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***Goldacre Paper*:**

Understanding meiosis and the implications for crop improvement

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Abstract. Over the past 50 years, the understanding of meiosis has aged like a fine bottle of wine: the complexity is developing but the wine itself is still young. While emphasis in the plant kingdom has been placed on the model diploids *Arabidopsis* (*Arabidopsis thaliana* L.) and rice (*Orzya sativa* L.), our research has mainly focussed on the polyploid, bread wheat (*Triticum aestivum* L.). Bread wheat is an important food source for nearly two-thirds of the world's population. While creating new varieties can be achieved using existing or advanced breeding lines, we would also like to introduce beneficial traits from wild related species. However, expanding the use of non-adapted and wild germplasm in cereal breeding programs will depend on the ability to manipulate the cellular process of meiosis. Three important and tightly-regulated events that occur during early meiosis are chromosome pairing, synapsis and recombination. Which key genes control these events in meiosis (and how they do so) remains to be completely answered, particularly in crops such as wheat. Although the majority of published findings are from model organisms including yeast (*Saccharomyces cerevisiae*) and the nematode *Caenorhabditis elegans*, information from the plant kingdom has continued to grow in the past decade at a steady rate. It is with this new knowledge that we ask how meiosis will contribute to the future of cereal breeding. Indeed, how has it already shaped cereal breeding as we know it today?

Additional keywords: *Asynapsis1*, chromosome pairing, meiosis, *Ph1*, recombination, synaptonemal complex, wheat.

Introduction

Given the importance of small grain cereals including wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.) and barley (*Hordeum vulgare* L.) in agriculture, there is constant demand to produce new varieties. With world wheat stocks declining and rice yield reaching a plateau in recent years, it is imperative that demand is met for an ever expanding global population. Meeting this demand will have its challenges but through the marriage of classical plant breeding and molecular approaches to create new varieties, we have already moved forward significantly in the past two decades. Underpinning significant yield improvements in many of the cereal crops is the understanding of how cellular processes work and how those processes can then be manipulated for the benefit of plant breeding programs. One such process, that many scientists and plant breeders alike consider as the 'holy grail' in significantly being able to enhance plant breeding strategies of the future, is meiosis.

Meiosis is required for the production of gamete cells that contain half of the genome content of a parental cell. This halving of genome content ensures that, upon fertilisation, the newly formed zygote contains the correct amount of genetic information, equal in quantity to that of the parents' cells. In addition, desirable combinations of alleles can be produced during meiosis. These combinations are the direct result of the recombination events that occur, ultimately leading to the genetic diversity that we see from generation to generation. However, strong selection pressure imposed through cereal breeding programs in the past has limited the genetic diversity that is readily available (Able *et al*. 2007).

Historically, meiotic studies in all eukaryotes have involved cytological analysis of cells by light and electron microscopy to understand key chromosomal events. Through such analysis the meiotic cycle has been divided into several stages, principally by the various changes in chromosome morphology that occur (Fig. 1). During one of the early stages, prophase I, there are a further five sub-stages (leptotene, zygotene, pachytene, diplotene and diakinesis), defined by cytological observations, during which three important meiotic events are occurring: chromosome pairing, synapsis and

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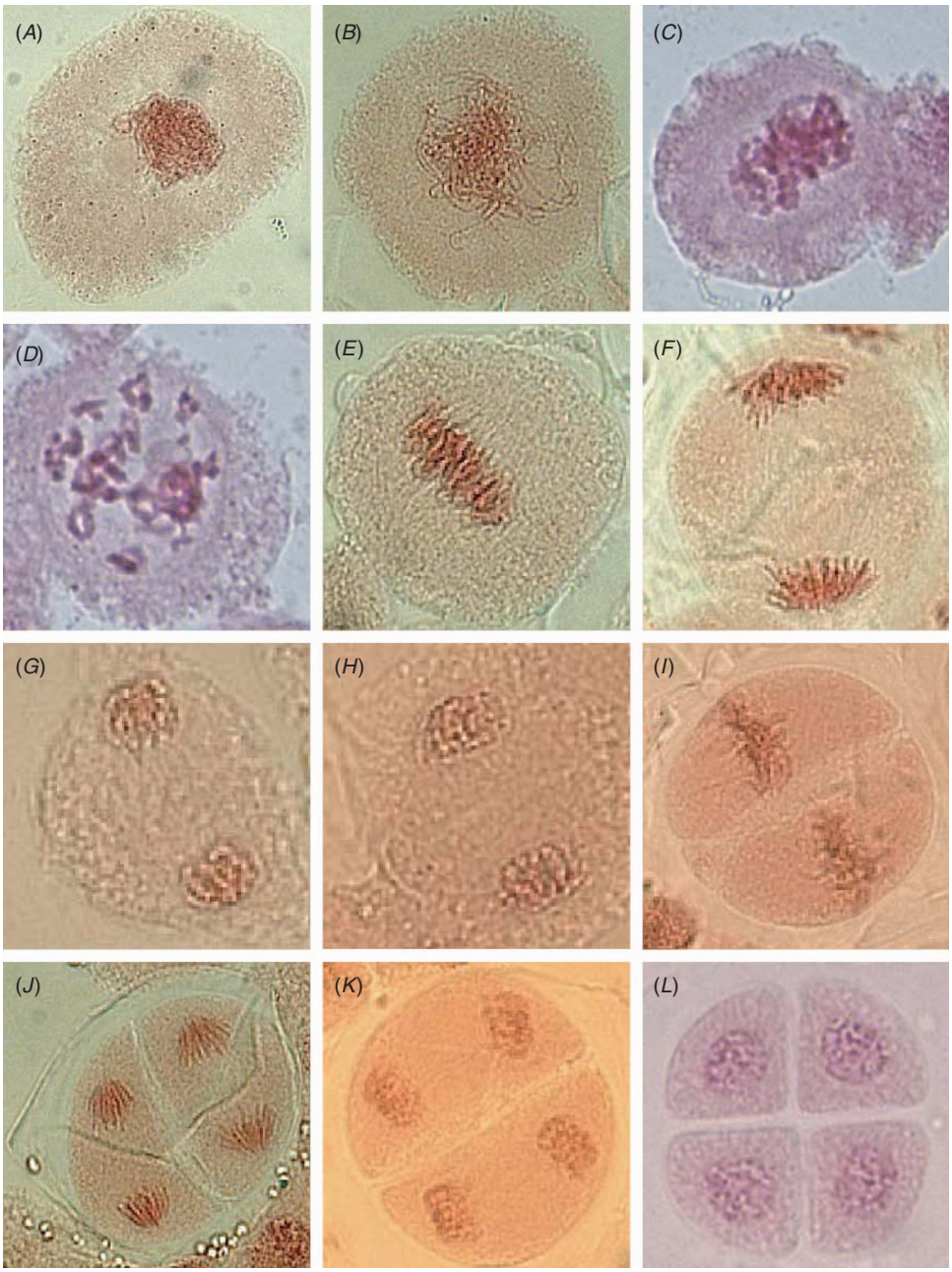

Fig. 1. Meiotic divisions I and II as observed in wheat (*Triticum aestivum*). (*A–E*) show prophase I which is represented by (*A*) zygotene, (*B*) pachytene, (*C*) diplotene and (*D*) diakinesis. (*E–G*) represent the remaining stages of the first meiotic division with (*E*) illustrating metaphase I, (*F*) anaphase I and (*G*) telophase I. The second meiotic division is shown in panels (*H–L*) with (*H*) representative of prophase II, (*I*) being metaphase II, (*J*) anaphase II, (*K*) telophase II and (*L*) tetrad formation. Images were captured using light microscopy (400× magnification).

recombination (Table 1). These three events are intimately associated with each other. Following the alignment of homologous chromosomes during leptotene, the inter-homologue interactions of synaptonemal complex (SC) formation and recombination occur. While recombination is generally recognised to initiate before SC formation, it is thought that the SC stabilises interactions between homologous chromosomes to allow for resolution of recombination events into either crossovers or non-crossovers (reviewed in Kleckner 1996; Börner *et al*. 2004; Page and Hawley 2004). Recombination and SC formation have been the subject of extensive molecular analysis, and both have been implicated in the alignment and recognition of homologous chromosomes.

Table 1. Glossary for selected terminology

Bivalent	A pair of homologous chromosomes, each consisting of two chromatids
Chiasmata	Cytological manifestation of crossing-over, typically visible as the cross-shaped exchange configuration that occurs between non-sister chromatids of homologous chromosomes
Chromatid	One of two identical longitudinal subunits produced by chromosome replication and joined at the centromere
Crossing-over	The process of exchange between non-sister chromatids of homologous chromosome pairs, resulting in recombination
Homoeologous chromosome pairing	Pairing of chromosomes that are very similar with respect to both gene content and order (differing in their repetitive DNA content)
Homologous chromosome pairing	Pairing of chromosomes that are identical with respect to both gene content and order
Landraces	Farmers' varieties, suited to the locale, produced over time by traditional breeding
Linkage drag	The transfer, in any particular cross, of unwanted genes with targeted genes that are linked to each other
Meiotic recombination	Exchange of DNA segments between paired chromosomes during prophase I of meiosis
Synapsis	The process in which two homologous chromosomes come in close proximity with one another during prophase I of meiosis, resulting in the formation of a bivalent
Synteny	The conservation of gene order between organisms
Transcriptomics	Typically utilises microarray technology to study the expression level of mRNA in a given cell population
Univalent	A chromosome that is not paired with its homologous partner
Wide cross breeding programs	Use of secondary, tertiary or quaternary gene pool material to improve the genetic base of elite germplasm and may require embryo rescue

Model organisms such as budding yeast (*Saccharomyces cerevisiae*) have proven to be influential in understanding the factors and mechanisms regulating such key events during meiosis. Given that meiosis is an evolutionarily conserved process, many of the molecular events identified in budding yeast are also shared by higher eukaryotes. Even so, this has not necessarily meant that the amino acid sequence of proteins involved in such events is well conserved between yeast and higher eukaryotes; as the isolation of key meiotic genes and proteins in plants and animals based on sequence homology alone has sometimes been difficult. This has particularly been the case for genes that have a role in synapsis of homologous chromosomes (Caryl *et al*. 2000; Higgins *et al*. 2005). However, one excellent example of where conservation of function has been demonstrated in a wide variety of organisms is HOmolog Pairing 1 (HOP1) isolated from yeast (Hollingsworth and Byers 1989), otherwise known as ASYnapsis 1 (ASY1) in *Arabidopsis* (*Arabidopsis thaliana* L.) (Ross *et al*. 1997; Caryl *et al*. 2000), *Brassica* spp. (Armstrong *et al*. 2002), bread wheat (Boden *et al*. 2007) or homologous Pairing Aberration In Rice meiosis 2 (PAIR2) in rice (Nonomura *et al*. 2004). Identified as an integral component in not only chromosome pairing of yeast (Hollingsworth and Byers 1989) but now also bread wheat (Boden *et al*. 2009), this gene will be the focus of discussion later.

The key events during early meiosis

Homologous chromosome pairing

There are many different factors which contribute to chromosome homology recognition; including chromosome morphology, chromatin re-modelling, regions of DNA sequence homology, and proteins that interact with chromatin (Hamant *et al*. 2006). The juxtaposition and alignment of homologous chromosomes during meiosis is the least well understood process of prophase I, with the mechanism by which homologous chromosomes align still remaining somewhat unresolved. Contributing to this is the difficulty in establishing whether a loss of bivalent formation in a given mutant is the consequence of defective pairing or synapsis, as deficiency in both processes could equally yield univalents. Furthermore, various studies in fruit fly (*Drosophila melanogaster*) and the nematode *Caenorhabditis elegans* have clearly demonstrated that a uniform mechanism for homologous chromosome alignment does not exist (when compared with other model organisms) (Carpenter 1975; Goldstein and Slaton 1982; Orr-Weaver 1995; Fung *et al*. 1998; MacQueen *et al*. 2005).

Various stages of the recombination pathway have been suggested to contribute to homologous chromosome recognition. For example, studies in maize (*Zea mays* L.) have shown that there is a significant decrease in the number of RADiation sensitive 51 (RAD51) foci from the beginning of zygotene compared with pachytene, and the high numbers of zygotene foci have been proposed to support a role for RAD51 in homology searching (Franklin *et al*. 1999). This has been supported by observations that maize mutants with abnormalities in the distribution and numbers of RAD51 foci during prophase I also display defects in homologous chromosome pairing (Pawlowski *et al*. 2003, 2004). Similarly, the *Arabidopsis asy1* mutant which fails to correctly synapse homologous chromosomes, also displays an abrupt decrease in Disrupted Meiotic cDNA 1 (DMC1) foci following its initial loading onto chromatin, relative to wild-type (Sanchez-Moran *et al*. 2007).

Another mechanism suggested to facilitate homologous chromosome alignment is the formation of a structure known as the telomere bouquet (reviewed in Zickler and Kleckner 1998; Harper *et al*. 2004). The telomere bouquet forms as telomeres of each chromosome attach to the nuclear periphery and cluster together during mid-prophase I (Hiraoka 1952; Zickler and Kleckner 1998). Formation of the telomere bouquet may assist homologous chromosome pairing by bringing the chromosomes into close association with one another, thereby decreasing the distance between homologous

chromosomes (Moses 1968; Hamant *et al*. 2006). Studies in maize support this theory as the *pam1* (*plural abnormalities in meiosis 1*) mutant, which displayed a loss of telomere bouquet formation, was also found to have a dramatic reduction in homologous chromosome pairing (Golubovskaya *et al*. 2002). However, there is also evidence to show that the telomere bouquet is not an essential requirement for homologous chromosome pairing, and that in several cases initial homologue interactions precede telomere bouquet formation (reviewed in Zickler and Kleckner 1998; Hamant *et al*. 2006).

Synaptonemal complex formation

The completion of homologous chromosome alignment and pairing is observed cytologically by the formation of a structure known as the SC. The SC is a tripartite protein structure that forms between non-sister chromatids of homologous chromosomes (von Wettstein *et al*. 1984; Fig. 2; also see Page and Hawley 2004). While its direct role in homologous chromosome interactions has been difficult to dissect, the evolutionary conservation of the structure across a wide range of species indicates that the SC does have a conserved role during meiosis (reviewed in Kleckner 1996; Hunter 2003).

In association with chromosome condensation that occurs through leptotene, sister chromatids become organised along structures known as axial elements. During the early stages of synapsis, the axial elements mature into lateral elements (Rockmill *et al*. 1995). The lateral elements of non-sister chromatids are linked through recombination-mediated induced double strand breaks (DSBs), and become joined through the recruitment and formation of transverse filaments (reviewed in Page and Hawley 2004). In yeast, correct localisation of transverse filament proteins requires the presence of proteins involved in chromosome condensation, indicating a coordination of chromosome synapsis with the process of chromosome condensation (Klein *et al*. 1999; Yu and Koshland 2003). At pachytene, when homologous chromosomes have completely synapsed, the cell contains a complete SC complement (Albini and Jones 1988). The complete SC includes the lateral elements and transverse filaments, as well as a dense region, at equidistance from each lateral element, known as the central element (reviewed in Page and Hawley 2004). Entering diplotene, the SC begins disassembly as the cell progresses towards metaphase and anaphase, where chiasmata form the sole physical union between non-sister chromatids.

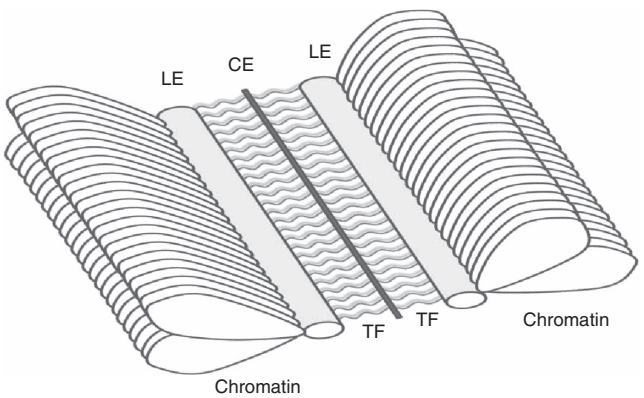

Fig. 2. A model sketch of the synaptonemal complex. A cross-section of the synaptonemal complex (SC) is shown highlighting the lateral elements (LE), central element (CE) and transverse filaments (TF). Chromatin of each homologue is attached to its corresponding lateral element. For a more comprehensive illustration showing the SC, see Page and Hawley (2004).

Recent evidence from studies in yeast, mammals and *Arabidopsis* indicate that formation of the SC and progression of the recombination pathway is intimately related (reviewed in Kleckner 2006). Studies in yeast and *Arabidopsis* indicate that components of the SC also facilitate homologous chromosome pairing (Higgins *et al*. 2005; Tsubouchi and Roeder 2005). Analysis in yeast showed that molecular ZIPper 1 (ZIP1) is required for the coupling of centromeres during early prophase I, and that homologous chromosomes failed to pair in its absence (Tsubouchi and Roeder 2005). Tsubouchi and Roeder (2005) proposed that the role for the coupling was to facilitate homologue pairing by holding chromosomes in close proximity while homology is being assessed. Further support of a role for SC-component proteins in homologous chromosome pairing was provided through analysis of ZYP1 (*Arabidopsis* homologue of yeast ZIP1) deficient *Arabidopsis* plants, which displayed recombination between non-homologous chromosomes (Higgins *et al*. 2005).

Evidence for a functional relationship between recombination and the SC has been provided through the analysis of yeast mutants with decreased activity of SPOrulation 11 (SPO11), a protein essential in the double strand break repair (DSBR) pathway (Henderson and Keeney 2004). In addition to displaying a decreased ability to generate DSBs, *spo11* mutants showed corresponding defects in SC formation (Henderson and Keeney 2004). These defects were caused by a decline in the number of ZIP3 complexes, which are thought to represent sites of SC initiation through their role promoting the recruitment of the transverse filament protein ZIP1 (Agarwal and Roeder 2000). Further evidence of a relationship between SC formation and recombination has been provided from *C. elegans*, *S. cerevisiae* and *Arabidopsis* mutants that are defective for a component of the central element (MacQueen *et al*. 2002; Börner *et al*. 2004; Higgins *et al*. 2005). All of these SC-component mutants displayed reduced levels of crossover formation, and immuno-localisation studies indicated that the defects may be caused by a loss of function in correct SC nucleation during leptotene and zygotene. These results therefore indicate a direct link between DSB initiation and SC formation, especially during the early stages of each process.

Recombination

Much of the early and current research on the DSBR pathway was performed in *S. cerevisiae* which led to the first model of the recombination pathway (Szostak *et al*. 1983). Since then, this model has been updated as further discoveries have been made (e.g. Allers and Lichten 2001; Bishop and Zickler 2004; Oh *et al*. 2007). Equivalent, extensive cytological and molecular analysis in plant species (excluding

Arabidopsis) has been limited. However, this has not prevented the recombination model to have been used as a framework for *Arabidopsis* (Sanchez-Moran *et al*. 2008). Further, through using such models as a starting point, the identification of several orthologues in agricultural crops including wheat, rice, barley, rye (*Secale cereale* L.) and maize has already been reported (and in some cases these genes have also been characterised) (Franklin *et al*. 1999; Pawlowski *et al*. 2003; Jenkins *et al*. 2005; Li *et al*. 2007; Khoo *et al*. 2008; Bovill *et al*. 2009).

Cytologically, recombination is observed as large multi-protein complexes called recombination nodules (RNs) (Zickler and Kleckner 1998, 1999). These nodules are found closely associated with the SC and are divided into two categories dependent on frequency and size, known as early (ENs) and late recombination nodules (LNs) (reviewed in Anderson and Stack 2005). ENs are associated with axial elements of the SC and appear from leptotene until pachytene, after which they detach from the SC (Stack and Anderson 1986*b*). Through the use of immuno-localisation data, Anderson and Stack (2005) have assigned recombination proteins with roles in DSB formation and single-end invasion of DNA strands as components of ENs. Based on the functions of the EN components and the large numbers of ENs, the ENs are hypothesised to have roles in searching for DNA homology, chromosome synapsis, and resolving recombination events into crossovers or non-crossovers (Carpenter 1979, 1987, 1988; Stack and Anderson 1986*a*, 1986*b*; Zickler and Kleckner 1999; Anderson *et al*. 2001; Moens *et al*. 2002). Involvement in the resolution of recombination events into crossovers or non-crossovers is supported by the fact that cytologically observed ENs are replaced by LNs at pachytene. The number of LNs is not only much fewer then ENs (1–6 per bivalent) but also reflective of the crossover frequency per bivalent (Stack *et al*. 1989; Anderson *et al*. 2003). Unlike ENs, LNs display interference patterns consistent with crossover interference and their location correlates well with chiasmata (Stack *et al*. 1989; Anderson *et al*. 2003). These observations, combined with immuno-localisation of proteins with essential roles in DNA mismatch repair strongly indicate LNs represent crossover sites (Moens *et al*. 2002).

Mining meiotic mutants in bread wheat: from classical genetics to molecular farming

The classical genetics

Approximately 70% of flowering plants are estimated to have experienced at least one polyploidisation event during their evolution (Bowers *et al*. 2003). Recent cytological and molecular analysis of other plants, which have previously been considered as diploids, reveals that they may in fact have been allopolyploids which have undergone diploidisation to now exist as paleopolyploids (Shoemaker *et al*. 1996; Gaut and Doebley 1997; Gomez *et al*. 1998; Grant *et al*. 2000; Vision *et al*. 2000; Gaut 2001). Such a widespread occurrence of this process is reflective of the potential for allopolyploid species to adapt to a wide range of environmental conditions, allowing these plants to survive in adverse environments when compared with their diploid progenitors (reviewed in Ma and Gustafson 2005). Although polyploids contain at least two sets of genomes per cell, such species frequently behave as cytological diploids during meiosis with only homologous chromosomes pairing with one another. The meiotic behaviour of several allopolyploid plant species has been, and continues to be, studied. These include bread wheat (Riley and Chapman 1958; Sears 1982; Martinez *et al*. 2001; Martinez-Perez *et al*. 2001; Griffiths *et al*. 2006; Colas *et al*. 2008; Boden *et al*. 2009), oilseed rape (*Brassica napus* L.) (Attia and Robbelen 1986; Jenczewski *et al*. 2003; Udall *et al*. 2005; Leflon *et al*. 2006; Liu *et al*. 2006; Nicolas *et al*. 2008, 2009), oats (*Avena sativa* L.) (Gauthier and McGinnis 1968; Rajhathy and Thomas 1972), cotton (*Gossypium hirsutum* L.) (Brown 1954; Reyes-Valdés and Stelly 1995; Ji *et al*. 2007; Vafaie-Tabar and Chandrashekaran 2007) and tobacco (*Nicotiana tabacum* L.) (Trojak-Goluch and Berbec 2003, 2007). Of all these plant species, the hexaploid genome of bread wheat has provided some of the most useful information to date.

Bread wheat is an allohexaploid with three genomes (AABBDD; $2n = 6x = 42$) derived from related progenitors. Studies on the origin of bread wheat have indicated that the genome complement formed ~10 000 years ago, through the hybridisation of the D genome progenitor, *Triticum tauschii* ($2n = 2x = 14$), and the tetraploid containing the A and B genome, *Triticum turgidum* (Feldman 2001). While it is well recognised that the progenitor of the A genome is *Triticum urartu* ($2n = 2x = 14$), the origin of the B genome is still open to conjecture (reviewed in Feldman and Levy 2005). An important behavioural characteristic of the wheat genome that ensures stabilisation of the hybrid condition is the diploid-like meiotic behaviour, with chromosome pairing occurring exclusively between homologues and not homoeologues. One of the central dangers to the establishment of a new species is the risk of homoeologous chromosome pairing due to the progenitor genomes usually being closely related, as this pairing would reduce fertility and therefore affect the fitness of the new species.

Studies in bread wheat have identified several loci that contribute to the exclusive pairing of bivalents, which ensures the maintenance of homologous chromosome pairing (Riley and Chapman 1958; Wall *et al*. 1971*a*; Driscoll 1972; Mello-Sampayo and Canas 1973; Riley and Chapman 1975; Sears 1982). Some of these loci have been termed *Pairing homoeologous* (*Ph*), for their ability to suppress interactions between homoeologous chromosomes (Wall *et al*. 1971*b*). Two examples are *Ph1* and *Ph2*, which are located on chromosome arms 5BL and 3DS, respectively (Riley and Chapman 1958; Driscoll 1972; Sears 1976).

Of the loci that contribute to the diploid behaviour of meiosis in bread wheat, the *Ph1* locus displays the strongest effect (Sears 1976; Feldman 1993; Moore 2002). Since its discovery some 50 years ago, cytological investigations of wheat mutants that lack the *Ph1* locus have shown that there are several defects that occur during pre-meiotic interphase and early meiosis that contribute to the homoeologous chromosome pairing observed at metaphase I (Riley and Chapman 1958; Sears 1977; Holm and Wang 1988). Initial studies showed that synapsis is arrested in *ph1* mutants, to a level of ~35–40% of wild-type wheat (Holm and Wang 1988).

In addition, multiple axial element associations that normally occur during zygotene are not resolved into homologous chromosome pairs in *ph1* mutants like they are in wild-type wheat (Holm and Wang 1988). Based on these observations, Holm and Wang (1988) proposed that the alignment of homologous chromosomes is affected in *ph1* mutants, preventing the correction of multiple axial element associations. Uncorrected associations are thought to be the prelude to the multivalents observed at metaphase I in *ph1* mutants (Holm and Wang 1988). Similarly, *Ph1* appears to be required for the synchronous remodelling of homologous chromosomes which occurs at the same time as telomere bouquet formation (Prieto *et al*. 2004; Colas *et al*. 2008). The absence of *Ph1* causes premature and asynchronous remodelling of homologous chromosomes, which leaves a chromosome just as likely to interact with a related homoeologue as with its true homologue (Martinez-Perez *et al*. 2001; Prieto *et al*. 2004; Colas *et al*. 2008). This has been confirmed by studies showing that *Ph1* regulates the specificity of chromosome interactions at sites of centromeres and telomeres, so that pairing only occurs between homologues (Martinez-Perez *et al*. 2001; Prieto *et al*. 2004).

In addition to the cytological investigations of meiosis in *ph1* mutants, genetic studies have been performed to identify the gene(s) responsible for the effect of the *Ph1* locus. The original *Ph1* deletion was defined to span a region of 70 Mbp; however, recent studies have reduced the size of this locus to 2.5 Mbp (Gill *et al*. 1993; Roberts *et al*. 1999; Griffiths *et al*. 2006). This refined locus was found to contain seven *Cyclin dependent kinase*-like (*Cdk*-like) genes and a segment of sub-telomeric heterochromatin, with the *Cdk*-like genes shown to be closely related to *Cdk2* of human and mouse (Griffiths *et al*. 2006; Martinez-Perez and Moore 2008). In addition, it has been shown that the *Cdk*-like genes of the 5B locus suppress the expression of the 5A and 5D *Cdk*-like loci, which are expressed at higher than normal levels in the absence of *Ph1* (Al-Kaff *et al*. 2008). This suggests that these genes coordinate chromatin remodelling of homologues to ensure that they are in the same conformation at the onset of pairing (Al-Kaff *et al*. 2008). Taken together, these studies indicate that by investigating the genes and proteins that are affected by deletion of *Ph1*, it may be possible to understand the mechanism that controls the diploid-like behaviour of bread wheat meiosis. Subsequently, ASY1 localisation has been shown to be perturbed in *ph1b* mutants (Boden *et al*. 2009).

Identification of the matchmaker: HOP1/ASY1 is required for chromosome synapsis and homologous chromosome pairing

In 1989, Hollingsworth and Byers identified a yeast gene with roles in SC formation and recombination by screening yeast mutants defective for homologous chromosome pairing during meiosis. Cytological analysis of the *hop1* mutant revealed that it failed to form a SC and displayed reduced levels of recombination (Hollingsworth and Byers 1989). Further evidence for a role in such processes was provided by identification of DNA interacting domains within HOP1, as well as immuno-localisation of the protein to sites directly adjacent to the lateral elements of the SC of homologous chromosome pairs (Hollingsworth *et al*. 1990; Muniyappa *et al*. 2000; Anuradha and Muniyappa 2004*a*, 2004*b*).

Immuno-localisation studies and the identification of proteins that interact with HOP1 also provided evidence for involvement in chromosome synapsis (Hollingsworth *et al*. 1990; Hollingsworth and Ponte 1997; Woltering *et al*. 2000). Examination of whole chromosome spreads from meiotic nuclei by electron microscopy following incubation with an anti-HOP1 primary antibody and a colloidal gold-conjugated secondary antibody revealed that the protein is closely associated with meiotic chromosomes (Hollingsworth *et al*. 1990). While HOP1 was proposed to serve as a component of the SC, comparisons of similar analysis with known SC components from mouse indicates that HOP1 is more likely to represent a non-SC component chromatin interacting factor (Hollingsworth *et al*. 1990; Schalk *et al*. 1998). The idea of HOP1 representing a non-SC protein is further supported by its dissociation from chromosomes at pachytene, when SC formation becomes complete (Smith and Roeder 1997).

So what is known about this gene in plant species? As highlighted earlier, identification and isolation of plant meiotic genes via sequence homology with yeast genes can be difficult. Using sequence alone, identifying a HOP1 orthologue in plants proved difficult, and at best returned low percentage matches. To overcome this, plant scientists used a reverse genetics approach by screening *Arabidopsis* T-DNA insertion lines for plants with reduced fertility and abnormal chromosome behaviour during meiosis. This led to the identification of *ASY1*, which is required for correct synapsis of homologous chromosomes (Ross *et al*. 1997; Caryl *et al*. 2000). Plants with a T-DNA disrupted *ASY1* gene display an absence of synapsed bivalents during pachytene, with unconnected homologues appearing as univalents at diplotene and diakinesis (Ross *et al*. 1997). This is followed by irregular chromosome distribution at metaphase I, and multiple non-disjunction events caused by equational segregation of chromosomes at anaphase I. Such chromosome behaviour led to a reduction in fertility to ~10% of the wild-type (Ross *et al*. 1997; Caryl *et al*. 2000). Similar analysis resulted in the identification of the rice *ASY1*/*HOP1* orthologue, termed *PAIR2* (Nonomura *et al*. 2004).

Complementing the forward genetics approach identifying *ASY1* and *PAIR2* in *Arabidopsis* and rice, a targeted genetic and protein approach was used to characterise the bread wheat orthologue, *TaASY1* (Boden *et al*. 2007, 2009). *TaASY1* displays significant genetic similarities with *ASY1* and *PAIR2*, with expression analysis revealing high levels of transcript at interphase and prophase I of meiosis (Boden *et al*. 2007). Immuno-gold and immuno-fluorescence localisation of *Ta*ASY1 in meiotic cells further supports a conserved role for this protein, with analysis in all three organisms showing that ASY1/PAIR2 localises to chromatin of lateral elements of the SC as chromosomes are condensing and pairing with their homologous partner (Armstrong *et al*. 2001; Nonomura *et al*. 2006; Boden *et al*. 2007, 2009). These analyses also reported a strict temporal localisation pattern for ASY1/PAIR2; with the protein first localising to chromatin at early leptotene as punctate foci that polymerise to form a

continuous signal throughout zygotene, before dissociating from the chromatin at the completion of synapsis, so that the signal diminishes during pachytene to be absent by diakinesis (Fig. 3). This suggested that ASY1/PAIR2 was required for either synapsis, by recruiting proteins to form the structures required for formation of the SC, or pairing by facilitating the chromosomes' search for their homologous partner.

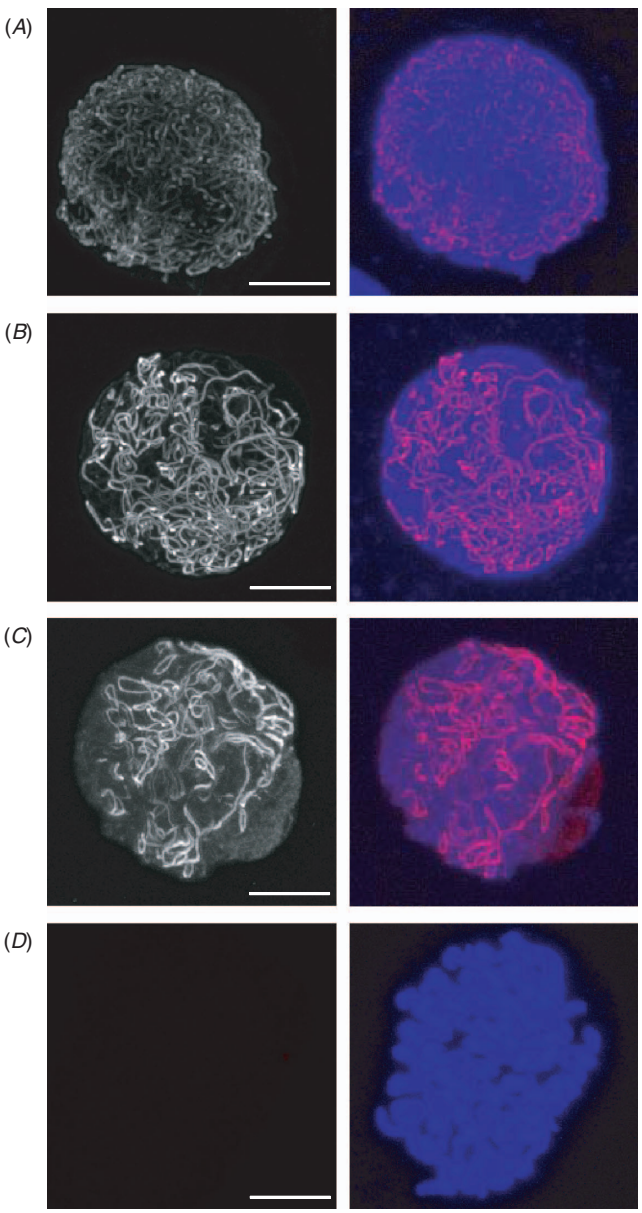

Fig. 3. *Ta*ASY1 localisation in wild-type wheat (*Triticum aestivum*) cv. Chinese Spring during prophase I. (*A*) represents leptotene where the loading of *Ta*ASY1 appears as punctuate foci. (*B*, *C*) show that the *Ta*ASY1 signal polymerises as the chromosomes roughly align during zygotene (*B*) and pachytene (*C*). By the completion of prophase I (diakinesis, *D*), there is no *Ta*ASY1 signal detected. Panels on the left display *Ta*ASY1 in white, while panels on the right display merged *Ta*ASY1 (red) with DAPI (blue). Scale bars, 10 μm.

Recent analyses performed in *Taasy1* RNA interference (RNAi) bread wheat lines and Chinese Spring *ph1b* bread wheat have indicated that a role in chromosome pairing is more likely. In the *Taasy1* lines with reduced levels of *TaASY1* transcript, the strict control of chromosome pairing between homologues was reduced, such that multivalents and univalents were observed at metaphase I (Boden *et al*. 2009). The metaphase I phenotype was reminiscent of that from *ph1* deficient lines previously reported (Sears 1977; Fig. 4). Transcript analysis of *TaASY1* in *ph1b* showed a significant 20-fold increase relative to wild-type. Interestingly, this observation is consistent with recent observations of *HOP1* gene activity in yeast meiosis following deletion of the *Cdk2* homologue, named *Inducer of meiosis 2* (*Ime2*) (Szwarcwort-Cohen *et al*. 2009), indicating the mechanism controlling chromosome pairing is conserved across eukaryotes. Additional evidence for *Ta*ASY1 being involved in bread wheat chromosome pairing was shown by Boden *et al*. (2009) with the localisation patterns in the *ph1b* mutant being disrupted and spiral-like in appearance. This observation is consistent with abnormalities in chromatin re-modelling and synapsis that are thought to lead to the homoeologous interactions observed in this mutant (Holm and Wang 1988; Prieto *et al*. 2004). Combined, these recent findings indicate that *TaASY1* is intimately involved with the *Ph1* dependent control of chromosome pairing, and that it might promote pairing between homologous regions of chromosomes. This activity is being controlled at a transcriptional level by *Ph1* in wild-type wheat so that regions of close homology (e.g. homoeologous sequences) are not promoted to interact with each other. An updated model illustrating how these new results contribute to understanding homologue pairing interactions during wheat meiosis was recently published (Moore and Shaw 2009).

Molecular farming to discover other orthologues and novel candidates

In the plant kingdom, *Arabidopsis* remains the favoured model organism because of its short life cycle, small size and small genome. With the genome having been sequenced in 2000, and the availability of an extensive T-DNA mutant collection with flanking sequence tags (Samson *et al*. 2002; Sessions *et al*. 2002; Alonso *et al*. 2003), extensive research on a gene of choice can be completed in a relatively short period of time when compared with some of the larger genomes such as barley and bread wheat. In a little over a decade of *Arabidopsis* research, various research groups have identified and characterised ~50 genes with roles in meiosis (Mercier and Grelon 2008). This list, while not exhaustive when compared with what has been reported in yeast, is comprised of a mixture of novel genes and those with orthologues in other taxonomic kingdoms.

While the sequencing and assembly of the barley and bread wheat genomes are in their formative years, comparative genetics using the rice genome sequence has enabled several regions that share synteny in these genomes to be identified (Sutton *et al*. 2003; Griffiths *et al*. 2006; Paux *et al*. 2006; Jardim 2007; Huang *et al*. 2008; March *et al*. 2008). One of

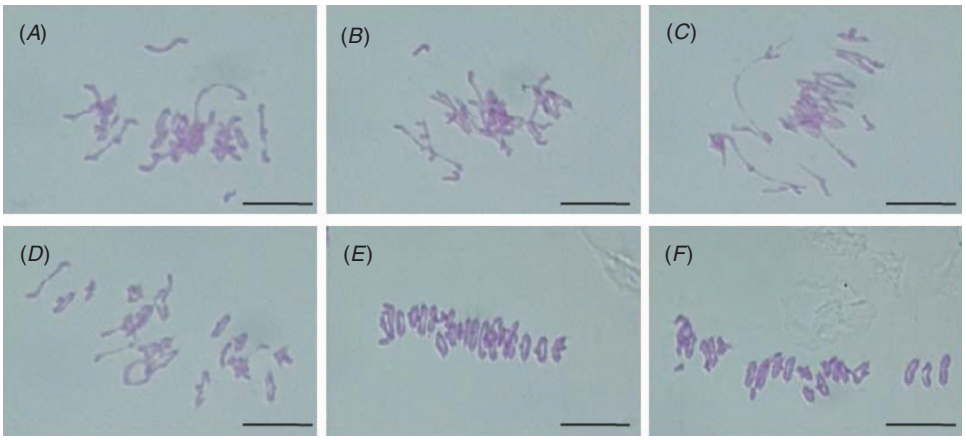

Fig. 4. Feulgen's-stained metaphase I chromosome spreads of independent transgenic *Taasy1* and control wheat plants. (*A–D*) metaphase I spreads from mutant lines typically displayed abnormal pairing behaviour, including the presence of univalents and multivalents. (*E*, *F*) the control transformed wheat variety (Bob White MPB26) displayed a normal metaphase I phenotype (ring bivalents). Scale bars, 25 µm.

the most appropriate studies to discuss here is the research conducted with the *Ph1* locus. The similarity between bread wheat (genome size of ~17 000 Mbp), rice (~490 Mbp) and *Brachypodium sylvaticum* (Huds.) Beauv. (~160 Mbp) genomes were used to create the framework for the bacterial artificial chromosomes (BACs) that contained sequence from the *Ph1* locus and also the homoeologous regions on the long arms of chromosomes 5A and 5D (Griffiths *et al*. 2006). This enabled the original fast-neutron irradiation-induced 70 Mbp deletion to be refined to a 2.5 Mbp region, and the identification of genes believed to be responsible for the action of *Ph1*. Using a similar approach Sutton *et al*. (2003) scrutinised the gene content of the *Ph2* locus, which as highlighted earlier, is another region that influences chromosome pairing behaviour in bread wheat. In identifying 280 expressed sequence tags (ESTs) from rice chromosome 1 which was 6.58 Mbp in length and syntenic to the *Ph2* locus, Sutton *et al*. (2003) mapped a subset of these ESTs and showed that 78% were located within the *Ph2* region. Information pertaining to putative genes within this region that may encode the action of *Ph2* was also reported.

More recently, a comparative genetics approach was used to identify meiotic gene candidates in the small grain cereals using the yeast and *Arabidopsis* sequenced genomes (Bovill *et al*. 2009). From 53 genes known to be involved in meiosis in either yeast and/or *Arabidopsis*, 30 or more orthologues from wheat, rice and barley were identified with an *E*-value > E^{-20}. This collection of ESTs (and full-length sequences in some instances) clearly demonstrates the level of DNA conservation across diverse organisms and is a valuable resource from which further studies can be launched, including transgenic studies of individual candidates in the cereals (see Table 2 for examples). As the diversity of technologies used for meiotic research increases, there will also be comparisons made between biological processes such as the transcriptomes of organisms and the biochemical pathways that they control. Indeed, one approach used to extract meaningful outcomes from vast amounts of data involves the constantly evolving microarray technology; initially designed as a high throughput platform to quantify gene expression (Schena *et al*. 1995).

Since its inception, reproductive processes including stages of meiosis, differences in germline and somatic tissues, and differences in male and female germlines have been investigated using microarrays. However not surprisingly, the majority of these studies were completed in model species including; *S. cerevisiae*, *Schizosaccharomyces pombe* (fission yeast), *C. elegans*, *D. melanogaster*, rats (*Rattus rattus*), and *Arabidopsis* (Chu *et al*. 1998; Andrews *et al*. 2000; Primig *et al*. 2000; Reinke *et al*. 2000; Mata *et al*. 2002; Schlecht *et al*. 2004). Some of the earliest meiotic microarray work investigated the transcriptional program of *S. cerevisiae* (Chu *et al*. 1998). Complementary DNA microarrays containing 97% of the known *S. cerevisiae* genes were used to increase the number of genes meiotically-regulated from ~150 which were identified using conventional methods (Chu *et al*. 1998; and references therein), to over 1000 using a microarray approach. Subsequently the two *S. cerevisiae* strains, SK1 and W303, which show different sporulation efficiencies, were compared. This revealed gene deletions, polymorphisms and ~1600 temporally-regulated genes in both strains (Primig *et al*. 2000). These genes were assigned into seven broad expression clusters; with some of them having previously been reported in DNA synthesis, recombination, the synaptonemal complex and sporulation. Of significance in this study was the identification of ~650 meiotically-regulated genes not previously mentioned in the literature (Primig *et al*. 2000).

More recently, Crismani *et al*. (2006) analysed a large-scale transcriptomics dataset across a meiotic time series in bread wheat. They showed that 1350 transcripts were temporally-regulated during the early stages of meiosis, in which 30 of these had at least an 8-fold expression change between different stages. While a significant proportion of the

Table 2. Selected meiotic candidates for wheat, rice and barley mined from public expressed sequence tag databases and/or isolated, with their proposed breeding benefit for cereals such as bread wheat

Each gene has been assigned to one of several key events that occur during early meiosis. Those listed, are proposed gene targets for cereal transgenic programs that currently exist (or that have already been analysed using such an approach, *ASY1* (Boden *et al*. 2009)). In developing transgenic cereals with these candidates, it would be desirable (where possible) to investigate multiple genes simultaneously (e.g. create double mutants, either through transgenesis or crossing two single mutants and analysing the progeny). Although these candidates affect processes such as chromosome pairing or recombination, there are subtle differences in how they would interplay with each other through meiosis. Known orthologues exist for all candidates listed, in at least *Arabidopsis* and/or yeast, except for *PHS1* and *RecG*. For references to the known orthologues and for further candidates that have been identified in the small grain cereals, see Bovill *et al*. (2009). *Ta*, *Triticum aestivum*; *Os,Oryza sativa*; *Hv, Hordeum vulgare*; *ASYnapsis 1, ASY1*; *Poor Homologous Synapsis 1, PHS1*; *SWItch 1, SWI1/DYAD*; *synaptonemal complex protein 1, ZYP1*; *Disrupted Meiotic cDNA 1, DMC1*; *MutL Homologue 1, MLH1*; *MutS Homologue 4, MSH4*; *MutS Homologue 5, MSH5*; *MutS Homologue 7, MSH7*; *ATP-dependent DNA helicase recG*, *RecG*; *SPOrulation 11-1, SPO11-1*; *SPOrulation 11-2, SPO11-2*

Gene acronym	Species	Proposed breeding benefit
		Pairing and synapsis
ASY1[A]	*Ta*, *Os*, *Hv*	Alien introgression, wide-cross breeding programs
PHS1[B]	*Ta*, *Os*, *Hv*	Silence/reduce *PHS1* expression, producing plants that would be useful for wide-cross breeding programs
SWI1/*DYAD*[C]	*Ta*, *Os*	Create *swi1* mutants in wheat for 2n gamete formation, leading to increased diversity in hybrids; perhaps useful for also investigating cereal apomixis
ZYP1	*Ta*, *Os*, *Hv*	Silence/reduce *ZYP1* expression to enhance homoeologous recombination
		Recombination and mismatch repair
DMC1	*Ta*, *Os*, *Hv*	Increasing *DMC1* expression could result in additional early recombination nodules forming; which may translate into more late recombination nodules, which would enhance the number of crossover/recombination sites
MLH1	*Ta*, *Os*, *Hv*	Increased expression may lead to enhanced recombination frequencies; perhaps particularly useful for cereals as they are known to have recombination poor regions
MSH4/*MSH5*	*Ta*, *Os*, *Hv*	Given that MSH4 is required for wild-type levels of crossing-over in yeast[D], increasing *MSH4* (which forms a dimer with *MSH5*) could lead to additional crossover sites being produced
MSH7	*Ta*, *Os*, *Hv*	Fertility decreased[E]; however, further analysis of *HvMSH7* knock-down lines may identify homoeologous recombination events; subsequent lines could then be used as a bridging tool in breeding programs
RecG[F]	*Ta*, *Os*, *Hv*	Enhancing levels of *RecG* may increase homologous recombination, thereby decreasing the number of crosses needed to obtain the desired elite germplasm
SPO11-1/*SPO11-2*	*Ta*, *Os*, *Hv*	Enhancing the expression of this candidate might result in increased recombination events that are site-specific

[A]Boden *et al*. (2009). [B]Pawlowski *et al*. (2004). [C]Motamayor *et al*. (2000); Agashe *et al*. (2002). [D]Novak *et al*. (2001). [E]Lloyd *et al*. (2007). [F]Lloyd and Sharples (1993); Whitby and Lloyd (1995).

1350 transcripts hit to uncharacterised sequences or did not share any sequence similarity with any database entry to date, several shared sequence similarity with genes which have roles in chromatin condensation, synaptonemal complex formation and recombination (Crismani *et al*. 2006). Where limited sequence information for the organism of choice exists, microarray analysis has therefore proven useful in identifying novel (and known) meiosis candidates to undertake further research on. Evidence that wide-scale synergies exist between the expression profiles of meiosis genes from wheat, poplar (*Populus trichocarpa* Torr. & Gray) and *Arabidopsis* have also been discovered (W. Crismani and J. A. Able, unpubl. data). Using comparative expression profiling may therefore be an additional approach to identify important meiotic genes and/or gene clusters between similar and/or divergent species of interest.

Implications for crop improvement: why manipulate meiosis?

For the majority of crop species we have access to genetic variation in the cultivated gene pool, amongst land races and in the wild relatives. Although these sources have been used for crop improvement, plant breeders have typically relied upon exploiting genetic variation present within cultivated and well adapted lines in order to improve their target phenotypes and to minimise the transfer of unwanted linkage blocks. As highlighted earlier in the case of bread wheat, recombination of wild chromatin into the genetic makeup of these elite lines is strongly suppressed and is a direct result of the tight meiotic controls prevalent in this species. As breeders continually face commercial pressures to generate new varieties quickly, this has meant that they are often reluctant to use poorly adapted lines, land races and wild relatives due to the slow and complex introgression of the desired alleles into commercial varieties. Given that speciation of many crops has occurred over thousands of years, the level of natural variability is invariably large. Just how much of this diversity has been captured, especially within the small cereal grain families, remains unclear. Estimates suggest that in the *Triticeae* alone, only ~10 to 15% of the gene pool has been utilised (Able and Langridge 2006). Significantly expanding the use of non-adapted and wild germplasm in breeding programs will therefore depend on the ability to manipulate key events such as meiotic recombination. With a greater ability to regulate the location and/or frequency of recombination events, undesirable linkage drag would be minimised in any particular cross. Reducing linkage drag would subsequently enhance the rate of genetic gain that breeding programs achieve, as target genes could be transferred independently of undesirable genes. Furthermore, producing highly recombinogenic lines would

enable plant breeders to reduce the size of populations used, while still obtaining the desired phenotypes.

While major advancements have been made over the past 50 years in various model and agriculturally important crop species, many key events during meiosis are far from being completely understood. This is because meiotic biochemical pathways operate through an integrated and complicated array of networks that are yet to be deciphered. This review has highlighted the importance of meiosis and the benefits of manipulating the key events of chromosome pairing and recombination, with a particular emphasis on bread wheat. From an applied perspective, and as described by Riley and Chapman (1958) with the discovery of *Ph1*, identification of the mechanisms that control homologous chromosome pairing in bread wheat would have both theoretical and practical implications. Future studies in bread wheat may indeed help to identify proteins that are involved in homology searching during prophase I in a way that is not possible in diploid organisms. In addition, by understanding the mechanisms that suppress homoeologous chromosome interactions, it should be possible to manipulate this process so that homoeologous chromosomes can interact in inter-specific hybrids, which would in turn facilitate the introduction of alien genes into wheat chromosomes by normal recombination. Given the recent research reported by Boden *et al*. (2009), the relationship between key genes such as *TaASY1* and the *Ph1* locus is now becoming more complete. Further research investigating other candidates in the *Ph1* background is underway and will no doubt lead to a more comprehensive dissection of how chromosomes pair and recombination events take place in this complex polyploid. Such knowledge will have significant implications for plant breeding strategies of the future.

Indeed, since the early 1990s, the adoption of technology such as marker assisted selection and other related marker-based strategies have enabled significant improvements in plant breeding programs to occur. Through further refinements of these current platforms and the development of further innovative assays, the identification and function(s) of new genes and proteins that the pre- and plant breeder will have at their disposal is virtually immeasurable. While some time exists before outcomes of the current 'omics' find an applied marker route, such reverse genetics strategies should also eventually find a path through to breeding programs. The power of all these modern day approaches, combined with classical knowledge will ultimately underpin the ability to successfully manipulate the meiotic process not only in commodities such as bread wheat but many crop species of agricultural importance.

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