

## Chapter 2

# Distant Hybridization: A Tool for Interspecific Manipulation of Chromosomes

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**Abstract** Wide or distant hybridization has been widely used as an important tool of chromosome manipulation for crop improvement. The chromosome behaviors in  $F_1$  hybrids provide us with the essential genetic basis for chromosome manipulation. The induction of homoeologous pairing in  $F_1$  hybrid plants followed by the incorporation of a single-chromosome fragment from an alien or a wild species into an existing crop species by translocating chromosomes has been used in the production of translocation lines. Most efforts to transfer a beneficial trait from wild plants into crops so far have bridged the species gap via alien chromosome translocation lines. Chromosome doubling in somatic cells or gametes of  $F_1$  hybrids followed by the incorporation of all alien chromosomes has been used in the production of amphidiploids. Amphidiploidy can be used for a bridge to move a single chromosome from one species to another or for the development of new crops. Chromosome elimination of a uniparental genome during the development of  $F_1$  hybrid embryos has been used in the production of haploids. Haploids are very useful in double-haploid breeding of a true-breeding crop such as wheat and rice since this method can quickly replace genetic recombination while enhancing breeding efficiency or facilitating genetic analysis.

**Keywords** Amphidiploidy • Chromosome manipulation • Gene introgression • Haploid • Translocation

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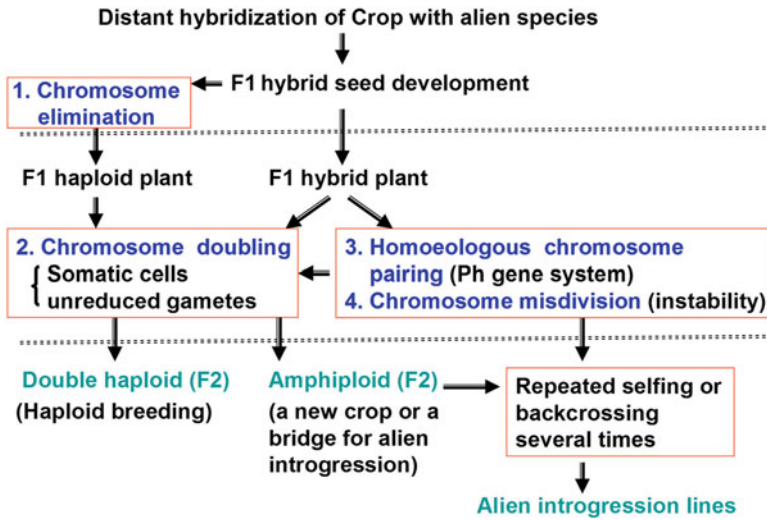
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## 2.1 Introduction

Wide or distant hybridization, a mating between individuals of different species or genera, provides a way to combine diverged genomes into one nucleus. Wide hybridization breaks what is known as the species barrier for gene transfer and thus makes it possible to transfer the genome of one species to another, which results in changes in genotypes and phenotypes of the progenies. It is very important for species evolution and speciation since chromosome doubling of wide hybrids is responsible for the origin of many allopolyploid species. Repeated backcrossing of wide hybrids to their parental species has also contributed to the evolution and speciation of some species by gene introgression, i.e., the infiltration of chromosomes or chromosome fragments from one species into another through repeated backcrossing of wide hybrids to their parental species (Anderson 1953; Stebbins 1971; Arnold 1997; Mallet 2007). Besides its role in evolution and speciation of species, gene introgression from crops, especially genetically modified crops, into the wild species, may increase the capability of the wild species to adapt to agricultural environments and compete with the cultivated forms, which is viewed as a possible threat to the environment and to agriculture (Ellstrand 2003; Weissmann et al. 2005). In application, distant hybridization and resulting wide hybrids have been widely used as an important tool of chromosome manipulation (also referred to as chromosome engineering) for crop improvement. Based on the chromosome behaviors of wide hybrids and the resulting chromosome constitutions in their progenies, chromosome manipulation of wide hybrids for crop improvement is classified into three main categories:

1. Incorporation of single-chromosome or chromosome fragment from a wild species (also referred to as alien) into an existing crop in order to enhance crop genetic diversity: The resulting alien chromosome substitution, addition, or translocation lines help breeders to transfer beneficial characteristics from wild and weedy plants to the cultivated crop species. Most efforts to transfer a beneficial trait from wild plants into crops so far have been bridged via alien chromosome translocation lines (Qi et al. 2007).
2. Incorporation of all the alien chromosomes by chromosome doubling in order to produce amphidiploid: Sometimes, the incorporation of partial alien chromosomes will lead to partial amphidiploid. Amphidiploid can be used for the development of a new crop. The man-made crop Triticale (*X Triticosecale* Wittmack) is an amphidiploid between wheat (*Triticum turgidum* L. or *Triticum aestivum* L.) and rye (*Secale cereale* L.) (Gupta and Priyadarshan 1982). Amphidiploid can be further used as a bridge for the development of alien gene introgression or alien chromosome substitution, addition, and translocation lines (Jiang et al. 1994).
3. Elimination of all alien chromosomes in order to induce crop haploid: Haploid is very useful in double-haploid breeding of a true-breeding crop like wheat and rice since it can quickly fix genetic recombination and thus enhance breeding efficiency or facilitate genetic analysis (Pratap et al. 2010).



**Fig. 2.1** Chromosome manipulation based on chromosome behaviors in  $F_1$  hybrids. Alien chromosome elimination during the development of  $F_1$  hybrid embryos to produce haploid; chromosome doubling in  $F_1$  hybrid plants to produce amphidiploid; homoeologous chromosome pairing or chromosome misdividing in hybrid plants to produce translocation line

Type 1 is the manipulation for single chromosome, while type 2 and 3 are the genome manipulation by the loss and the addition of alien genome, respectively. Chromosome manipulation of wide hybrids for crop improvement is involved in some key steps that may vary according to different wide hybrids. Anyway, a  $F_1$  hybrid between a crop and an alien species is the first step (Fig. 2.1). Crossability of different species is an important genetic character to strongly affect the wide cross. Some genes or QTL for crossability have been found in plants, for example in tribe Triticeae species tetraploid wheat (*T. turgidum* L.) and common wheat (Riley and Chapman 1967; Krowlow 1970; Zheng et al. 1992; Tixier et al. 1998; Liu et al. 1998a, b, 1999, 2002; Alfares et al. 2009; Bertin et al. 2009; Mishina et al. 2009; Zhang et al. 2008a, 2011a). With combined crossable genes/QTL with the application of techniques like embryo rescue and hormone treatment on post-pollination, successful production of  $F_1$  hybrid can be achieved (Jiang et al. 1994; Sharma 1995). In most cases, the production of  $F_1$  hybrid is not a barrier for chromosome manipulation.

## 2.2 Chromosome Manipulation for Crop Improvement

The chromosome behavior in  $F_1$  hybrid provides us the essential genetic basis of chromosome manipulation. In this review, we focus on the chromosome manipulations based on the chromosome behaviors of wide  $F_1$  hybrids: (1) alien chromosome elimination during the development of  $F_1$  hybrid embryos to produce haploids,

(2) chromosome doubling in somatic cells or gametes in  $F_1$  hybrid plants to produce amphidiploid, and (3) induction of homoeologous pairing in  $F_1$  hybrid plants and then the fixation of translocated chromosomes in their progenies to produce translocation lines (Fig. 2.1).

## 2.2.1 Chromosome Elimination and Haploid Crop

Chromosome elimination of one parental or uniparental genome after fertilization of the egg by the sperm of another species can occur in intraspecific, interspecific, intergeneric, or more distant hybrids (Dunwell 2010). This phenomenon results in haploid embryo formation of only one of the parents. It is, therefore, a barrier for breeding new crop cultivars by gene introgression from alien species into crop. However, it offers a shortcut for plant breeding by the production of doubled haploids (DH). Plant breeding needs to obtain high levels of homozygous lines with consistent phenotypes. However, the production of such a homozygous line usually requires several generations of selfing or backcrossing even if under the help of molecular markers (Chan 2010). A DH is a homozygous line that can be immediately achieved by artificial (chemical treatment) or spontaneous chromosome doubling of a haploid plant. In fact, doubled-haploid technology can accelerate the breeding of new cultivars, and the time to develop new cultivars may be reduced by 50 % in winter-grown crops compared to classical pedigree breeding (Forster et al. 2007).

Chromosome elimination was observed in interspecific hybridization within a genus like *Nicotiana* (Kostoff 1934; Burk et al. 1979), *Portulaca grandiflora* (Okura 1933), *Hordeum* (Kasha and Kao 1970; Houben et al. 2011), *Solanum* (Uijtewaal et al. 1987; Peloquin et al. 1996; Maine 2003), and *Elymus* (Lu 1992). In genus *Hordeum*, during early development stages of a hybrid embryo of between cultivated barley (*H. vulgare*) as the female and wild species *H. bulbosum*, chromosomes of *H. bulbosum* are eliminated and then lead to the formation of a haploid embryo only containing barley chromosomes. After grown in vitro, a haploid barley plant will be produced. The “*bulbosum*” method was the first haploid induction method to produce large numbers of barley haploids used in crop breeding programs (Choo et al. 1985; Devaux and Pickering 2005). Haploid formation has also been observed in hybrid combination between *H. vulgare* and other species in genus *Hordeum* (Jorgensen and von Bothmer 1988; Houben et al. 2011).

Chromosome elimination has also been shown to exist in many instances of intergeneric or more distant hybridization, such as *Cichorium intybus* × *Cicerbita alpina* (Doré et al. 1996), pear × apple (Inoue et al. 2004), *Brassica napus* × *Orychophragmus violaceus* (Cheng et al. 2002), *B. rapa* × *Isatis indigotica* (Tu et al. 2009), *Avena sativa* × *Zea mays* (Rines and Dahleen 1990; Kynast et al. 2012), *A. sativa* × *Pennisetum americanum* (Matzk 1996), *A. sativa* × Triticeae species (Ishii et al. 2010), *Triticum ventricosum* × *H. bulbosum* (Fedak 1983), *T. turgidum* × *Zea mays* (Almouslem et al. 1998), *T. aestivum* × Triticeae species (*H. vulgare* and

*H. bulbosum*), and *T. aestivum*  $\times$  its more distantly related species (*Zea mays*, *Pennisetum glaucum*, *Sorghum bicolor*, *Coix lacryma-jobi*, *Imperata cylindrica*, etc.) (Barclay 1975; Fedak 1980; Laurie and Bennett 1986, 1988; Laurie 1989; Matzk and Mahn 1994; Inagaki and Mujeeb-Kazi 1995; Mochida and Tsujimoto 2001; Gernand et al. 2005; Komeda et al. 2007; Pratap et al. 2005, 2006; Pratap and Chaudhary 2012; Chaudhary et al. 2013). Of them, efficient induction of haploids by hybridization with maize (*Zea mays* L. ssp. *mays*) has been widely reported in wheat (*T. turgidum* and *T. aestivum*), and wheat–maize hybridization is currently a preferred method for producing haploid wheat (Jauhar et al. 2009; Tayeng et al. 2012).

Uniparental chromosome elimination in wide hybrids should be a result of different chromosome behaviors of two parents. There are some assumptions that have been proposed to account for uniparental chromosome elimination in wide hybridization (see review by Houben et al. 2011). One hypothesis is that centromeres from two parents interact unequally with the mitotic spindle, leading to selective chromosome loss (Bennett et al. 1976; Finch 1983; Laurie and Bennett 1989; Kim et al. 2002; Jin et al. 2004; Mochida et al. 2004). Centromeres are the chromosomal loci that attach to spindle microtubules to mediate faithful inheritance of the genome during cell division. They are epigenetically specified by incorporation of the essential kinetochore protein CENH3 (CENP-A in humans or HTR12 in *Arabidopsis thaliana*) (Earnshaw and Rothfield 1985; Talbert et al. 2002), a histone H3 variant that replaces conventional H3 in centromeric nucleosomes (Henikoff and Dalal 2005). The chromosomal location of CENH3 is the assembly site for the kinetochore complex of active centromeres. The loss of CENH3 results in the failure of centromere formation and chromosome segregation (Allshire and Karpen 2008). Recent works on intraspecific (Ravi and Chan 2010) and interspecific hybrids (Sanei et al. 2011) provided the experimental link evidences between the loss of CENH3 and the occurrence of uniparental chromosome elimination. Sanei et al. (2011) studied the mechanism underlying selective elimination of the paternal chromosomes during the early development of *Hordeum vulgare*  $\times$  *H. bulbosum* embryos and gave the conclusions regarding the role of the centromere-specific histone CENH3 in the process of chromosome elimination: (1) centromere inactivity of *H. bulbosum* chromosomes triggers the mitosis-dependent process of uniparental chromosome elimination in *H. vulgare*  $\times$  *H. bulbosum* hybrids; (2) centromeric loss of CENH3 protein rather than uniparental silencing of CENH3 genes causes centromere inactivity. They also proposed a possible model of how the mitosis-dependent process of uniparental chromosome elimination works in *H. vulgare*  $\times$  *H. bulbosum* hybrid embryos. After fertilization, two parental CENH3 genes are transcriptionally active. CENH3 is then loaded into the centromeres of *H. vulgare* but not of *H. bulbosum*, which may be due to cell cycle asynchrony of the two parental genomes during mitotic G2 phase. This leads to *H. bulbosum* chromosome lagging because of centromere inactivity during anaphase, subsequently forming micronuclei. Finally, micronucleated *H. bulbosum* chromatin will degrade, and a haploid *H. vulgare* embryo will develop.

In another experiment, Ravi and Chan (2010) found that haploid *Arabidopsis thaliana* plants can be easily generated through seeds by manipulating the single-centromere protein CENH3. When *cenh3* null mutants expressing altered CENH3 proteins are crossed to wild type, chromosomes from the mutant are eliminated, producing haploid progeny. This process seems a mimic of genome elimination seen in wide hybridization. It is unclear, however, whether a comparable haploidization process takes place between the intraspecific hybrids of *A. thaliana* *cenh3-1* null mutants with its wild type (Ravi and Chan 2010) and the interspecific hybrids of *H. vulgare*  $\times$  *H. bulbosum* (Sanei et al. 2011). From the viewpoints of crop improvement, the production of double haploids has been greatly advanced by the manipulation of CENH3 since the frequency of genome elimination by this kind of centromere-mediated method is higher than any previously reported wide hybridization and thus might improve the efficiency of haploid production in crops (Chan 2010). In addition, crossing a mutant with altered CENH3 proteins (as female) with a wild-type male can shift paternal chromosomes into maternal cytoplasm. This character can be used to develop cytoplasmic male sterility that is very useful for the production of hybrid seeds.

### 2.2.2 Unreduced Gametes and Amphidiploid

Wide  $F_1$  hybrids from interspecific and intergeneric hybridization usually are amphihaploid with two parental genomes if chromosome elimination does not occur. Due to the absence of only one set of homologous chromosomes, meiosis in  $F_1$  amphihaploid plants (analogous to haploid plant as described above) may result in sterile gametes with incomplete chromosome by meiosis, so there is no seed set. To convert sterile amphihaploids into fertile, duplication of the chromosome complement and then the production of amphidiploids are therefore necessary. Besides restoring fertility, amphidiploids are valuable for alien gene transfer as mentioned in introduction. Chromosome doubling can be carried out through the treatment with anti-microtubule drugs. Colchicine (originally extracted from autumn crocus (*Colchicum autumnale*)) is the most widely used doubling agent although it is highly toxic. This anti-microtubule drug inhibits microtubule polymerization by binding to tubulin. Other doubling agents, such as oryzalin, amiprophosmethyl (APM), trifluralin, and pronamide, all of which are used as herbicides, are also used in the doubling induction with variable degree of success in diploidization.

Some interspecific or intergeneric  $F_1$  amphihaploids can also set grains by selfing and give rise to amphidiploids by spontaneous chromosome doubling. Spontaneous chromosome doubling usually results from unreduced gametogenesis and a union of unreduced female and male gametes leads to the formation of a spontaneous amphidiploid from a wide hybrid. It is believed that unreduced gametes (with somatic chromosome number) played a predominant role in polyploidization (Harlan and De Wet 1975; Ramsey and Schemske 1998, 2002; Cai and Xu 2007; Jauhar 2007; Matsuoka 2011; Silkova et al. 2011), leading to the origination of both

autopolyploids, such as potato (Peloquin et al. 1999), and allopolyploids, such as wheat (Kihara and Lilienfeld 1949). Besides the origin of polyploid species, unreduced gametes can help in crop genetics and breeding, not only in production of amphidiploids in a large scale (Zhang et al. 2010), which is the bridge of alien gene introgression into crop (Yang et al. 2009), but also in the production of doubled haploids (Ramana and Jacobsen 2003; Zhang et al. 2007). Recently, Zhang et al. (2011b) described a simple method for synthesizing DHs (SynDH) especially for allopolyploid species by utilizing unreduced gametes. The method involves three steps: hybridization to induce recombination, interspecific hybridization to extract haploids, and spontaneous chromosome doubling by selfing the interspecific  $F_1$ s. SynDHs produced in this way can only contain recombinant chromosomes in the partial genome(s) of interest in a homogeneous background (Zhang et al. 2012; Hao et al. 2013). No special equipment or treatments are involved in the SynDH production and it can be easily applied in any breeding and/or genetic program. Unreduced gametes provide a strategy to fix translocated chromosomes, derived from homoeologous pairing of  $F_1$  hybrids, into their progenies.

Unreduced gametes can be generated by a variety of cytological mechanisms. They are generally formed by anomalies of meiotic cell division in plants. These defects include abnormal spindle orientation, defected synapsis, and omission of chromosome segregation at one of the two meiotic divisions (Veilleux 1985; Bretagnolle and Thompson 1995; Peloquin et al. 1999; Ramana and Jacobsen 2003; Cai et al. 2010; Kynast et al. 2012). The production of unreduced gametes has been largely observed in amphihaploid hybrids of the big tribe Triticeae, including the important polyploid crops like common wheat, durum wheat, barley, rye, triticale ( $\times$ Triticosecale), and many forage species (for examples, Aase 1930; Kihara and Lilienfeld 1949; Maan and Sasakuma 1977; Islam and Shepherd 1980; Blanco et al. 1983; Fukuda and Sakamoto 1992; Xu and Dong 1992; Li and Liu 1993; Xu and Joppa 1995, 2000; David et al. 2004; Matsuoka and Nasuda 2004; Zhang et al. 2007, 2008b, 2008c, 2010, 2011b, Tiwari et al. 2008; Loureiro et al. 2009; Yang et al. 2010; Matsuoka 2011; Silkova et al. 2011). This haploidy-dependent unreductional meiotic cell division (UMCD), resulting in unreduced gametes, has been considered the mechanism for chromosome doubling in the origins of allopolyploid species in Triticeae and other allopolyploid plant species (Cai and Xu 2007; Jauhar 2007; Matsuoka 2011; Silkova et al. 2011). Two main cytological processes leading to unreductional meiosis were described in *Triticeae* genotypes. First division restitution (FDR) was used to describe the lack of chromosome segregation at anaphase I followed by nuclear restitution and second meiotic division in hybrids between *T. turgidum* L. and *Ae. tauschii* Coss. (Xu and Joppa 2000). On the other hand, also in hybrids of *T. turgidum* with *Ae. tauschii*, other authors described a single-division meiosis (SDM) characterized by a mitosis-like equational division with sister chromatid segregation at anaphase I (Zhang et al. 2007). Both types of divisions, FDR and SDM, may coexist in a same hybrid (Xu and Joppa 2000; Zhang et al. 2007; Silkova et al. 2011; Ressurreição et al. 2012). The divergence in terminology reflects the lack of knowledge regarding the mechanisms for the production of unreduced gametes in amphihaploid genotypes. It should be mentioned that both FDR and



SDM have exactly the same genetic outcome, i.e., formation of two genetically identical unreduced gametes since cell division only involves sister chromatid segregation. That means that no matter which division failed, sister chromatids of a chromosome separated at metaphase of the normal division, like they do in mitosis, leading to formation of unreduced gametes possessing the two non-sister chromatids and consequently retained equivalent levels of parental heterozygosity and epistasis. Zhang et al. (2007), therefore, proposed to call the two mechanism as “mitotic-like meiosis” since it resembles a mitosis by having only one equational division.

Cai et al. (2010) further studied the cytological mechanism of UMCD by using the polyhaploids of wheat cv. Langdon (LDN) and its amphidiploid hybrids with *Aegilops tauschii*. LDN has normal meiosis, but its polyhaploid and amphidiploid have UMCD. They found that sister kinetochores oriented syntelically at meiosis I in LDN but amphitelically in LDN polyhaploid and amphidiploid hybrid. Moreover, sister centromere cohesion persisted until anaphase II in LDN, LDN polyhaploid, and amphidiploid hybrid. Meocytes with all chromosomes oriented amphitelically underwent UMCD in LDN polyhaploid and amphidiploid, suggesting the tension created by the amphitelic orientation of sister kinetochores, and persistence of centromeric cohesion between sister chromatids at meiosis I contributed to the onset of UMCD. They suggested that some ploidy-regulated genes were responsible for kinetochore orientation at meiosis I in LDN and LDN-derived polyhaploids. In addition, since sister kinetochores of synapsed chromosomes oriented syntelically and asynapsed chromosomes oriented either amphitelically or syntelically, synapsis probably is also a factor for the coordination of kinetochore orientation in LDN. This is agreed with that a high level of chromosome pairing will prevent meiotic restitution and formation of unreduced gametes (Wang et al. 2010), while a low pairing is apparently not sufficient to prevent restitution in interspecific hybrids (Xu and Joppa 2000; Zhang et al. 2008c) or even common wheat itself (Ressurreição et al. 2012). Additionally, in fact, this is also the case observed here for the N5DT5B line under asynaptic conditions. This suggests that processes leading to the previously described haploid-dependent formation of unreduced gametes in F1 hybrids or polyhaploids also occur when two homologous chromosomes are present if synapsis is inhibited.

Second division restitution (SDR): It can also result in unreduced gametes in some diploid or hybrids involving autopolyploids. SDR was used to describe the normal first meiotic division followed by sister chromatid separation but failed to migrate to opposite poles at meiosis II. Two nuclei with unreduced chromosome number form at the end of meiosis II. Because sister chromatids are kept together in SDR-type gametes, the genetic makeup of these gametes is characterized by high levels of homozygosity, leading to the loss of the majority of parental heterozygosity, and epistatic interaction is lost (Cai and Xu 2007). SDR could occur after the first meiotic division, which should be completely normal, as is the case with meiosis in autopolyploid potato. However, since reductional division and segregation of univalents in anaphase I in wide haploid or amphiploid hybrids do not ensure a balanced chromosome set, SDR is hardly to occur. Therefore, SDR may be not the



pathway for the production of unreduced gametes in wide amphihaploid hybrids as in Triticeae.

Production of unreduced gametes in wide hybrids can be stimulated by both genetic (Xu and Joppa 2000; Zhang et al. 2010; Brownfield and Kohler 2011 and the references therein) and environmental (Bretagnolle and Thompson 1995; Ramsey and Schemske 1998; Mable 2004; Pécrix et al. 2011; Mason et al. 2011) factors as well as the interaction between these two (Bretagnolle and Thompson 1995; Zhang et al. 2010; Mason et al. 2011). Genetic studies on mutant alleles responsible for the formation of unreduced gametes in a number of crop species have shown that this phenotype is usually monogenic (Bretagnolle and Thompson 1995; Ramsey and Schemske 1998; Xu and Joppa 2000; Storme and Geelen 2011). Recently, several genes, such as DYAD/SWITCH1 (SWI1), OSD (omission of the second division), CYCA1; 2 (TAM, tardy asynchronous meiosis), AtPSI (Arabidopsis thaliana Parallel Spindles 1), and JASON for unreduced gametes, have been recently identified from the model diploid plant *Arabidopsis thaliana* (Andreuzza and Siddiqi 2008; Ravi et al. 2008; d'Erfurth et al. 2008, 2009; Storme and Geelen 2011). However, the molecular characterization of gene for haploidy-dependent UMCD in wide hybrids has not been reported although this kind of gene is very important for the origin of allopolyploids.

### 2.2.3 Homoeologous Chromosome Pairing and Translocation Lines

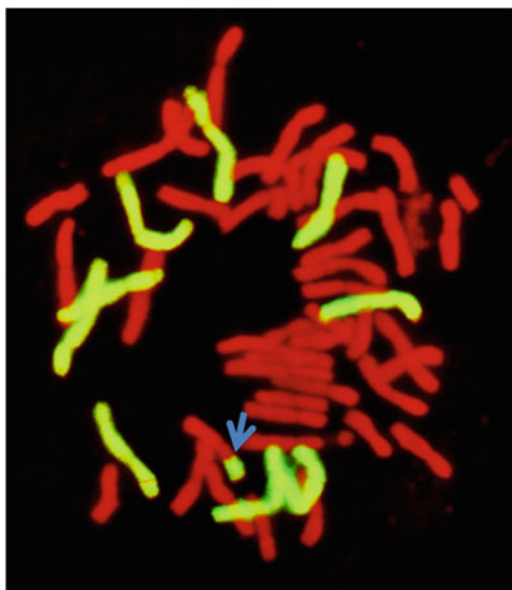
Wild species provides a vast gene pool for crop improvement. Most pioneering efforts in chromosome engineering have involved the *Triticum* species in Triticeae, with the greatest emphasis being placed on improving common wheat (*T. aestivum* L.,  $2n=6x=42$ , AABBDD) (Qi et al. 2007; Crouch et al. 2009; Reynolds et al. 2009; Wang 2009). Common wheat has more than 300 relative species in the fairly big tribe *Triticeae* (Clayton and Renvoize 1986; Watson and Dallwitz 1994). These species are important resources for broadening the genetic diversity of wheat. Wide hybrids of wheat have been studied since 1876 when Wilson (1876) made the first hybrid between common wheat (*Triticum aestivum* L.,  $2n=6x=42$ , AABBDD) and rye (*Secale cereale* L.,  $2n=2x=14$ , RR).

Translocation lines have been recognized as means for providing the most promising pathway for the utilization of alien germplasm (Qi et al. 2007). Translocations can occur in terminal, intercalary, or centric positions. Centric translocations can be produced by the misdivision of univalents at meiosis and subsequent random fusion of telocentric chromosomes, i.e., centric break-fusion (Lukaszewski and Gustafson 1983). In wide hybrids, unpaired chromosomes are present as univalents and thus give a chance to misdivide and then re-fuse. Centric translocation is frequently observed in wide hybrids. However, translocations in other positions are not common since the homoeologous chromosomes between wheat and alien species in wide hybrids show a low pairing level at meiotic metaphase I (MI) due to the action

of pairing homoeologous (*Ph*) gene system in wheat, which restricts the production of wheat–alien translocations (Sears 1976; Martinez-Perez and Moore 2008). This system includes a major pairing gene, *Ph1*, on 5B (Okamoto 1957; Riley and Chapman 1958); an intermediate pairing gene, *Ph2*, on 3D (Mello-Sampayo 1971; Sutton et al. 2003); and several minor loci (Sears 1976). The *Ph1* locus is related to a cluster of genes similar to Cdk2 (cyclin-dependent kinase) in mammals (Griffiths et al. 2006; Al-Kaff et al. 2008; Yousafzai et al. 2010a, b) and has a downstream effect on the synapsis gene *TaASY1* by reducing its expression level (Boden et al. 2009). Cdk2 has been shown to participate in the transition from G1 into S phase and also to affect DNA replication. Although the 5B Cdk-like genes are transcribed, they all seem to be defective copies. These defective Cdk-like genes are responsible for reducing Cdk-type activity, and this leads to the *Ph1* effect. However, the increased Cdk-type activity can phenocopy the effect of deleting the *Ph1* locus (Greer et al. 2012). The intermediate pairing gene *Ph2* is involved in the progression of synapsis (Martinez-Perez et al. 2001; Prieto et al. 2004) although the gene responsible for the phenotype is still to be isolated (Sutton et al. 2003). Pairing restriction by *Ph1* and *Ph2* involves not only wheat homoeologues but also wheat–alien chromosomes in wide crosses containing a haploid set of related chromosomes. However, homoeologous chromosomes can pair in hybrids of Chinese Spring (CS) mutant lines *ph1b*, *CSph2a*, and *CSph2b* and related alien species enabling gene transfer from alien species to wheat (Wall et al. 1971; Sears 1982; Martinez-Perez and Moore 2008). Moreover, gene *Ph'* from *Aegilops speltoides* can repress the action of *Ph1* and induce homoeologous chromosome pairing (Chen et al. 1994). A new strategy by increasing Cdk-type activity may be used in the induction of homoeologous chromosome pairing (Greer et al. 2012). The manipulation of *Ph1* gene can relieve the restriction of homoeologous chromosome pairing and thus improve the efficiency of alien translocation development.

On the other hand, natural phenotypic differences in homoeologous pairing have been observed among the hybrids of wheat and alien species (Driscoll and Quinn 1970; Dvorak and McGuire 1981; Farqoo et al. 1990; Ma et al. 1999; Ozkan and Feldman 2001) or in haploids from different common wheat cultivars (Martinez et al. 2005). Of which, Chinese common wheat landrace Kaixian-luohanmai (KL) exhibits homoeologous pairing in hybrids with *Secale cereale* L. ( $2n=2x=14$ , RR) and *Aegilops variabilis* Eig. ( $2n=4x=28$ , UUS<sup>L</sup>S<sup>L</sup>) at levels between those of hybrids involving Chinese Spring *ph1b* (*CSph1b*) or *CSph2b/CSph2a* (Luo et al. 1992; Liu et al. 1998c, 2003; Xiang et al. 2005). However, KL  $\times$  *Psathyrostachys huashanica* Keng ex Kuo ( $2n=2x=14$ , NsNs) hybrids showed significantly higher chromosome pairing than *CSph1b*  $\times$  *Psa. huashanica* (Kang et al. 2008). The lower pairing in *CSph1b*  $\times$  *Psa. huashanica* may be caused by a suppressor in *Psa. huashanica* (Sun and Yen 1994). Recently, meiotic phenotypic differences on homoeologous chromosome pairing at metaphase I between hybrids of *CSph1b* and KL with rye were studied by genomic in situ hybridization (GISH). Although the frequency of wheat–wheat associations was higher in *CSph1b*  $\times$  rye than in KL  $\times$  rye, frequencies of wheat–rye and rye–rye associations were higher in KL  $\times$  rye than in *CSph1b*  $\times$  rye (Hao et al. 2011). These differences may be the result of different mechanisms of control between the *ph*-like gene(s) controlling

**Fig. 2.2** One wheat–rye translocation chromosome (*arrow*) observed at mitotic metaphase in root-tip cells of the Syn-SAU-6/Qinling  $F_2$  plants



homoeologous chromosome pairing in KL and *CSph1b*. These lines promoting homoeologous chromosome pairing can also be used in alien translocation development.

Another problem for alien translocation development is that randomly separated chromosomes in wide hybrids move towards opposite poles in meiotic anaphase I (AI) and thus result in reduced gametes with absent chromosomes. This sets a barrier for developing translocation lines since the translocated chromosomes may be not contained in reduced gametes or cannot be transmitted into progenies due to the sterility of reduced gametes. High pairing in the inactive *Ph1* gene further reduces fertility of gametes that probably attributed an increase in meiotic disturbances (Ceoloni and Donini 1993). The efficiency of genetic manipulations of *Ph1* gene for the production of wheat–alien translocations in past years was not as good as expected (Miller et al. 1998). How to efficiently transmit the translocated chromosomes induced in  $F_1$  hybrid into following generations still needs to be resolved for translocation line development. As mentioned above, unreduced gametes may be used in the fixation of translocation chromosomes in wide progenies. Translocated chromosomes occurred in meiotic metaphase I in hybrids can be transmitted into amphidiploids by the union of fertile unreduced gametes. Haploid wheat–rye hybrids and its derivatives usually have very low fertility because their reduced gametes are often nonfunctional. However, some synthetic hexaploid wheat Syn-SAU-6/Qinling  $F_1$  plants had relatively high seed set. Syn-SAU-6 was derived from spontaneous chromosome doubling of hybrids between *T. turgidum* L. ssp. *durum* cv. Langdon and *A. tauschii* accession AS65 and inherited the gene(s) for the formation of

unreduced gametes from Langdon (Zhang et al. 2007, 2010). We observed some translocation chromosomes in some F<sub>2</sub> Syn-SAU-6/Qinling hybrid seeds, thus demonstrating that unreduced gametes are capable to fix chromosome rearrangements into progenies. Of which, one wheat-rye translocation chromosome is shown in Fig. 2.2.

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