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ORIGINAL PAPER

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Durum wheat as a candidate for the unknown female progenitor of bread wheat: an empirical study with a highly fertile F_1 hybrid with *Aegilops tauschii* Coss.

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Abstract Hexaploid bread wheat was derived from a hybrid cross between a cultivated form of tetraploid *Triticum* wheat (female progenitor) and a wild diploid species, *Aegilops tauschii* Coss. (male progenitor). This cross produced a fertile triploid F_1 hybrid that set hexaploid seeds. The identity of the female progenitor is unknown, but various cultivated tetraploid *Triticum* wheats exist today. Genetic and archaeological evidence suggests that durum wheat (*T. turgidum* ssp. *durum*) may be the female progenitor. In previous studies, however, F_1 hybrids of durum wheat crossed with *Ae. tauschii* consistently had low levels of fertility. To establish an empirical basis for the theory of durum wheat being the female progenitor of bread wheat, we crossed a durum wheat cultivar that carries a gene for meiotic restitution with a line of *Ae. tauschii*. F_1 hybrids were produced without using embryo rescue techniques. These triploid F_1 hybrids were highly fertile and spontaneously set hexaploid F_2 seeds at the average selfed seedset rate of 51.5%. To the best of our knowledge, this is the first example of the production of highly fertile F_1 hybrids between durum wheat and *Ae. tauschii*. The F_1 and F_2 hybrids are both similar morphologically to bread wheat and have vigorous growth habits. Cytological analyses of F_1 male gametogenesis showed that meiotic restitution is responsible for the high fertility of the triploid F_1 hybrids. The implications of these findings for the origin of bread wheat are discussed.

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Introduction

Bread wheat (*Triticum aestivum* L. ssp. *aestivum*) has a hexaploid genome (genome constitution AABBDD) derived from a hybrid cross between a form of tetraploid *Triticum* wheat (*T. turgidum* L., genome constitution AABB) as the female parent and a wild diploid species *Aegilops tauschii* Coss. (genome constitution DD) as the male parent (Kihara 1944; McFadden and Sears 1944). The hybrid cross is supposed to have produced a fertile triploid F_1 hybrid that spontaneously set hexaploid seeds by producing unreduced gametes in male and female gametogenesis (Kihara and Lilienfeld 1949). Because the primary habitat areas of the wild *T. turgidum* (*T. turgidum* ssp. *dicoccoides*) and *Ae. tauschii* do not overlap, the hybrid cross that gave rise to bread wheat is thought to have taken place after domestication of *T. turgidum* in the Fertile Crescent and the subsequent spread of its cultivated forms to the western part of the *Ae. tauschii* distribution—Transcaucasia and northern Iran (Zohary and Hopf 2000). Although this framework of bread wheat evolution is well established, several questions still must be addressed regarding the origin of bread wheat. One is what kind of cultivated *T. turgidum* provided the AB genome to bread wheat given the diverse array of existing *T. turgidum* cultivars. This question is important because ascertaining the source would help us to better understand the nature of the AB genome of bread wheat and, in turn, help guide genetic, evolutionary, and breeding studies on this plant.

The existing forms of cultivated *T. turgidum* are phenotypically and genetically diverse. Taxonomically, they are classified in seven subspecies (Slageren 1994): *carthlicum*, *dicoccon*, *durum*, *paleocolchicum*, *polonicum*, *turanicum*, and *turgidum*. On the assumption that the ancestral cultivated *T. turgidum* still exists, one approach to identify the AB genome donor of bread wheat is to artificially cross the existing *T. turgidum* cultivars with *Ae. tauschii*, then analyze the fertility, morphology, and genetic features of their triploid F_1 and hexaploid F_2 hybrids. This empirical approach has the potential to reproduce the natural process that gave rise to bread wheat

approximately 10,000 years ago by taking advantage of the relative readiness of crossing *T. turgidum* with *Ae. tauschii* without the use of embryo rescue techniques.

Embryo rescue-free, artificial-cross studies have provided valuable information on the identification of the AB genome donor of bread wheat: ssp. *carthlicum* is crossable with *Ae. tauschii*, and the selfed seedset rates of ssp. *carthlicum-Ae. tauschii* triploid F_1 hybrids are high (roughly 15–57% depending on the parental genotypes) (Kihara et al. 1965; Fukuda and Sakamoto 1992a). In contrast, selfed seedset rates of F_1 hybrids between other forms of *T. turgidum* cultivars and *Ae. tauschii* are about 10% at most (Tanaka 1961; Fukuda and Sakamoto 1992a). Moreover, the hexaploid F_2 that arose spontaneously from the ssp. *carthlicum-Ae. tauschii* triploid F_1 hybrids shows great morphological similarity to bread wheat (Kihara and Lilienfeld 1949). These and other lines of evidence have led some researchers to consider that ssp. *carthlicum* may have been the source of the AB genome of bread wheat (Tanaka 1961; Mackey 1963; Kerber and Bendelow 1977; Bushuk and Kerber 1978). Furthermore, ssp. *carthlicum* has genetic factors that control unreduced gametogenesis in its triploid F_1 hybrids with *Ae. tauschii* (Fukuda and Sakamoto 1992a).

Subspecies *carthlicum* is distinct from the other forms of cultivated *T. turgidum* in that it has remarkable morphological similarity to bread wheat (Zhukovsky 1923). The cultivation area of ssp. *carthlicum* is narrow —restricted to the Transcaucasus region—but the hybrid cross with *Ae. tauschii* could have occurred because populations of *Ae. tauschii* are present in that region. These points support ssp. *carthlicum* being the AB genome donor of bread wheat. The close morphological similarities may, however, indicate that ssp. *carthlicum* is a descendent of bread wheat, rather than a progenitor, derived from a hybrid cross between bread wheat and some unknown *T. turgidum* cultivar in the Transcaucasus region (Kucuck 1979). If so, the high selfed seedset rates for ssp. *carthlicum-Ae. tauschii* F_1 hybrids would not support the ancestry of bread wheat being ssp. *carthlicum* because the rates could be the result of inheriting of the genetic factors that control the production of unreduced gametes from bread wheat to ssp. *carthlicum*. In fact, the chromosomal structures of ssp. *carthlicum* and the AB genome of bread wheat differ, indicative that ssp. *carthlicum* may not have been involved in bread wheat's origin (Riley et al. 1967). A similar hybrid origin model has been proposed for ssp. *paleocolchicum* (Dvorák and Luo 2001).

The presumed hybrid origin of ssp. *carthlicum* and ssp. *paleocolchicum* requires further study to clarify the origin of the AB genome of bread wheat. In particular, the possibility that other forms of cultivated *T. turgidum* were involved in the origin of bread wheat needs to be investigated. Durum wheat (*T. turgidum* ssp. *durum*), one of the most common forms today of the cultivated *T. turgidum* wheats, has existed since ancient times (Araus et al. 2001) and is sometimes referred to as the AB genome progenitor of bread wheat (Kellogg 2003, for example). Durum wheat, however, produces F_1 hybrids with low fertility (0.0–9.7% selfed seedset rate) when crossed with *Ae. tauschii* if embryo rescue techniques are not used (Tanaka 1961; Fukuda and Sakamoto 1992a), indicative that some cultivars of durum wheat may not be capable of producing fertile F_1 hybrids with *Ae. tauschii* under natural conditions. Recently, a cultivar of durum wheat which carries a gene for meiotic restitution has been reported, and the same or a similar gene is probably shared with some durum cultivars (Xu and Joppa 1995, 2000). These findings suggest that embryo rescue-free, artificial-cross studies may furnish the empirical basis for the theory that durum wheat is the unknown female progenitor of bread wheat if the F_1 hybrids of such durum wheat cultivars with *Ae. tauschii* have degrees of fertility comparable to those found for the ssp. *carthlicum-Ae. tauschii* F_1 hybrids.

We report here our findings for the F_1 and F_2 hybrids of the durum wheat cultivar Langdon and an *Ae. tauschii* line. Langdon has a gene for meiotic restitution (Xu and Joppa 1995, 2000). Triploid F_1 hybrids were obtained by hand pollination without the use of embryo rescue techniques. The average selfed seedset rate of the triploid F_1 hybrids was 51.5% under our conditions, which is comparable to the rates that have been reported for ssp. *carthlicum-Ae. tauschii* F_1 hybrids. The fertility, morphology, and meiotic behavior of the triploid F_1 hybrids and their hexaploid F_2 descendants are described and the implications of our findings for the origin of bread wheat discussed.

Materials and methods

Plant materials

The parental materials were the durum wheat cultivar Langdon (*Triticum turgidum* ssp. *durum* cv. Langdon; subsequently referred to as Ldn) and an *Aegilops tauschii* (accession YM9508) line. YM9508, obtained from S. Yokota, was originally derived from an accession of *Ae. squarrosa* (syn. *Ae. tauschii*) (KU-2088) that is maintained at the Plant Germ-plasm Institute of Kyoto University.

Production of hybrids

Seeds were sown in December and the plants grown individually in pots in a greenhouse at Fukui Prefectural University. The greenhouse was slightly heated for the first 3–4 weeks to enhance early development but was unheated thereafter. To produce F_1 hybrids, we emasculated Ldn spikes and pollinated these by hand with *Ae. tauschii* YM9508 as the pollen parent. No gibberellic acid solution was applied to the embryos after pollination. Following harvest, crossability was calculated as the number of seeds obtained/number of florets pollinated × 100. Well-developed F_1 seeds were selected and analyzed further. These seeds were germinated at 23°C in

petri dishes, then transplanted. Chromosomes in the root tips of a few individuals were counted by the aceto-carmine squash method. Neither colchicine nor similar chemicals were applied to the F_1 plants. Spikes on well-developed tillers were bagged before flowering. The selfed seedset rate was calculated as the number of seedsets/number of well-developed florets × 100. F_2 hybrid plants were grown and analyzed similarly.

Hybrid growth habits

Plant height and tillering, the two growth-habit traits of the hybrids that we selected for analysis, were compared with those of the parental strains. Plant height was measured as the length of the longest tiller—from the ground to the tip of the spike—awns being excluded. Tillering was measured as the effective number of tillers—the number of spike-set columns per plant.

Cytological observations

Analyses of chromosome behavior in male sporogenesis in the triploid F_1 plants were performed by the conventional aceto-carmine squash method. Stages of meiosis and post-meiotic mitosis were determined in aceto-carmine squashes of one of three anthers per flower. If appropriate stages were present, the remaining two anthers were fixed in a mixture of absolute ethanol and acetic acid (3:1) and kept in a refrigerator for up to 3 months. For the cytological analysis, anthers were hydrolyzed in 1 *N* HCl at 60°C for 10 min, stained with Schiff's Reagent (Wako, Japan) for several hours, then squashed in a drop of aceto-carmine. Observations and documentation were made with an Olympus BX-60 microscope coupled with a Photometrics SenSys CCD camera. Images were captured and processed by the computer programs IPLAB ver. 3.1 and PHOTOSHOP ver. 4.0.

Pollen fertility was measured for pollen grains sampled from mature anthers at flowering. The grains were stained in a 2% aceto-carmine solution with glycerin. At least 1,000 grains were observed per plant. Pollen fertility was calculated as the number of normal pollen grains/total number of pollen counted × 100.

Results

We crossed Ldn with *Ae. tauschii* YM9508 in the spring of 1999, 2002, and 2003. Average crossability was 44.8% for 1999 (174 florets crossed), 19.6% for 2002 (191 florets crossed), and 52.9% for 2003 (34 florets crossed). Similar degrees of crossability have been reported for other crosses of durum wheat with *Ae. tauschii* (Kihara et al. 1965; Fukuda and Sakamoto 1992a).

Growth habits, morphologies, and seedsets of the F_1 and F_2 hybrids

F_1 seeds were sown in 2001 and 2002, resulting in a total of 96 plants. The selected F_1 seeds had a high germination rate (average: 95.8%). Root tips sampled from a few plants confirmed that they were triploids with 21 chromosomes. All of the F_1 plants grew vigorously, and none showed symptoms of hybrid lethality (Nishikawa 1960). As expected, the F_1 plants were uniform in appearance and had some obvious traits inherited from *Ae. tauschii*, including non-waxiness and tough glume (non-free-threshing spike). F_1 plants had spikes with lax internodes, shortened awns, and very sharply keeled, empty glumes—all of which are characteristics typical of durum wheat-*Ae. tauschii* F_1 hybrids (Kihara et al. 1950). The selfed seedset rate was 51.5% in 2001 and 52.8% in 2002 (total average 51.5%) (Table 1). These are substantially higher values than those reported for durum wheat-*Ae. tauschii* F_1 hybrids produced by embryo rescue-free artificial crosses (0.0–9.7%) (Tanaka 1961; Fukuda and Sakamoto 1992a).

F_2 seeds obtained from a single F_1 plant were sown in 2002. The root-tip chromosome count revealed that of the 12 plants grown nine were euhexaploids with 42 chromosomes; the other three plants were aneuploids with 40 (two plants) and 43 (one plant) chromosomes, respectively. All of the seeds germinated and grew vigorously. The morphology of the F_2 plants was similar to that of the F_1 plants except that the former appeared more robust. There was no apparent morphological difference between the euhexaploids and aneuploids. The average selfed seedset rate was 97.4% for the euhexaploids and 86.1% for the aneuploids (Table 1).

Table 1 Seedset rate and pollen fertility of hybrids of *Triticum turgidum* ssp. *durum* cv. Langdon (Ldn) with *Aegilops tauschii* YM9508 (NA Not available)

Plant type	Year	Seedset				Pollen		
		Number of plants	Number of florets	Number of seeds	Rate[a] (%)	Number of plants	Number of pollen	Fertility[a] (%)
F_1	2001	35	9,070	4,671	51.5 (39.0–63.6)	NA	NA	NA
	2002	4	180	95	52.8 (46.9–62.5)	4	4,473	46.9 (26.8–66.4)
F_2 (euhexaploid)	2002	9	460	448	97.4 (95.0–100)	4	5,904	96.2 (93.6–97.6)
F_2 (aneuploid)	2002	3	180	155	86.1 (78.3–90.0)	2	2,406	83.0 (71.9–94.9)
Ldn (control)	2002	1	34	28	82.4	NA	NA	NA

[a]Value ranges per plant are given in parentheses

Both the F_1 and F_2 plants had vigorous growth habits, as shown by enhanced plant height and tillering (Table 2), so the hybrids were easily identified by their heights. In fact, both the F_1 and F_2 hybrids were significantly taller than Ldn ($P<0.05$, Tukey-Kramer's HSD test). The effective number of tillers was significantly higher in the F_1 hybrids than in the F_2 and Ldn ($P<0.05$, Tukey-Kramer's HSD test).

Male gametogenesis of Ldn-*Ae. tauschii* YM9508 hybrids

Chromosome numbers in the root tips of the F_2 plants (mostly $2n=42$) suggest that they underwent chromosome doubling through the union of the male and female unreduced gametes ($n=21$) produced by the F_1 plants (see Kihara and Lilienfeld 1949). Moreover, the frequency of functional unreduced gametes should be high in F_1 plants, given the high selfed seedset rate (Table 1). We tested these inferences by observing male gametogenesis of the F_1 plants.

Cytological observations showed that an atypical type of meiosis, which we have named "single-division meiosis" (hereafter SDM), predominated in many anthers of the F_1 plants. Unlike normal meiosis, the SDM pathway involves a single division (Figs. 1, 2). The same, or a similar, type of meiosis has been described for some triploid hybrids in *Triticum* and *Aegilops* (Maan and Sasakuma 1977; Maan et al. 1980; Xu and Dong 1992). At metaphase in SDM, there was no chromosome pairing in 30 pollen mother cells (PMCs) (Fig. 1), indicative that homoeologus pairing is a rare occurrence due to the presence of the suppresser gene, *Ph*, of Ldn (Okamoto 1957; Riley and Chapman 1958). Initially, univalent chromosomes were randomly distributed in the PMCs (Figs. 1, 2d), subsequently becoming aligned at the equator at metaphase (Fig. 2e). Separation of sister chromatids occurred during late metaphase (Fig. 2f, g). Chromosomes of the PMCs underwent equational division at anaphase (Fig. 2h) and started to decondense at telophase (Fig. 2j). Symmetric dyad daughter cells were the final products of meiosis (Fig. 2l). SDM may have resulted in the production of aneuhaploid sporocytes because chromosomes often failed to align at the metaphase plate (Fig. 3a, b), and there were lagging chromosomes (Fig. 3c–e) and bridges (Fig. 3e, f). Apparently, the dyads proceeded to normal pollen mitosis (data not shown). In fact, pollen fertility of the F_1 generation was high for a triploid (average 46.9%, range: 26.8–66.4%) (Table 1), evidence that the predominant SDM contributed to the high pollen fertility of the F_1 plants. Pollen fertility was 96.2% (range: 93.6–97.6%) for the euhexaploid F_2 and 83.0% (range: 71.9–94.9%) for the aneuploid F_2 (Table 1). We found no PMCs with the donut- and/or dumbbell-shaped nuclei typical of some *T. turgidum-Ae. tauschii* hybrids that produce functional unreduced gametes through a process that includes the formation of restitution nuclei (Fukuda and Sakamoto 1992b; Xu and Joppa 1995, 2000).

In addition to symmetric dyads, triads and tetrads with small nuclei were present as final meiotic products (Fig. 4a–d). These abnormal triads and tetrads are probably products of meiotic pathways that involve two consecutive divisions, with a random assortment of univalents at the first meiotic division, the subsequent formation of two nuclei with different amounts of chromatin, and equational division at the second meiotic division. Those triads and tetrads were present at frequencies that varied from one anther to another, but in general they represented relatively minor portions of our sporocyte preparations, indicative that meiotic pathways that produced sporocytes with small nuclei are not common. Some sporocytes with small nuclei seemed to

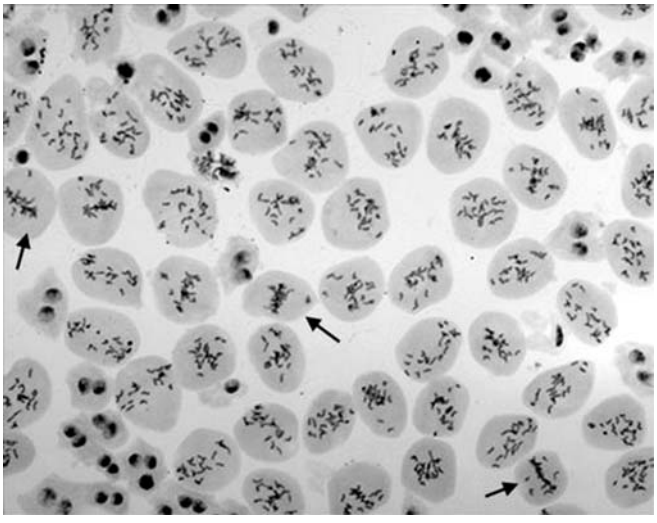

Fig. 1 Pollen mother cells of triploid F_1 hybrids of *Triticum turgidum* ssp. *durum* cv. Langdon (Ldn) with *Aegilops tauschii* YM9508 at meiotic metaphase. Single-division meiosis (SDM) proceeds synchronously in an anther. Chromosomes are completely asynaptic, as seen by the presence of 21 univalents. Note that univalents are scattered in most pollen mother cells (PMCs), some being aligned at the equator (*arrows*). This indicates their movement to the equator as cell division progresses

Table 2 Vigor of hybrids of Ldn with *Ae. tauschii* YM9508

Plant type	Number of plants	Plant height		Effective no. of tillers	
		Average[a] (cm)	Standard deviation	Average[a] (cm)	Standard deviation
F_1	13	120.0	9.5	**8.5**	1.9
F_2 (euhexaploid)	9	126.0	6.7	6.4	0.5
Ldn	2	**97.9**	4.1	4.5	0.7

[a]Averages shown in bold type differ significantly from the others at the 5% level (Tukey-Kramer's HSD test)

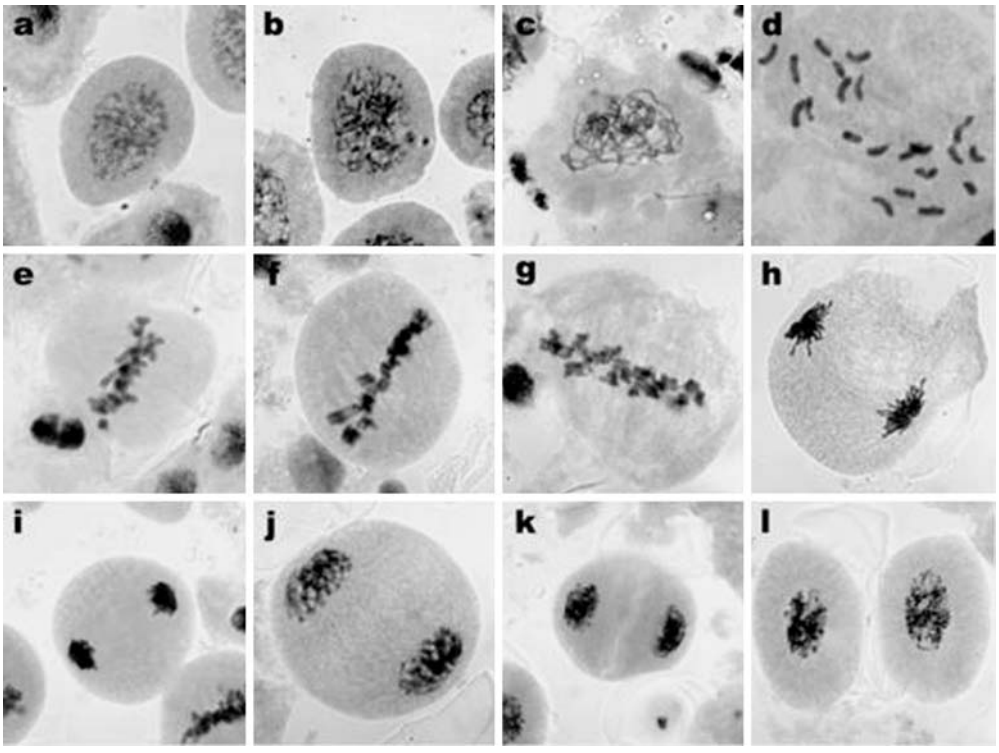

Fig. 2 Cytological observations of SDM stages in triploid F_1 hybrids of Ldn with *Ae. tauschii* YM9508. **a**, **b** PMCs, **c** prophase, **d** early metaphase, **e** metaphase, **f, g** late metaphase, **h** anaphase, **i** late anaphase, **j** telophase, **k** late telophase, **l** dyad. Note that sister chromatids start to separate during late metaphase (**f**, **g**). Neither chromosomes nor chromatid bridges are present in anaphase (**h**, **i**). Soon after telophase, chromatin is decondensed (**j**)

proceed to pollen mitosis and produced small abnormal pollen grains at maturity (data not shown).

Discussion

Durum wheat as a candidate for the unknown female progenitor of bread wheat

We here reported that: (1) Ldn, a cultivar of durum wheat, is crossable with an *Ae. tauschii* line (YM9508) by hand pollination; (2) vital triploid F_1 hybrids can be obtained without the use of embryo rescue techniques; (3) the triploid F_1 hybrids spontaneously set hexaploid seeds at a rate (51.5%) comparable to those reported for ssp. *carthlicum*-*Ae. tauschii* F_1 hybrids (15–57%); (4) the hexaploid F_2 plants are vital, fertile, and morphologically close to bread wheat plants. These findings suggest that at least some cultivars of durum wheat are capable of producing vital, fertile hybrids with *Ae. tauschii* under natural conditions, thereby lending support to durum wheat being a candidate for the unknown AB genome progenitor of bread wheat. Our findings have evolutionary importance in that, to the best of our knowledge, they provide the first empirical evidence for the presence of a cultivar of *T. turgidum* ssp. *durum* that produces highly fertile F_1 hybrids when crossed with an *Ae. tauschii* of the appropriate genotype. As a caveat we note that, because Ldn is a modern cultivar, the high fertility of Ldn-YM9508 hybrids may be a byproduct of modern breeding that may have created a novel genotype in Ldn. To clarify this point, further artificial-cross studies using the land races of durum wheat are required.

Other lines of evidence also support durum wheat being a candidate for the AB genome progenitor of bread wheat. Of the five subspecies of cultivated *T. turgidum* (*dicoccon*, *durum*, *polonicum*, *turanicum*, *turgidum*, excluding *carthlicum* and *paleocholchicum*), *durum* is one of the subspecies for which archaeological antiquity is reported (10,000 cal BP) (Araus et al. 2001). Because some of the oldest archaeological remains of free-threshing-type hexaploid wheat date from 9,700–8,600 cal BP (Hillman 1978; see also Salamini et al. 2002), the antiquity of durum wheat remains (10,000 cal BP) does not preclude the possibility that ssp. *durum* (or its free-threshing ancestors) came into existence before the emergence of bread wheat. In contrast, ssp. *polonicum*, and *turanicum*, *turgidum*, differ from ssp. *durum* in only a few characters and, therefore, are probably of relatively recent origin (Feldman 2001). Moreover, there is genetic proof that ssp. *durum* shares with bread wheat the *Q* gene on chromosome 5A which controls the free-threshing trait (Muramatsu 1986), whereas cultivars of ssp. *dicoccum* (syn. ssp. *dicoccon*, non-free-threshing), with few exceptions, have a recessive allele for this gene (Muramatsu 1985). This second point is important because there is cumulative genetic and archaeological evidence for the model that bread wheat evolved from a hybrid between a *Q*-carrying, free-threshing tetraploid wheat and *Ae. tauschii* (see Salamini et al. 2002 for review).

In conclusion, all of this evidence supports durum wheat being suitable as a candidate for the unknown AB genome progenitor of bread wheat, whereas the possibility for the other forms of tetraploid *Triticum* wheat having been involved in the evolution of bread wheat remains to be investigated. In terms of human-plant interactions in

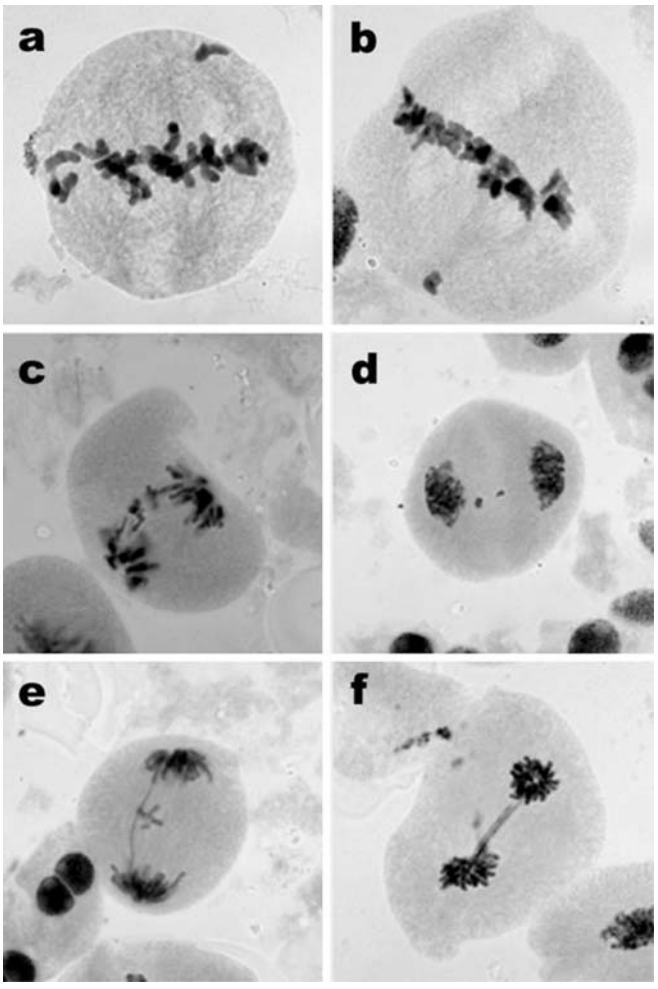

Fig. 3 PMCs with abnormal morphology during SDM. These cells have produced aneuhaploid sporocytes owing to unaligned chromosomes at metaphase (**a**, **b**) and lagging chromosomes (**c**–**e**) and bridges (**e**, **f**) at ana/telophase.

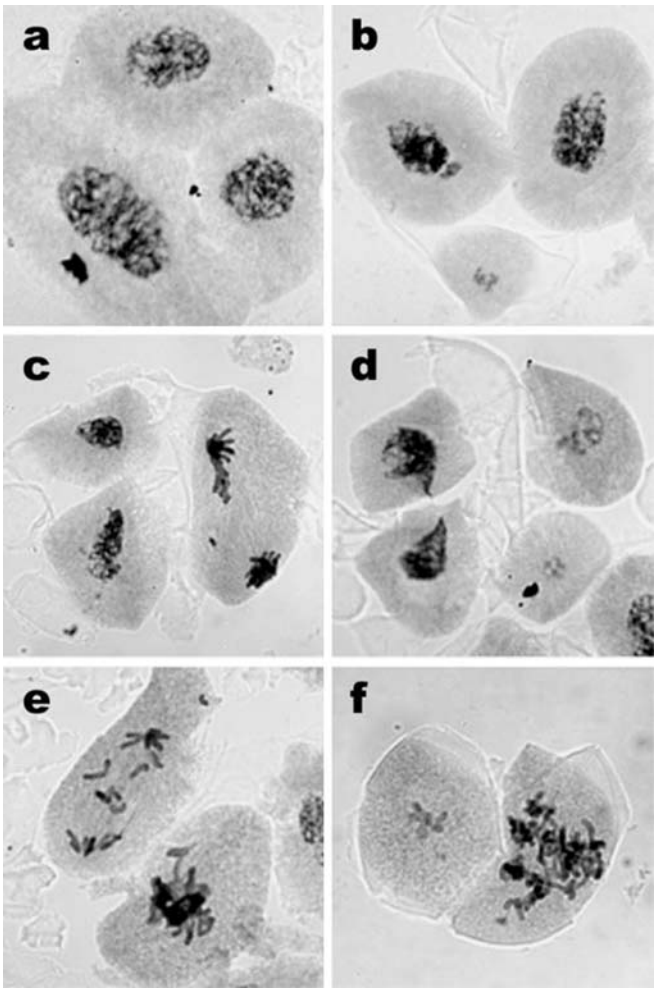

Fig. 4 Triads (**a**, **b**) and tetrads (**c**, **d**) seen together with symmetric dyads. These sporocytes have different amounts of chromatin. Asymmetric dyads proceed to the second meiotic division asynchronously (**e**, **f**)

crop evolution, the hybrid vigor of Ldn-*Ae. tauschii* hybrids is of particular interest (Table 2). In the early stages of crop evolution, plants with morphological peculiarities may have been collected and used for breeding by agriculturists. We postulate that in the case of bread wheat, traits such as the vigorous plant height and tillering shown by the Ldn-*Ae. tauschii* hybrids may have been those that first caught the attention of early agriculturists.

Meiotic mechanism for the production of unreduced gametes in *T. turgidum* wheat-*Ae. tauschii* F_1 hybrids

The production of functional gametes in the triploid F_1 hybrids between *T. turgidum* wheat and *Ae. tauschii* was a significant biological step that led to the emergence of bread wheat. To understand the mechanism that underlies this phenomenon, various investigators over the years have analyzed meiotic behavior in several *T. turgidum-Ae. tauschii* F_1 hybrids (Kihara and Lilienfeld 1949; Fukuda and Sakamoto 1992a, b; Xu and Dong 1992; Xu and Joppa 1995, 2000). These studies showed that meiotic restitution is the mechanism responsible for the production of functional unreduced gametes in *T. turgidum-Ae. tauschii* hybrids. Meiotic restitution is controlled genetically in *T. turgidum-Ae. tauschii* F_1 hybrids (Fukuda and Sakamoto 1992a; Xu and Joppa 1995, 2000). Actually, Ldn does have a gene for meiotic restitution which is probably shared with other durum wheat cultivars to which Ldn is related (Xu and Joppa 1995, 2000). Interestingly, meiotic restitution occurs in synthetic haploids of Ldn that set diploid seeds (Jauhar et al. 2000; Jauhar 2003).

Two types of restitutive meiotic pathways for the production of functional unreduced gametes have been described for *T. turgidum-Ae. tauschii* F_1 hybrids. In one, PMCs produce dyads as final products through a process that includes the failure of chromosomes to move to the poles at anaphase I, the formation of restitution nuclei at telophase I, and equational division at anaphase II (Kihara and Lilienfeld 1949; Fukuda and Sakamoto 1992b; Xu and

Joppa 1995, 2000). This pathway is called first-division restitution (FDR) (Xu and Joppa 1995, 2000). The name FDR implies that there are two consecutive divisions in this meiotic pathway—a first division with atypical chromosome behavior and a normal second division—whereas actual cell division occurs only once at anaphase II. In the other pathway, PMCs undergo a process that includes a single equational division at anaphase, with dyads as the final meiotic product. Restitution nuclei are not seen at telophase, indicative that, unlike in FDR, their formation, if at all, is rare. This type of meiosis also has been reported in a highly fertile triploid F_1 hybrid between an *Aegilops* species (the female parent) and durum wheat (the male parent) (Maan and Sasakuma 1977; Maan et al. 1980).

Similar to the latter meiotic pathway, we found a type of meiosis that involves a single division (SDM) during male sporogenesis of Ldn-YM9508 F_1 hybrids. In our case, SDM appears to be the major meiotic pathway for the PMCs in many of the anthers sampled from F_1 hybrids that set hexaploid seeds at a high rate (51.5%). Triads and tetrads with small nuclei were also present along with the symmetric dyads produced as final products by SDM (Fig. 4). This means that PMCs may use other types of meiotic pathways that include two consecutive divisions. The symmetric dyads appear to undergo normal pollen mitosis and to produce functional pollen grains. The correlation between the frequent occurrence of SDM and high pollen fertility (Table 1) is clear evidence that the former contributes to the high selfed seedset rate of Ldn-YM9508 F_1 hybrids by producing functional unreduced gametes. Meiotic restitution through SDM, therefore, is concluded to be responsible for the high fertility of Ldn-YM9508 F_1 hybrids. Strict asynapsis (Fig.1) may be a prerequisite for the expression of SDM in Ldn-YM9508 F_1 hybrids as may also be the case for the meiotic process observed in *Ae. heldrechii*-durum wheat F_1 hybrids (Maan et al. 1980). To date, it is unknown whether or not SDM and FDR are independent meiotic pathways, but they are distinct in forming restitution nuclei. The expression of restitution nucleus formation may be affected by certain environmental conditions (e.g., temperature) or certain genetic factors (e.g., parental genotypes), or both.

Xu and Joppa (1995) produced F_1 hybrids of Ldn with a line of *Ae. tauschii* (accession RL5286) by means of embryo rescue techniques and analyzed their meiotic behavior. FDR was shown to be responsible for the relatively high seedset rate of these hybrids (average: 18.6%; range: 0.9–32.4%). Unlike in the case of Ldn-YM9508 hybrids, SDM does not seem to be prominent in Ldn-RL5286 hybrids, whereas Xu and Joppa (2000) observed equational division at an increased rate at the first meiotic division in hybrids between a Langdon durum D-genome disomic substitution line and RL5286. The formation of restitution nuclei, however, is not prominent in Ldn-YM9508 hybrids, as we did not find PMCs with the donut- and/or dumbbell-shaped nuclei typical of PMCs undergoing a meiotic process that includes the formation of restitution nuclei (Fukuda and Sakamoto 1992b; Xu and Joppa 1995, 2000). This suggests a role for *Ae. tauschii* genotypes in the expression of restitution nucleus formation in Ldn-*Ae. tauschii* hybrids. Comparative analyses of the chromosomal behavior of Ldn hybrids with various *Ae. tauschii* genotypes should provide valuable insights into the cytology and genetics of the meiotic process that gave rise to bread wheat.

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