hybrid varieties may be a passing phase in wheat breeding. There may, however, be functional or operational advantages in heterozygosity at some loci, for example, those controlling dwarfness or disease resistance.

23. The relationship of recombination nodules to chiasmata in *Dendrocoelum lacteum*

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The fresh water planarian *Dendrocoelum lacteum* provides a useful system in which to examine the hypothesis that recombination nodules (RNs) are organelles directly involved in the recombination events which lead to crossing-over and chiasma formation. This flatworm is hermaphrodite and consequently male and female meiosis can be studied within the same individual. Cytological investigations have shown that spermatocytes and oocytes within the same individual differ significantly in their chiasma frequency and distribution (Pastor and Callan, *J. Genet.*, *50*, 449, 1952). Our own observations confirmed that oocytes form 1·6 times as many chiasmata as spermatocytes.

RNs were recorded in three dimensional reconstructions of 10 spermatocytes and 10 oocytes of *D. lacteum*. The numbers of RNs associated with the synaptonemal complex (SC) at pachytene were in close agreement with the numbers of chiasmata observed in later stages of oocytes and spermatocytes. It was also observed that the total SC length of oocytes is 1·6 times longer than that of spermatocytes. The proportionality observed between SC lengths and RN/chiasma frequencies in *D. lacteum* suggests a possible mechanism of chiasma frequency regulation based on SC length. Such a mechanism has also been proposed to explain observations made in *Mea mays* (Gillies 43, 145, 1973; Morgansen, *Carlsberg Res. Commun. 42*, 475, 1977) and humans (Holm and Rasmussen, *Carlsberg Res. Commun. 42*, 283, 1977.

24. Recombination nodules in *Allium* species

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Structures termed recombination nodules (RNs) have been observed associated with pachytene synaptonemal complexes (SCs) in many organisms and it has been proposed that they occur at crossover sites since the frequencies and distributions of RNs are similar to those of chiasmata and/or genetical crossovers (Carpenter, *Genetics*, *92*, 511, 1979). To further examine the coincidence of RNs and chiasmata two species of *Allium* were investigated. *Allium fistulosum* and *Allium cepa* are two closely related onion species which have very different chiasma distributions. *Allium fistulosum* has proximally localised chiasmata whereas 90 per cent of the chiasmata in *Allium cepa* occur in distal and interstitial locations. The technique of whole mount surface spreading of SCs was adapted for use on these species (Albini and Jones, *Exp. Cell. Res.*, *155*, 588, 1984). It was found that at pachytene RNs were associated with the SCs and their distribution closely matched the chiasma distribution in both species.

The stage of prophase at which RNs first appear is not clear. RN-like structures have been observed during zygotene in several species (*e.g.*, Holm and Rasmussen, *Carlsberg Res. Commun.*, *48*, 351, 1983; Stack and Anderson, *Amer. J. Bot.*, *73*, 264, 1986). In zygotene nuclei of the *Allium* species, small spherical structures which are intimately associated with closely aligned axial cores, prior to pairing, have been observed. They persist in the SC but disappear abruptly at the end of zygotene. In view of their apparent close association with SC formation these structures have been termed pairing nodules (PN). Similarities and differences between PNs and RNs are discussed.

25. Chromosomal DNA changes and recombination in *Lathyrus*

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Variation in chromosome size and total nuclear DNA amounts is large among diploid species ($2n = 14$) of *Lathyrus*. The chromosome shapes and karyotype arrangements are similar in the complements of most diploid species irrespective of a five fold increase in nuclear DNA amounts. The excess DNA acquired during evolution are preponderantly repetitive in nature and are distributed equally in all chromosomes within each complement.

The present investigation was to find out whether the recombination in *Lathyrus* species was related to the DNA content in chromosomes. The DNA content and chiasma frequency were measured separately for each bivalent and metaphase I of meiosis for eight *Lathyrus* species. The variation in genome size was two fold between the 8 species investigated. The results showed that within each complement the chiasma frequency per bivalent was directly correlated with its DNA amount. However, between complements the amount of recombination per unit amount of DNA decreased with increase in genome size.

The location of c-band heterochromatin in the chromosomes of the eight species was also determined. The effect of heterochromatin on the location and frequency of chiasma in the chromosome bivalents is discussed.

26. Induction of recombination between homoeologous chromosomes of wheat and rye

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The suppressive effect of the *Phl* gene in bread wheat on allosyndetic recombination has been known for many years, and its exploitation in gene introgression from related domesticated and wild Triticeae species has been advocated as a tool for extending the gene pool in cultivated wheat. Cytological investigations of metaphase I chromosome associations in *Phl*-deficient wheat-rye hybrids have suggested a low frequency of wheat-rye chromosome synapsis, and on this basis it has been thought that introgression from rye by *Phl* manipulation would not be practicable. Recent results, using selectable genetic markers, have demonstrated that recombination does occur at a significant frequency. Rye chromosome arm 1RS carries *SrR*, a gene conferring resistance to stem rust, but the complete arm Robertsonian translocations to wheat chromosomes 1BL or 1DL produce flour

giving weak dough unsuitable for breadmaking. Allosyndesis in translocation heterozygotes was induced and various physiological, biochemical and molecular markers were employed to select and characterise a number of wheat-rye recombinants. In particular, two reciprocal-type recombinants with a common length of rye chromatin (including *SrR*) were obtained. Preliminary assessment of back-cross derivatives of one of these indicates a dough strength intermediate between the recurrent (normal) and the translocation parents. This line lacks one of the three known storage protein loci on 1DS, whose products are expected to influence dough quality. The two recombinants have been intercrossed in order to extract homologous recombinants carrying an intercalary segment of 1RS, together with all three storage protein loci. This genotype is expected to have a dough quality equal to a normal wheat, and will allow the exploitation of *SrR* in breeding programmes.

27. Meiotic chromosome pairing and recombination in the human male

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There is generally a good agreement between initiation and progression of homologous synapsis and chiasma localisation in the human male with proterminal synaptic initiation and clustering of chiasmata, the pericentromeric regions the last to pair and the heterochromatic blocks differentially delayed, correspondingly to the lack of chiasmata in these segments.

EM investigations of surface spread Synaptonemal Complexes from eight structural heterozygotes indicate, on the one hand, that initial homologous synapsis is efficient and precise, and that, on the other hand, exchange pairing may be selectively prohibited with non-homologous synaptic adjustment at later stages of pachytene. The occurrence of asymmetric pachytene crosses in reciprocal translocations, interpreted to indicate central asynapsis followed by non-homologous synapsis, is of particular interest, as this may explain the well documented changes in chiasma pattern and recombination within the interstitial segments.

Interstitial pairing initiation, regularly seen at the mid-point of two comparatively large and loop forming pericentric inversions, speak against predetermined pairing sites, and may lead to a strictly localised chiasma at this site, while insufficient homologous synapsis at the base of the loop be associated with crossing-over suppression. In contrast, a smaller, largely non-loop-forming pericentric inversion (having one break point the heterochromatic p arm), showed mainly asynapsis or non-homologous synapsis expected to be associated with crossing-over suppression; and the question arises if the recombinant offspring (2/8) could be the result of an aberrant chiasmatic exchange of U- rather than X-type.

28. A fertile mule and hinny in China

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Anecdotal reports of fertility in female mules (mare × jack donkey) and hinnies (jenny donkey × stallion) have appeared in the literature over the years, but scientists have generally regarded them with scepticism (Chandley, *Genet. Res. Camb.*, *37*, 105, 1981). The fact that these hybrids can come into oestrous at irregular intervals makes fertility a possibility, given that opportunity for mating arises. In China, where mules are bred extensively for work on the farms, a fertile female mule (Rong *et al.*, *J. Roy. Soc. Med.*, *78*, 821, 1985) and a fertile female hinny have now been verified by chromosomal investigation. Each had mated with a donkey and produced a female foal. The foals show unique hybrid karyotypes different from the mule or hinny, and different from each other. Both have inherited a mixture of horse and donkey chromosomes via the ovum. A fertile female mule has also been verified by chromosomal and biochemical investigation in the U.S.A. (Ryder *et al.*, *J. Hered.*, *76*, 379, 1985).

29. The control of double reduction in natural and experimental polyploids

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Double reduction is a feature of multivalent forming polyploids. It involves chiasmata at right-angles to the normal line of orientation and results in products of replication, distal to the point of crossing-over, being included in the same nucleus after the second meiotic division. "Side-on" chiasmata are characteristic of multivalents in adjacent orientation and their frequency sets an upper limit to the incidence of double reduction. Direct investigations of double reduction, using gene markers, are laborious and inappropriate for most organisms. In theory the frequency of double reduction could reach 50 per cent for genes in distal segments; in practice it rarely exceeds 16 per cent. The frequency of double reduction is compared between sites on acrocentric and metacentric chromosomes in autotetraploids, between experimental and natural polyploids and between individuals in natural populations. The resulting estimates have been inserted into models of selfing and response to selection under polysomic inheritance.

30. Effects of hydrozyurea inhibition of DNA synthesis on meiosis

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The role of late replicating meiotic DNA in grasshopper spermatocytes has been examined by using hydroxyura (HU) to inhibit semiconservative DNA synthesis. The results were as follows: (i) spermatogonia and S-phase meiotic cells were killed; (ii) late S-phase meiotic cells were arrested but not killed; (iii) very late S-phase/pre-leptotene cells underwent normal synapsis and crossing-over as demonstrated by normal chiasmata, but showed a failure to resolve sister chromatids, leading to bridges at anaphase I and/or II. In many cells, chromosome fragmentation occurred after metaphase I to give around 30 "sticky" pieces. These were eventually incorporated into irregular early spermatids but did not progress to elongation. Labelling with ^{3}H-thymidine suggests that the sensitive period was less than 24 hours after the star of S-phase; (iv) later-stages-zygotene onwards-were not affected by HU; (v) No delays were seen in passage of labelled cells through meiosis, although HU was present for 48 hours of the 130 hours of meiosis. This implies that (a) synapsis and recombination use DNA repair synthesis systems and (b) late replicating meiotic DNA is related to sister chromatid adhesion. Sister chromatid adhesion is in turn related to the major difference in segregation at meiotic metaphase I and mitosis.

31. Hypervariability in a conservative sex-chromosome system

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The subgenus *Acetosa* of the genus *Rumex* is characterised by highly-differentiated sex-chromosomes. Females of all seven species have a pair of metacentric X-chromosomes twice the length of the longest autosomes. Males have an X and two non-homologous distinguishable Y-chromosomes which form a convergent trivalent during meiosis. The Ys are entirely heterochromatic but despite this there is no variation in length relative to each other or to the X within species. Between some species, however, the sex-chromosome proportions are different. In contrast to this stability the structure of each Y is continuously variable in terms of the centromere position such that every other male is distinguishable by its karyotype. This hypervariability is found in all species. The statics and dynamics of this sex-chromosome system will be considered.

32. Complex, SOS-independent regulation of the *Escherichia coli* K-12 *uvrC* gene

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The *E.coli uvrC* gene encodes one subunit of the endounclease which removes UV-induced

pyrimidine dimers from damaged DNA. The regulatory region of the gene has been analysed by subcloning appropriate restriction fragments into the promoter probe vector pPV502, generating operon fusions to the chloramphenicol acetyltransferase (*cat*) gene. We have identified at least three promoters capable of controlling *uvrC*, the majority of the transcripts originating from the most distal of these promoters. Partial transcription termination of the major transcript apparently plays a role in the control of the gene. *In vivo* and *in vitro* studies reveal no evidence for control by the *recA-lexA* regulatory circuit. The complex control of *uvrC* differs from that of *uvrA* and *uvrB* and implies an important role in cell function.

33. Combining ability and heterosis for quantitative powdery mildew resistance in barley

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The estimation of combining abilities and heterosis for quantitative resistance against *Erysiphe graminis* f. sp. *hordei* of eight spring barley (*Hordeum vulgare*) varieties is presented. For this purpose, a half diallel cross and its parents were arranged in five Latin squares, each inoculated with a different mildew isolate. Significant general combining ability was found, whereas specific combining ability was non-significant. A great part of the general combining ability was conditioned by additive variety effects. Significant variety heterosis was obtained too. Referring to the analysis of a fixed set of parents, 'Grit' and 'Hora' were the best parents for further crosses. Significant average heterosis was obtained, but its effect was small. Artificial crossing does not influence quantitative resistance of F_1 plants in these experiments. Data are discussed for their relevance of breeding pure lines.

34. Relations between parthenogenesis, heterozygosity and environmental sensitivity

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Seed apomicts are of potential interest in plant breeding and genetic engineering because they can combine the advantages of genetic uniformity and heterosis. All mechanisms of parthenogenesis promote genetic uniformity but, while pre-meiotic restitution conserves heterozygosity, post-meiotic doubling eliminates it. At meiosis, heterozygosity around the centromere is preserved through first division failure but lost if it is the second division which fails. Lower levels of heterozygosity are associated with increased environmental sensitivity which may not always be desirable but is at least readily detectable in seed apomicts. Frequent first and second division failures occur at male meiosis in tetraploid *Hierochloe odorata* from Scotland both separately to give unreduced tetraploid products and consecutively to produce octaploid nuclei. Neither octaploid *H. odorata* from Swedish Lapland at least on the male side. Seminferous clones of *Poa alpina* vary in environmental sensitivity, largely in relation to natural habitat rather than chromosome number. Electrophoretic comparisons of enzyme markers have been used to investigate levels of heterozygosity in these species.

35. Overdominance in heterosis: indirect gene action through general resistance to adverse environments

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A model for heterosis is presented which could be general for any situation, in contrast with all the diverse ones as yet studied. Instead of looking for a genetic effect, cause of heterosis, in genes responsible for the metric or productive trait, this model considers the heterosis as an indirect effect of loci responsible for vigour or resistance to adverse environments. Heterozygosity in those vigour loci will produce strong organisms which will be active

in adverse or stress conditions; the homozygous individuals will be weaker and they should be depressed on those same conditions (overdominace in vigour). In those adverse environments the active individuals will express their genetic capacity to produce much better than the depressed ones. In optimum environment that difference will be lesser or not observed because both types will be active. So the heterosis should be more a maintenance of the genetic potential for production in stress situations rather than an increase of it in the cross. Even though there is not a definite proof to accept this model, some basis in favour of it are also presented: heterosis more conspicuous in bad environments and clear overdominance for vigour traits. Finally, since heterosis is a general phenomenon observed, more or less, in any productive trait, it seems logical to look for an unified model of genetic effect, rather than to try to explain each case by a different mechanism.

36. The transfer of diploidizing genes by backcrossing

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Tetraploid hybrid cultivars of *Lolium perenne* × *Lolium multiflorum* are extensively used in U.K. grassland farming. Tetrasomic inheritance modified by the effect of some preferential pairing of homologous chromosomes gives populations which are genetically more stable than comparable diploids.

Genotypes of both parental species have been identified which contain genes capable of suppressing the degree of homoeologous chromosome association at metaphase I of meiosis in both diploid and tetraploid hybrids with *L. temulentum* and in tetraploid hybrids with each other. A diploidising effect is thus achieved which is considered ideal for improving still further the genetic stability of commercial hybrids of *L. perenne* × *L. multiflorum*.

The transfer of these diploidising genes from the agronomically inferior donor genotypes into genotypes of both *L. perenne* and *L. multiflorum* which can be used by the breeders is being carried out through an extensive programme of recurrent backcrossing at the diploid level. Identification of backcross progeny containing the diploidising genes is achieved by test crossing to *L. temulentum* Ba3081 and subsequent cytological screening of testcross progeny for those families showing low bivalent frequency. From the data already collected from two generations of backcrossing it is apparent that the genes are easily transferred.

37. Distribution and divergence during evolution of classes of repetitive DNA sequences in *Lathyrus* species

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Repeated DNA sequences in the genomes of higher plants vary in base sequence complexity and in their copy number. A class of repeated DNA similar enough to form stable duplexes are defined as a family of repetitive sequences. Different families differ in the extent of base sequence divergence between their members which may reflect the time interval since the family was first formed. It may also suggest conservation of certain repeated sequences.

In *Lathyrus* 56–70 per cent of the total DNA is made up of base sequences which are repetitive. Cross reassociation among repetitive and among non-repetitive fractions from different species has shown substantial divergence in DNA composition. High resolution denaturation profiles of the reassociated DNA duplexes were analysed for 7 *Lathyrus* species using higher derivative analysis to distinguish thermal classes which characterise families of repetitive sequences. The seven species embraced a two fold variation in nuclear DNA amount. In six out of the seven species investigated the number of thermal classes were similar. Within each species the amount of DNA contained in different thermal classes varied. The degree of base sequence divergence in different thermal classes as estimated from the thermal stability of the DNA duplexes also varied within each species. Between species the amount of repetitive sequences contained in each thermal class increased with increase in genome size. In *L. tingitanus* a limited number of thermal classes were distingished but each contained a greater proportion of the total repetitive sequences. The significance of the origin and divergence of classes of repetitive sequences during the evolution of *Lathyrus* species is discussed.

38. Chiasma frequency of the individual bivalents of wheat

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By crossing the 21 tetrasomic lines of *Triticum aestivum* cv. Chinese Spring with rye, *Secale cereale*, 21 hybrid genotypes were produced, each with a single different homologous pair of wheat chromosomes. The chiasma frequency of each individual wheat bivalent was scored and significant differences were found. The differences could not be attributed to chromosomes from the different constituent genomes nor from differences in chromosome length. It is therefore concluded that chiasma frequency is specific for each bivalent. The study of isolated wheat bivalents in the hybrid situation is considered valid as the sum of the chiasma frequencies of the 21 bivalents from the hybrids was close to the total chiasma frequency of wheat itself. The fact indicates that chiasma formation of individual bivalents in wheat is independent of other bivalents and there is no interbivalent competition.

The chiasma frequencies of the constituent wheat genomes were close to those of the donor species indicating that the frequency of chiasma formation has remained fairly constant during the evolution of polyploid wheat.

39. Repeated sequencies in *Staurodens scalaris* (Orthoptera)

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The grasshopper *Staurodens scalaris* has large blocks of centromeric heterochromatin. Highly repeated simple sequences often lack normally common restriction enzyme sites. *In situ* digestion of chromosomes has been used to reveal local variation within the blocks of repeated sequences where an irregular distribution of recognition sites leads to uneven removal of DNA.

40. Non-homologous pairing in four heterozygote translocation human male carriers

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An EM study of synaptonemal complexes was performed on testicular biopsies from carriers of 4 translocations each with a different fertility status. As expected, quadrivalents were observed in the two reciprocal translocations: t(9;21)(q22.33;q11.2) and t(4;16)(p14;p11.2) and trivalents in the two Robertsonian translocations: t(13q;14q). In addition, non-homologous pairing was detected among 3 per cent of t(9;21) cells, 22 per cent of t(4;16) cells, 8 per cent of t(13q;14q) cells but none from t(13q;14q). We believe that delayed synapsis within the interstitial segments gives rise to this non-homologous pairing and that its frequency is correlated with the length of the translocated segments. This may explain the well documented changes in frequency and distribution of chiasma within the interstitial segments.

Meiotic NOR association between 13p and 14p was observed only in the Robertsonian translocation in which non-homologous pairing occurred and a mechanism for this association and its possible effects on fertility is discussed in the text.

41. Synapsis, chiasma formation and DNA quantity

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Closely-related species may be very similar in overall karyotype while differing in the quantity of DNA they contain. This observation is clearly pertinent to the mechanism of genome evolution but studies of hybrids between such species may also give insights into the process of chromosome pairing itself. Meiosis has been examined in three hybrids with very large DNA differences between the parents: 75 per cent, 55 per cent and 50 per cent, respectively. In these hybrids pairing and chiasma formation is very regular. There is little univalence and chiasma frequency and distribution is identical in parents and hybrids. Despite the massive DNA difference homoeologues are completely paired from telomere to telomere with no asynapsis or loops and buckles. It is clear that pairing is precise at the light microscope level but that the opposed chromosomes differ in size. The evolution of these species pairs has involved chromomeric DNA but apparently not the DNA

associated with the synaptic process or the mechanism of chiasma formation.

42. Surface spreads of synaptonemal complexes in *Crepis capillaris*

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Pollen mother cells of diploid *Crepis capillaris* (2n = 6) were spread using detergent as the spreading agent, fixed with paraformaldehyde (Albini and Jones, *Exp. Cell. Res.*, *155*, 588, 1984), and stained using silver nitrate. From pachytene spreads the length of the synaptonemal complexes could be measured and, in conjunction with markers such as the nucleolar organiser region, a synaptonemal complex karyotype constructed. Examination of zygotene spreads has provided data on the pattern of pairing in *C. capillaris*. The technique developed here is currently being applied to both structural and numerical variants of *C. capillaris*.

43. Unequal crossing-over in *Escherichia* K12: the question of mechanisms

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We are studying amplification of a genomic 1S1-flanked unit in *E. coli* K12. The initial step in the amplification is an unequeal exchange between the 1S1 repeats, to give a tandem duplication; further unequal exchanges result in a 45-fold increase in copy number. The first step occurs only if the F factor is integrated *in cis* to the unit, while the subsequent steps are independent of the F factor. We will present data on two aspects of this system.

(1) The effects of mutations in the *E. coli rec* genes on the unequal exchanges occurring (i) between the 1S1 repeats in Hfr strains (ii) between the tandem repeats to give further amplification, or to decrease the copy number.
(2) Generation of the amplification from the duplication under conditions that suggest that DNA replication additional to normal cell-cycle DNA replication is occurring. We will consider possible models.

44.

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