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Haploid Independent Unreductional Meiosis in Hexaploid Wheat

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1. Introduction

Polyploidy correspond to the presence of more than two complete sets of chromosomes and is considered a major plant evolutionary force connected with adaptive plasticity (review in Comai, 2005). Within angiosperms it is estimated that at least 50% of its members have suffered one or more rounds of polyploidization (Wendel, 2000). Formation of functional unreduced gametes ($2n$) due to meiotic abnormalities is considered the key event associated with chromosome doubling and has been described in several dicot and monocot plant species (Ramanna and Jacobsen, 2003, Fawcett and Van de Peer, 2010). While autopolyploids are a direct result of duplication thus having multiple chromosome sets of the same origin, allopolyploids result from interspecific or intergeneric hybridization associated or followed by chromosome doubling, allowing for the emergence of new sexually reproduced species. Among sexual polyploids are many of the most important crops worldwide as it is the case of bread wheat (*Triticum aestivum* L.).

Triticum aestivum L. is an allohexaploid with 3 genomes designated A, B and D ($2n = 6x = 42$, AABBDD). It is believed that the formation of hexaploid wheat has occurred about 8000 years ago (Huang et al., 2002) through the cross between *Aegilops tauschii* Coss. ($2n = 2x = 14$) donor of genome D, and *Triticum turgidum* L. ($2n = 4x = 28$; AABB) (McFadden and Sears, 1946). By its turn *Triticum turgidum* L. (durum or macaroni wheat) is an allotetraploid resulting from the hybridization between *Triticum urartu* Tumanian ($2n = 2x = 14$) and *Aegilops speltoides* Tausch ($2n = 2x = 14$) the diploid donors of the genomes A and B, respectively (Dvorak et al., 1993). Since wheat progenitor species are close related, pairing can occur between corresponding (homoeologous) chromosomes of the distinct genomes. This phenomenon is however suppressed by the *Pairing homoeologous* gene (*Ph 1*) mapped in the long arm of chromosome 5B (Riley and Chapman, 1958). The presence of *Ph 1* results in a diploid-like meiosis both in tetra- and hexaploid wheat and is believed to have arisen by mutation at the time of the tetraploid formation (Riley and Chapman, 1958; Jauhar, 2007).

It is accepted that formation of unreduced gametes is the most important mechanism for fertile allopolyploid formation. Two main pathways are associated with meiotic

restitution according with the composition of the duplicated meiotic products: First Division Restitution (FDR) and Second Division Restitution (SDR). FDR and SDR correspond in *sensu lato* to the omission of the first division or the second meiotic division respectively, this is failure of either homologous chromosome segregation or sister chromatid segregation (Ramanna and Jacobsen, 2003). Meiotic restitution corresponding FDR has been described in *Triticeae* as a haploid-dependent process and repeatedly addressed through the use of intergeneric hybrids (between wheat and related species) and wheat polyploids (recovered from hybridization with maize) (Islam and Shepherd, 1980; Balatero and Darvey, 1993; Jauhar, 2007; Matsuoka and Nasuda, 2004; Shamina, 2011).

In summary it has been shown that the haploid dependent meiotic restitution trait is genetically controlled and is only present in some wheat genotypes. When meiotic restitution trait is present, unreduced gametes result from lack of univalent segregation at meiosis I and subsequent sister chromatid disjunction at anaphase although the level of penetrance is generally very low. Analysis of microtubule cytoskeleton revealed that haploid unreductional meiosis depends on the bipolar attachment of univalents (Cai et al., 2010). In addition, it was also recently shown that even in genotypes with meiotic restitution, formation of unreduced gametes is obstructed by the occurrence of some level of homologous pairing (Wang et al., 2010).

So far, in wheat meiotic restitution was only described for haploid genotypes in which asynapsis results from the absence of homologous chromosome pairs. Here we investigated the influence of induced asynapsis in the progression of meiosis in a diploid context. For this purpose we took advantage of aneuploid hexaploid wheat line nulisomic for 5D and tetrassomic for 5B (N5DT5B) derived from cv Chinese Spring that display inducible asynapsis. This phenotype is associated with the lack of *Low temperature pairing* (*Ltp*) gene mapped in the long arm of chromosome 5D. N5DT5B plants are fertile with regular diploid-like meiosis when grown at temperatures ranging from 19 to 29°C, however for temperatures lower than 15°C or higher than 30°C meiocytes are asynaptic (Bayliss and Riley, 1972a). Moreover it has been established that the sensitive state for asynapsis is the last interphase prior to meiosis and not the meiotic division itself (Bayliss and Riley, 1972b).

2. Material and methods

2.1 Plant material and growth conditions

We analyzed the chromosome and cytoskeleton behaviour during male meiosis in aneuploid lines N5DT5B and N5DT5A derived from hexaploid wheat (*Triticum aestivum* L.) cv Chinese Spring. Plants were continuously grown at 22°C or exposed to 10°C for 15-20 days prior to meiosis (Queiroz et al, 1991). Under the low temperature regime N5DT5B line is completely asynaptic while N5DT5A line displays a low level of asynapsis (Riley et al., 1966, Bayliss and Riley, 1972a). In these lines all chromosomes are present as homologues pairs with exception of chromosome 5B or 5A that are present in four copies in N5DT5B and N5DT5A, respectively. Wheat x rye F1 hybrid between hexaploid wheat cv. Chinese Spring and Portuguese rye (*Secale cereale* L.) landrace Centeio do Alto continuously grown at 22°C was also analyzed corresponding to an haploid-dependent asynaptic genotype.

2.2 Cytological analysis of meiocytes

Anthers selected for all meiotic stages were fixed in 4% (w/v) formaldehyde in MTSB (50 mM piperazine-N,N-bis(2-ethanesulfonic acid), 5 mM MgSO₄·7H₂O, 5 mM EGTA, pH 6.9) for 45 min at room temperature, and then rinsed twice in MTSB. Meiocytes were processed for subcellular localization of microtubules (MT) by indirect immunofluorescence. Briefly, fixed anthers were dissected permitting meiocyte dispersal in multiwell slides coated with aminopropyltriethoxysilane (Sigma) and left to air dry. The cells were then permeabilized in 0.5% Triton X-100 in MTSB for 15 min and rinsed prior to labeling. MT were localized with mouse monoclonal antibody against alpha-tubulin DM1A (Serotec) diluted 1 : 100 in MTSB, which recognizes alpha-tubulin a component of MT. Indirect detection of DM1A was performed with a secondary antibody conjugated with fluorescein isothiocyanate, diluted 1 : 300 in MTSB. DNA was counterstained 4',6-diamidino-2-phenylindole hydrochloride (DAPI) in Citifluor antifade buffer (AF1; Agar Scientific, Stansted, U.K.).

Immunofluorescence was recorded using an epifluorescence microscope Zeiss Axioskop2 equipped with a Zeiss AxioCam MRc 5 digital camera. Images were captured using the appropriate excitation and emission filters and composited using Adobe Photoshop 7.0 (Adobe Systems Inc.) software. For N5DT5B and N5DT5A in both growth conditions and for wheat x rye F1 hybrid several plans were analyzed and at least 100 meiocytes were scored at each stage (prophase I, metaphase I, anaphase/telophase I, prophase II and anaphase/telophase II).

3. Results

N5DT5B and N5DT5A lines grown at 22°C have a regular meiotic chromosome behaviour as previously described (Bayliss and Riley, 1972a). Also the microtubule dynamics follows the typical *Triticeae* meiotic pattern (Shamina, 2005, Cai et al., 2010). During the first meiotic division prophase a perinuclear ring is formed, from which microtubules emanate into the nuclear area with progression of prophase (Figure 1 a). Metaphase I and anaphase I are characterized by the presence of a spindle where microtubules converge at two polar foci forming a clear fusiform spindle responsible for homologous chromosome segregation (Figure 1 b and c, respectively). At telophase I a prominent fragmoplast is formed resulting in cytokinesis and formation of two reduced dyads (Figure 1 d). In the second meiotic division in each dyad following a brief prophase a spindle is observed at metaphase/anaphase leading to sister chromatid segregation and a fragmoplast is formed at telophase producing a tetrad with four haploid microspores (Figure 1 e and f).

As previously described (Bayliss and Riley, 1972a), in N5DT5B plants exposed to 10°C prior to meiosis asynapsis is induced. Under these asynaptic conditions at first meiotic division 81.6% of the meiocytes present a low level of bivalent formation (3-6 bivalents per cell). In these cases a spindle is formed although major disturbances such as twisted spindles are common. Syntelical orientation to the spindle (monopolar attachment) of sister kinetochores is observed for both bivalents and univalents (Figure 2 a). This results in the gathering of bivalents at the metaphase plate and their correct segregation while univalents are dispersed and randomly segregated. Progression into meiosis II occurs with sister chromatid segregation and cytokinesis with consequent uneven meiotic products and high level of micronuclei (Figure 2 d, left).

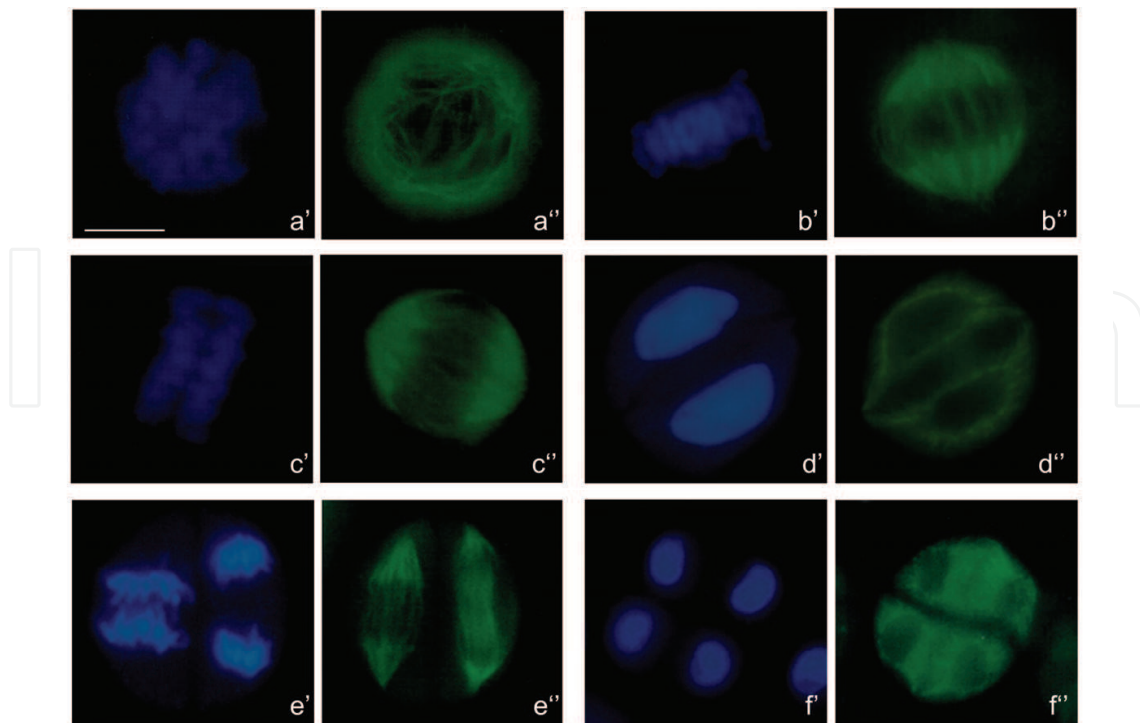


Fig. 1. Regular meiosis of the aneuploid line N5DT5B derived from hexaploid wheat cv Chinese Spring grown at 22°C. a. prophase I, b. metaphase I, c. anaphase I; d. telophase I, e. anaphase II, f. telophase II. Chromosome DAPI staining is shown in blue (a', b', c', d', e' and f') and microtubule cytoskeleton in green (a'', b'', c'', d'', e'' and f''). All images have identical magnification, bar = 10µm.

However, a significant proportion of the meiocytes (18.4%) present complete asynapsis. These cells undergo sister chromatid separation with tendentially equational chromatid segregation originating diads that further progress to interphase with a cytoskeleton organization characteristic of young pollen grain (Figure 2 d, right). Interestingly, the level of micronuclei in dyads is much low than in tetrads indicating high probability of balanced division. This results in the formation of unreduced gametes what is also supported by the fact that dyads nuclei are considerably larger than those of tetrads although the compaction level of chromatin is similar (Figure 2 d). At this stage, a high proportion (27%) of dyads are observed although simultaneously with tetrads, triads and other highly unbalanced meiotic products since unreductional division only occurs in some meiocytes within the same anther.

In the N5DT5B line under asynaptic condition we found that unreductional division can occur by two distinct pathways (Figure 2 b and c). (i) Segregation of chromatids during the first division and blockage of second division. In this case sister kinetochores orient amphitelicly to the spindle (bipolar attachment) and chromosome arm cohesion is lost. At anaphase sister chromatids are pulled to opposite poles although one or two lagging chromosomes can occur (Figure 2 b). (ii) Failure of first division with formation of a restitution nucleus encaging all univalents coincident with chromosome decondensation (Figure 2 c). The monads formed undergo to second division where sister chromatids are segregated.

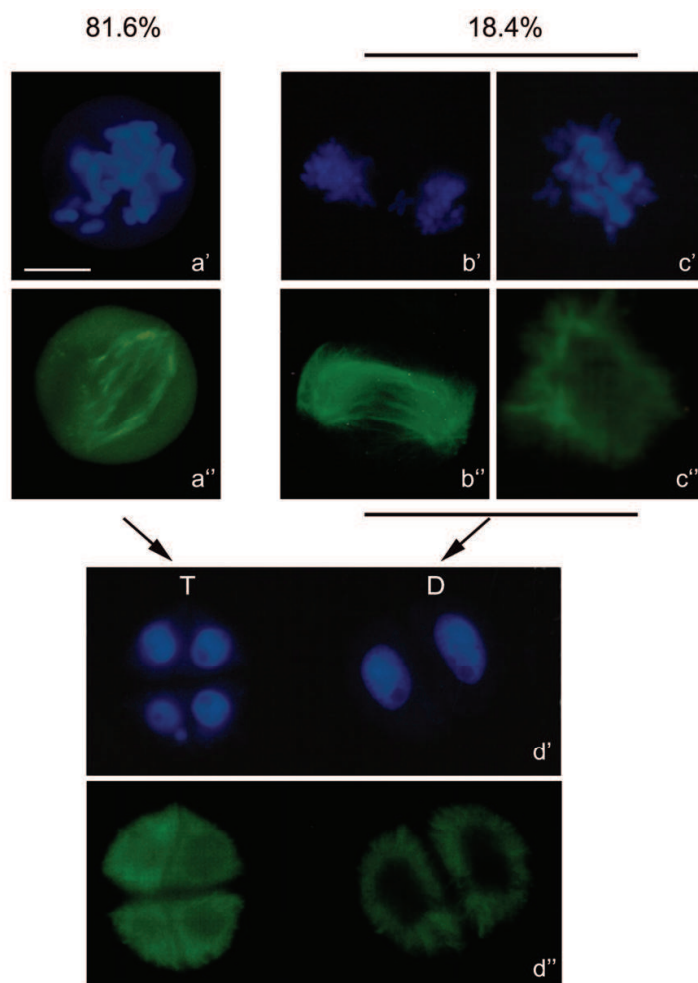


Fig. 2. Aspects of asynaptic meiosis in the aneuploid line N5DT5B due to exposure to 10°C prior to meiosis. a. Univalents at metaphase I (a') with bipolar spindle (a'') corresponding to 81.6% of the meiocytes at this stage b. and c. The remaining 18.4% of meiocytes undergo unreductional meiosis either through segregation of sister chromatids (b') with formation of bipolar spindle (b'') or through nuclear restitution and (c') absence of spindle (c''). d. Distinct meiotic products at the end of meiosis, a tetrad on the left (T) and a dyad on the right (D) are simultaneously observed in a single microscopic field. All nuclei show identical chromatin condensation but dyad nuclei are larger than tetrad nuclei, a micronuclei is present in the tetrad (d'). Microtubule organization characteristic of young pollen grain stage is present in both cell sets (d''). All images have identical magnification, bar = 10µm.

The meiotic behaviour of N5DT5A line under asynaptic conditions differs from that of N5DT5B line in the level of asynapsis that is much lower. Only a small fraction of meiocytes display complete or nearly complete asynapsis (10% of meiocytes with less than 6 bivalents). Meiocytes with a low number of bivalents behave as described for N5DT5B, while the majority of meiocytes undergo regular meiotic division although with a high frequency of micronuclei.

In the hexaploid wheat × rye F1 hybrid asynapsis at 22°C occurs due to haploid condition. Meiosis progress with a high level of irregularities as previously described for other wheat hybrid genotypes. Metaphase I form irregular spindles that result from monopolar

attachement of univalents and at anaphase/telophase I univalents are randomly segregated. Meiocytes progress into meiosis II with formation of highly unbalanced gametes (Figure 3 b). Importantly, the hybrid does not display any of the characteristic features of unreductional meiosis, although it has as female parent Chinese Spring wheat from which N5DT5B and N5DT5A are derived. Neither first division nuclear restitution or sister chromatid segregation are ever observed. Occasionally meiocytes (8,6% at metaphase I) present premature sister chromatid separation but in contrast with N5DT5B this is always associated with spindle collapse and consequently impairment of sister chromatids segregation (Figure 3 a).

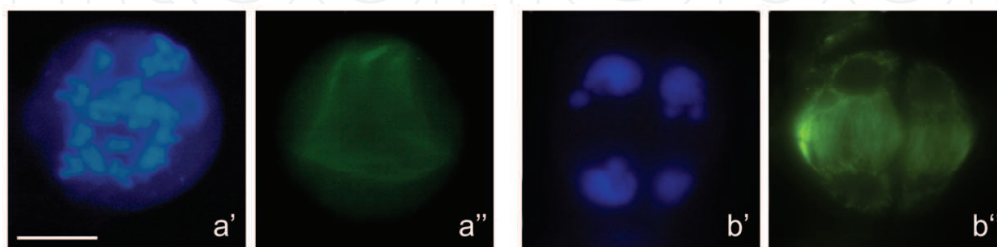


Fig. 3. Aspects of asynaptic meiosis in the hexaploid wheat cv Chinese Spring x rye Centeio do Alto F1 hybrid. a. Premature sister chromatid separation at first division (a') associated with spindle collapse (a''). b. Unbalance telophase II with several micronuclei. DAPI staining (b') and microtubule cytoskeleton (b'') reflects the random univalent segregation at previous anaphase I since both nuclei on the left have very distinct size from those on the right and dyad cleavage divides left and right nuclei. All images have identical magnification, bar = 10 μ m.

4. Discussion

Our results show that unreductional meiosis occurs in the aneuploid wheat line N5DT5B with formation of 2n pollen grains. To our knowledge this is the first time that unreductional meiosis is described in a wheat line with homologous pairs for all chromosomes present. Formation of unreduced gametes has recurrently been reported as a characteristic of some wheat genotypes described as having meiotic restitution trait. However, this characteristic was always considered as a haploid dependent process occurring in either interspecific F1 hybrids (for review see Silkova et al., 2011) or in the polyhaploid plants (Jauhar, 2007, Cai et al., 2010). In the case of N5DT5B this phenomena is induced under low temperature conditions as the meiotic behaviour of this line is completely regular at 22°C. N5DT5B was characterized by inducible asynapsis by low temperature exposure prior to meiosis due to the absence of the *Ltp* gene mapped in the in the long arm of chromosome 5D (Bayliss and Riley, 1972a). This implies that in wheat asynapsis rather than haploid condition is the key feature for unreduced pollen grain formation. Supporting this hypothesis is the recent demonstration that the meiotic restitution phenotype observed in F1 hybrids between *T. turgidum* with diploid *Ae. tauschii* is completely abolished when tetraploid *Ae. tauschii* is used due to the formation of bivalents between the homologues chromosomes of *Ae. tauschii* (Wang et al 2010).

Distinct cytological processes leading to unreductional meiosis were described in distinct *Triticeae* genotypes using distinct terminology. 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. ssp. *durum* cultivars Langdon and Golden Ball and *S. cereale* L. cultivar Gazelle or *Ae. tauschii* Coss. (Xu and Joppa, 2000). More recently the designation unreductional meiotic cell division (UMCD) was used to describe this meiotic behavior (Cai et al., 2010). On the other hand, in very close related hybrids between *T. turgidum* L. ssp. *turgidum* and *Ae. tauschii* Coss., other authors described a single-division meiosis (SDM) characterized by a mitosis-like equational division with univalent sister chromatid segregation and blockage of second division (Zhang et al., 2007). The divergence in terminology reflects the lack of knowledge regarding the mechanisms that govern meiotic division in haploid genotypes. It should be emphasized that either nuclear restitution at meiosis I followed by regular meiosis II or sister chromatid segregation at anaphase I and absence of the second division have exactly the same genetic outcome, i.e. formation of two genetically identical unreduced microspores since cell division only involves sister chromatids segregation. Additionally, it has been shown that both types of division coexist with various frequencies depending on the genotype analysed (Xu and Joppa, 2000, Zhang et al., 2007, Silkova et al., 2011). 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.

Interestingly, when the wheat cv Chinese Spring, the genotype from which N5DT5B line is derived, is crossed with Portuguese rye Centeio do Alto, the F1 hybrid does not present meiotic restitution features since at meiosis I univalents are either randomly segregated or if sister chromatid cohesion is lost microtubule spindle collapses and therefore no segregation of chromatid is observed. Similarly, Zhang et al. (2007) found no evidence of meiotic restitution in the F1 hybrid between Chinese Spring wheat and a Chinese rye landrace or *Ae. variabilis*. On the other hand, analysis of polyhaploid lines derived from hexaploid wheat cv Chinese Spring showed that although meiotic restitution can occur with seed production (Jauhar, 2007) the level of seed set is much lower than that observed in polyhaploid lines derived from the tetraploid wheat Langdon, one of the most studied genotypes for its haploid dependent meiotic restitution trait (Cai et al., 2010). Together these observations indicate that hexaploid wheat cv Chinese Spring genotypes cannot be characterized as having haploid dependent meiotic restitution trait as previously assumed by Zhang et al. (2007). This does not exclude however that a high level of meiotic restitution can occur in some in wheat cv Chinese Spring interspecific hybrids as has been observed with *Hordeum vulgare* cv. Betzes (Islam and Shepherd, 1980) since this phenomenon is influenced by both parental genomes.

The present results show that meiotic restitution and unreduced gamete formation can occur in hexaploid wheat genotypes without meiotic restitution trait in a haploid independent manner in conditions of induced asynapsis. These observations raise the hypothesis that in some step of hexaploid wheat evolution interspecific hybridization could result from unreduced gamete fertilization.

Taken together, this challenges the widely accepted notion that interspecific hybridization has taken place prior to chromosome duplication in wheat evolution. Considering that formation of $2n$ gametes in sexual species is rare and highly dependent on environment

(Ramanna and Jacobsen, 2003), it is plausible that allopolyploidization results from fusion of unreduced gametes which in turn are the result of environmental conditions in established species sharing the same geographical niche. In fact, it has been proposed that this is the primarily process in the formation of neopolyploids in flowering plants (Ramsey and Schemske, 2002).

From the extensive data on wheat haploid-dependent meiotic restitution it is clear that this genetically controlled trait occurs in some genotypes of tetraploid wheat but not in others. If we consider that haploid dependent restitution is the genesis of wheat species it must be assumed that at least in some genotypes controlling gene(s) were conserved throughout wheat evolution, although only effective in the haploid condition. Based on our observations, we are proposing the alternative hypothesis that the haploid-dependent meiotic restitution trait has been acquired in some genotypes after allopolyploidization and that this acquired trait resulted from a loss or reduction in function of genes involved in promoting meiotic pairing.

Several genes promoting meiotic pairing have been identified in wheat (Feldman, 1966, Riley, 1974, Queiroz et al., 1991). The most well studied genes involved in wheat meiotic chromosome pairing are *Ph* (*Pairing homoeologous*) genes, which ensure that pairing is limited to homologous rather than between homoeologous chromosomes. We suggest that in genotypes without haploid-dependent meiotic restitution, promoting pairing genes allow transient chromosome synapsis and thus result in a dysfunctional meiosis. On the other hand, in genotypes with haploid-dependent meiotic restitution, reduced pairing capacity could lead to a situation similar to that observed in the N5DT5B line at low temperatures. In this case, absence of meiotic synapsis can be attributable to defective initiation of meiotic chromosome pairing therefore becoming reminiscent of a mitotic division.

Our hypothesis that haploid-dependent meiotic restitution in wheat evolved more recently is supported by phylogenetic evidence. Chromosome structure of Chinese Spring wheat, which does not have the haploid-dependent meiotic restitution trait, is more similar to the primitive tetraploid wheat than other wild tetraploids (Kawahara, 1988). Also significantly, a recent report showed that tetraploid wheat genotypes without haploid-dependent meiotic restitution have less meiotic abnormalities in conditions of heat stress than tetraploid genotypes with this trait, suggesting that haploid-dependent meiotic restitution is directly associated with less efficient meiotic control (Rezaei and Sayed-Tabatabaei, 2010). Taken together, we believe our results provide a novel and comprehensive view of wheat evolution.

5. Conclusion

Unreductional meiosis and formation of $2n$ gametes is the main mechanism in the emergence of sexual polyploids. Bread wheat (*Triticum aestivum* L.) is a natural allohexaploid with regular diploid-like meiosis resulting from two sequential events of hybridization associated with chromosome doubling. Several studies have addressed the question of chromosome duplication considering that this is a haploid-dependent process. We show here that unreductional meiosis occurs in hexaploid wheat genotypes where two homologues are present for each chromosome as an asynapsis dependent process controlled

by a genotype-temperature mechanism. This is the first time that formation of 2n microspores is observed in wheat as a haploid independent process. The present results raise the hypothesis that wheat evolution could result from unreduced gamete fertilization challenging the generalized idea that wheat intergeneric hybridization occurred prior to chromosome duplication.

6. Acknowledgements

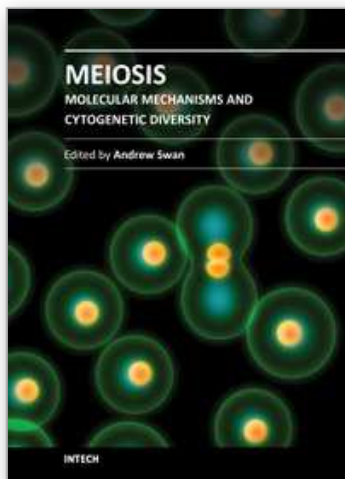
This work was funded by Pest-OE/AGR/UIO240/2011, FCT-Portugal

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Meiosis - Molecular Mechanisms and Cytogenetic Diversity

Edited by Dr. Andrew Swan

ISBN 978-953-51-0118-5

Hard cover, 472 pages

Publisher InTech

Published online 29, February, 2012

Published in print edition February, 2012

Meiosis, the process of forming gametes in preparation for sexual reproduction, has long been a focus of intense study. Meiosis has been studied at the cytological, genetic, molecular and cellular levels. Studies in model systems have revealed common underlying mechanisms while in parallel, studies in diverse organisms have revealed the incredible variation in meiotic mechanisms. This book brings together many of the diverse strands of investigation into this fascinating and challenging field of biology.

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Filipe Ressurreição, Augusta Barão, Wanda Viegas and Margarida Delgado (2012). Haploid Independent Unreductional Meiosis in Hexaploid Wheat, *Meiosis - Molecular Mechanisms and Cytogenetic Diversity*, Dr. Andrew Swan (Ed.), ISBN: 978-953-51-0118-5, InTech, Available from:
<http://www.intechopen.com/books/meiosis-molecular-mechanisms-and-cytogenetic-diversity/haploid-independent-unreductional-meiosis-in-hexaploid-wheat>

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