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ORIGINAL PAPER

Transfer of resistance against soil-borne wheat mosaic virus from *Triticum monococcum* to hexaploid wheat (*T. aestivum*)

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Abstract
Resistance to soil-borne viruses as Soil-borne Wheat Mosaic Virus (SBWMV) has gained evident importance in wheat research and breeding. Very few varieties of bread and durum wheat are resistant to these viruses. Search for new sources of SBWMV is conducted worldwide and loci causing resistance have been described on the B and D genomes of tetraploid and hexaploid wheat. In the present study, a gene locus was identified on the A genome of *Triticum monococcum* and was successfully transferred to hexaploid wheat. In hexaploid wheat, it is expressed in a stable dominant manner. As this is the first SBWMV resistance gene located on the A genome, this locus is proposed as *Sbm3*.

Keywords *Triticum monococcum* · Hexaploid wheat · Furovirus · Soil-borne Wheat Mosaic Virus (SBWMV) · Resistance · Screening · Gene transfer · Introgression

Introduction

Soil-borne viruses, such as wheat mosaic virus (SBWMV), became a serious threat for European wheat production. In infested fields, yield losses of up to 70% are recorded (Budge et. al. 2008, Ziegler et al. 2015). SBWMV is considered to be one of the most important diseases in winter wheat, especially in the central and eastern US, while in Germany it was found on few fields (Kastirr and Ziegler 2018). It is persistent and can practically destroy an entire crop of a susceptible cultivar when the weather conditions are particularly favourable for disease development (Myers et al. 1993). Koenig and Huth (2000; 2003) were the first to report on severe damages of wheat caused by SBWMV in Germany. Just, a few varieties show reasonable tolerance to these viruses (Kanyuka et al. 2004; Huth et al. 2007). Therefore, there is a big need for new sources of resistance to broaden the genetic base of resistance. Some variability among registered wheat varieties was reported by Ay et al. (2008). Since the diversity with respect to resistance in the group of hexaploid wheats is limited, resources from related genera can be an alternative.

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Introgression experiments with *T. monococcum*–as one of the progenitors of bread wheat–have been part of the repertoire of wheat breeding for decades. A large number of characteristics such as grain quality, protein composition of the flour, resistance to fungal leaf diseases, or salt tolerance were considered (Gale and Miller 1987).

A first report about SBWMV in wheat dated back to 1919 when McKinney (1925) described a mosaic-like leaf mottling that he called rosette disease in the USA. The causal virus was SBWMV, the type member of the genus Furovirus. SBWMV is naturally transmitted only by its vector, *Polymyxa graminis*, and a eukaryotic obligate biotrophic plasmodiphorid parasite of plant roots (Rao and Brakke 1969). Virus particles are encapsulated within *P. graminis* resting spores and protected from the environment. They may remain dormant but viable for decades, probably until a suitable host plant is encountered (Brakke and Langenberg 1988). There are currently no efficient chemical agents for the control of *P. graminis*. Therefore, breeding of resistant varieties to SBWMV seems to be the only way to avoid high yield losses (Ordon et al. 2009).

Soil-borne cereal mosaic virus (SBCMV) was considered to be a European strain of Soil-borne Wheat Mosaic Virus (SBWMV), but the proposed species name has later been approved by the International Committee on Taxonomy of Viruses. SBCMV was first detected by Clover et al. (2001) in the UK in Wiltshire in 1999 and subsequently has been

detected at several other locations in Europe (Kanyuka et al. 2004).

Until now, different modes of inheritance were postulated for the resistance to SBWMV/SBCMV in hexaploid wheat: a single dominant gene (Miyake 1938; Modawi et al. 1982), two genes (Shaalan et al. 1966; Merkle and Smith 1983; Barbosa et al. 2001), and three genes (Nakagawa et al. 1959). Meanwhile, a dominant gene was mapped on the long arm of chromosome 5D (5DL) of the winter varieties "Tremie" and "Claire", which is allelic to that of the resistant spring varieties "Cadenza" (Bass et al. 2006; Perovic et al. 2009). It was designated as *Sbm1*. A second gene, *Sbm2*, was localized on the short arm of chromosome 2B (2BS) in tetraploid durum wheat (Bayles et al. 2007; Maccaferri et al. 2011). Up to now, no resistance gene against SBWMV was mapped on the A genome.

During a perennial pre-screening over eight years 46 genotypes of wheat and wheat relatives were tested for SBWMV both in greenhouse and field experiments. One accession turned out to be persistently resistant to SBWMV. It was considered for the following introgression experiment.

Materials and methods

Plant material

One strain of diploid wild wheat, *Triticum monococcum,* (kindly provided by N. I. Vavilov Research Institute of Plant Industry, St. Petersburg, Russia) was used for the initial crossing with hexaploid wheat. However, it segregated for resistance to SBWMV. Therefore, the strain was purified by strong selection and isolation of resistant genotypes, resulting in the accession number "PC2205". The same procedure was carried out with the susceptible genotypes that were personally collected by R. Schlegel in 1996 at Kjustendil, Bulgaria and designated as No. PC2204. As female crossing parents the hexaploid wheat varieties "Chinese Spring" (susceptible) and/or "Asano" (susceptible) were chosen. The hexaploid wheat varieties "Avalon" (susceptible), "Cadenza" (resistant), and "Cezanne" (susceptible) served as additional controls.

Screening and field testing

The resistance test of wheat material was carried out as a pre-screening under greenhouse conditions. Pre-selected material resistant to SBCMV (Soil-borne Cereal Mosaic Virus), SBWMV (Soil-borne Wheat Mosaic Virus), or WSSMV (Wheat Spindle Streak Mosaic Virus) was then studied under field conditions on virus-infested locations and under different environments. However, for the introgression experiment, the resistance to SBWMV was only considered.

In greenhouse, the accessions were sown in multi-pot plates (2 replications and 10 plants per replication) with infectious soil and incubated at + 17 °C under greenhouse conditions. Field testing was performed as microplots with two replications on six test sites of Gödnitz, Thören, Eickleoh, Heddesheim, Westerrade, and Schleesen (Germany) within eight years. Each replication included 10 single plants. Eight and twelve weeks after sowing, the virus titres in the leaves were determined by means of DAS-ELISA as given below (Kastirr and Ziegler 2018).

Production of introgression lines

Triticum monococcum shows a high degree of progamous incompatibility in crosses with hexaploid wheat. Therefore, a bridging cross with the wheat variety "Chinese Spring" was conducted, which is known as a carrier of the dominant gene *Kr1* on chromosome arm 5BL determining a higher crossability than the common varieties but low agricultural performance. Therefore, the F1 progeny was in a next step backcrossed to the adapted wheat variety "Asano" (cf. Figure 1). "Asano" is a winter wheat breed of Breun Seed Co. from Germany released in 2008. It shows early maturity, very high yield, very high TGW and good agronomic adaptability (Anonymous 2020).

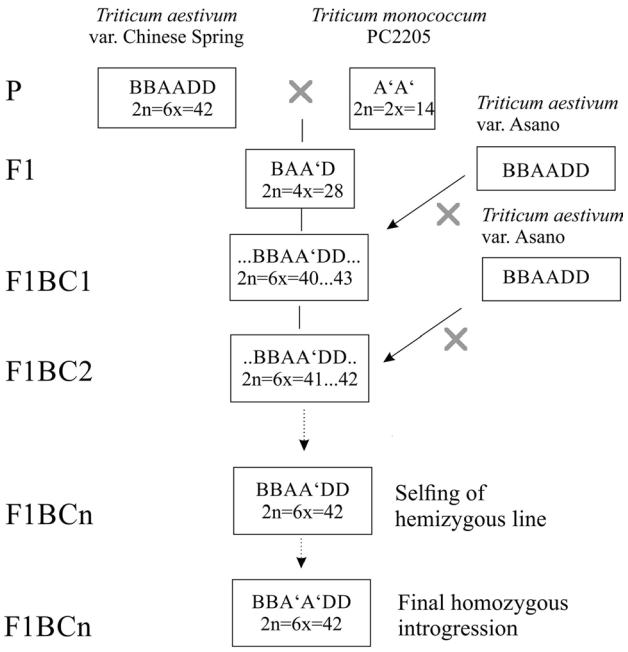

Fig. 1 Crossing scheme for production of wheat-*Triticum monococcum* introgression lines

Cytological studies

Chromosome counting was performed on root tips. They were removed from primary roots and treated in ice water (0 °C) for 24 h in order to increase contraction of chromosomes. Three hours before microscopic analysis root tips were transferred to 1% aceto carmine and then analysed by the squash method. For meiotic chromosome studies excised anthers were fixed with a mixture of 3:1 alcohol-acetic acid for 48 h. The fixed material was treated for 8–10 min with 1 N HCl in a water bath at + 60 °C. Afterward, the anthers were immediately transferred into Schiff's reagent at room temperature. The material was then squashed in aceto-orcein according to Schlegel and Gill (1984).

ELISA based testing of genotypes for resistance to SBWMV

Pre-germinated seeds were transplanted to pots ($V = 520$ ml) filled with the mixture of infested soil (Elxleben, Germany) and coarse sand (1:3), with final number of 5 plants per pot. Plants were grown in the cooled green house chamber under the following conditions: temperature between 16 and 18 °C and 16 h photoperiod, 60% humidity with first 4 weeks waterlogging and after that daily watering. The plants were weekly trimmed to about 10 cm from the soil level until 2 weeks before sampling to stimulate systemic virus movement.

After 10–11 weeks post-incubation, plants were screened for leaf symptoms and harvested for the detection of SBWMV by Double Antibody Sandwich Enzyme-Linked Immunosorbent Assay (DAS-ELISA) according Clark and Adams (1977). In case of wheat lines, the youngest leaves were harvested from each of the 4–5 individual plants. In case of plants from F1BC2 generation, two replicate samples were harvested from the single plants. The extraction was performed similarly as in Kanyuka et al. (2004). Fresh leaf material (50 mg) in the presence of 500 µl extraction buffer (phosphate-buffered saline buffer pH 7.4 containing 0.05% Tween 20, 2% polyvinylpyrrolidone MW 44,000, and 0.2% non-fat dry milk) was grinded with steel balls by tissue homogenizer (Precellys 24, Bertin GmbH, Germany). Leaf extracts were cleared in wide bore tips and 100 µL aliquots of each extract were applied to a microtiter plate previously coated with SBWMV IgG. After incubation overnight at 4 °C, plates were washed three times and the alkaline phosphatase-conjugated IgG were added. After incubation for 4 h at 37 °C and a further washing step, *p*-nitrophenyl phosphatase substrate was added and absorbance was measured at 405 nm (A_{405nm}) using a TECAN microplate reader (SUNRISE), after one hour. Polyclonal antiserum to SBCMV was produced according to Kastirr et al. (2006). Samples were considered to be positive when the A_{450} value was more than 0.1.

Results

Screening

Over eight years, 46 different wheat genotypes from distant gene pools were examined. Resistance to SBWMV on the phenotypic level was tested both under controlled conditions in the greenhouse and in the fields that are contaminated with the various viruses, as described above and in several reports (Kastirr et al. 2004, 2006; Kastirr and Ziegler 2018). Field testing showed great variability concerning infestation of plants. In some years the testers were classified to be resistant, e. g. "Asano" or "Chinese Spring", while they had to be declared as susceptible at other locations. Therefore, it was extremely difficult to select the populations with virus resistance for the subsequent introgression to common wheat.

From all entries that were tested, just one turned out to be resistant against SBWMV. It was a diploid wheat, *Triticum monococcum* ($2n = 2x = 14$) that was earlier described by Kanyuka et al. (2004). However, there was a genetic segregation within this wild population from Macedonia. Therefore, resistant genotypes were subsequently isolated and purified resulting in the accession number "PC2205". Because of the stably inherited resistance "PC2205" was determined for the initial crossing with the recipient varieties "Asano" and "Chinese Spring".

Hybridization

For the production of introgression lines initial crosses between *Triticum aestivum* var. "Chinese Spring" as well as "Asano" as female parent and *T. monococcum* (PC2205) as male parent were initiated in 2016. *T. monococcum* (PC2205) showed the typical grassy growth habit of einkorn wheat. As compared to a susceptible einkorn (PC2204), the "PC2205" strain exhibits an earlier growth and maturity, longer straw, a weak anthocyanin expression in the coleoptile, susceptibility to mildew but resistance to soil-borne viruses.

Since seed setting was extremely rare on the female parent quite a lot of spikes were emasculated by hand and subsequently pollinated. Altogether 334 spikes were prepared within three years crossing (2016 to 2018). That means about 10,000 florets were emasculated and pollinated. There was some setting of caryopses, slightly more with "Chinese Spring" (0.3%) as compared to "Asano" (0.2%). Since no embryo rescue could be applied almost all of those caryopses died during germination. Just one

Fig. 2 Somewhat shrivelled and greenish F1 caryopsis (K16-100–1) from the cross of hexaploid wheat var. "Chinese Spring" x *Triticum monococcum* "PC2205" (left), as compared to maternal seed of "Chinese Spring" (right)

viable seed was observed in 2017 with the "Chinese Spring" genotype (cf. Figure 2).

This single seed showed a slightly greenish seed colour, probably caused by anthocyanin pigments within the aleurone layer as a consequence of the dominant inheritance of *T. monococcum* gene(s) and xenia formation on the pale grained "Chinese Spring" female. This led to the assumption that the F1 caryopsis is a true hybrid and not derived from selfing.

The F1 seed slowly germinated. It was subsequently grown under optimal conditions in the greenhouse for a cytological check of true hybrid character. Its growth habit was strongly related to the female parent "Chinese Spring", but it was completely male sterile because of the irregular chromosome constitution (Fig. 3). The F1 hybrid should carry the haploid genome of hexaploid wheat $n = 21$ (BAD) and the haploid genome of einkorn wheat $n = 7$ (A') giving rise for 28 somatic chromosomes (BAA'D).

Out of five spikes, which could be produced, one was used for determination of chromosome number and for studying the meiotic chromosome pairing during metaphase I. The chromosome number of $2n = 4x = 28$ was confirmed (cf. Table 1 and Fig. 4). Moreover, 100 pollen mother cells (PMCs) were scored. They showed besides univalents quite a high frequency of rod and ring bivalents, totally 4.42 bivalents per PMC. Even trivalents were detected demonstrating the chromosomal homoeology between the A, B, and D genomes.

The high frequency of bivalent formation points to a close genomic relationship between the A genome of "Chinese Spring" and the A' genome of *T. monococcum* (PC2205). As a consequence, about six chiasmata per PMC were formed (Table 1), i.e. a high degree of recombination between the A and A' genomes can be expected in the progeny. This may facilitate the stable and rapid introgression of *T. monococcum* genes into the hexaploid wheat.

Fig. 3 F1 plant (K16-100–1) during anthesis from the cross of hexaploid wheat var. "Chinese Spring" x *Triticum monococcum* "PC2205"

Backcrossing

The variety "Chinese Spring" derived from a Chinese landrace shows low agronomic performance and susceptibility to several leaf diseases (Sears and Miller 1985). It was only included in the experiment because of its good cross-compatibility with related wild species of wheat. This became evident by the fact that only the cross combination with "Chinese Spring" resulted in a viable hybrid. The subsequent backcrosses were performed with the hexaploid wheat variety "Asano". Four male sterile F1 spikes were pollinated several times until seed setting was observed. It resulted in six viable F1BC1 caryopses that were germinated and planted on a SBWMV infested soil in the greenhouse.

Leaf symptoms could not be estimated in plants; however, a retarded growth of three plants (F1BC1-2, F1BC1-4, and F1BC1-5) could be detected pointing to a certain degree of virus susceptibility, while the remaining three plants

Table 1 Mean chromosome pairing at metaphase I of an F1 plant (2n = 28, BAA'D) from the cross of hexaploid wheat var. "Chinese Spring" x *Triticum monococcum* "PC2205" (range in brackets)

Hybrid K16-100–1	No. PMCs scored	No. associations/PMC					No. chiasmata/PMC
		Univalents	Bivalents			Trivalents	
			rods	Rings	Total		
Total	100	18.56 (7–28)	3.22 (1–6)	1.20 (0–4)	4.42 (0–7)	0.20 (0–1)	6.32 (0–16)

Fig. 4 Meiotic metaphase I spread of F1 plant (K16-100–1) from the cross of hexaploid wheat var. "Chinese Spring" x *Triticum monococcum* "PC2205" with 6 heteromorphic rod bivalents + 16 univalents = 28 chromosomes, after Feulgen staining

Fig. 5 Vigorous F1BC1 plant from cross of "Chinese Spring" wheat with *Triticum monococcum* (PC2205) and backcrossing to "Asano" wheat (centre) on SBCMV/SBWMV infested soil from Walternienburg (Germany) as compared to sensitive "Asano" (left and right)

(F1BC1-1, F1BC1-3, F1BC1-6) seemed to be resistant (cf. Figure 5). The latter were again backcrossed to "Asano" while the weak (susceptible) plants were eliminated.

From all six F1BC1 plants (susceptible and resistant) the somatic chromosome numbers were determined. Table 2 shows that just one plant carried the complete hexaploid chromosome set of $2n = 42$. The remaining plants were aneuploid within the range of $2n = 39$ to 44 chromosomes (Table 2). One plant showed even a telocentric chromosome ($2n = 41 + t$).

The second backcross was made with the F1BC1-1, F1BC1-3, and F1BC1-6 plants. They still showed a high degree of male sterility. Only, hand-pollinated florets yielded 31 F1BC2 seeds that were viable and germinated. As expected the percentage of aneuploid offspring decreased below 50% (Table 2 and Fig. 6). Most of the plants were already stable euploids with $2n = 42$ chromosome.

Screening of plant material for resistance to SBWMV

In order to investigate the susceptibility of F1BC2 plants to virus infestation 15 plants, i.e. five plants per each of F1BC2-1, F1BC2-3, and F1BC2-6 progeny, were grown on the virus-contaminated soil from Elxleben under controlled greenhouse conditions. The soil was collected in 2019 and the contamination with SBWMV was previously shown. In addition, two cultivars, "Avalon" and "Cezanne", known to be susceptible to virus under field condition, were used in the experiment. The infection rate of the virus-contaminated soil was about 80%. All plants of cultivar "Cadenza", which was used as negative control, were resistant. The same was true for the resistant parent "PC2205". All plants of the susceptible parent "Asano" (PC2241) of the backcross progeny were infected (Fig. 7). From the 15 germinated seeds of

Table 2 Somatic chromosome numbers in the progeny from the cross of hexaploid wheat var. "Chinese Spring" x *Triticum monococcum* "PC2205" and twice backcrossing to hexaploid wheat var. "Asano"

Material	Somatic chromosome numbers 2*n* =									Total plants
	28	39	40	40 + t	41	41 + t + t	42	43	44	
F1	1									1
F1BC1	–	1	–	1	2	–	1	–	1	6
F1BC2	–	–	3	4	6	1	16	1	–	31

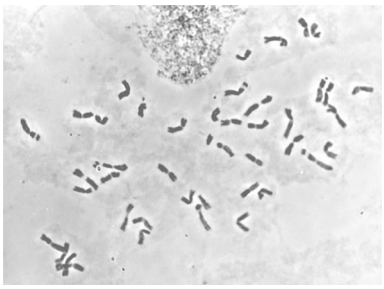

Fig. 6 Wheat-*Triticum monococcum* introgression plant "F1BC2-3" from the cross of hexaploid wheat var. ("Chinese Spring" x *Triticum monococcum* "PC2205") // "Asano", resistant to SBCMV and SBWMV, with $2n = 6x = 41 + 2t$ chromosomes, after carmine staining

F1BC2-1, F1BC2-3, and F1BC2-6 progeny 3, 5, and 3 vigorous plants finally remained for ELISA testing, respectively.

Each of the progeny showed a clear differentiation between susceptible and resistant offspring when the exceeded threshold of infestation 0.10 is considered. Thus, two plants of F1BC2-1, four plants of F1BC2-3, and one plant of F1BC2-6 were resistant to SBWMV. It is very likely that these resistant offspring represent recombinants with a dominant *T. monococcum* gene, because the offspring can only carry the allele in a hemizygous constitution due to the backcrossing.

Discussion

Crossing

Hexaploid bread wheat is the most extensively cultivated cereal crop worldwide, supplying the most important grain source for human nutrition and animal feed. SBWMV is considered to be one of the most important diseases in winter wheat, especially in central and eastern USA and in several European countries, particularly in France, Italy, Germany, Poland, and Denmark (Kastirr and Ziegler 2018). The persistent, soil-borne nature of SBCMV and SBWMV makes the use of resistant cultivars currently the only practical, environmentally friendly and sustainable means of control. Wheat cultivars with resistance or partial resistance to these virus diseases are available, e.g. "Charger", "Claire" and "Hereward", or "Cadenza" (cf. Figure 7; Kanyuka et al. 2004; Perovic et al. 2009). At least two loci determining resistance were described within the B and D genomes of hexaploid wheat. Therefore, a further search for new genetic sources of resistance became an important task of breeding research.

There is renewed interest for first cultivated wheat einkorn (*Triticum monococcum*) due to the nutritional qualities of its grain, its adaptation to low-input agriculture and high level of resistance to pests and diseases. Several resistance genes

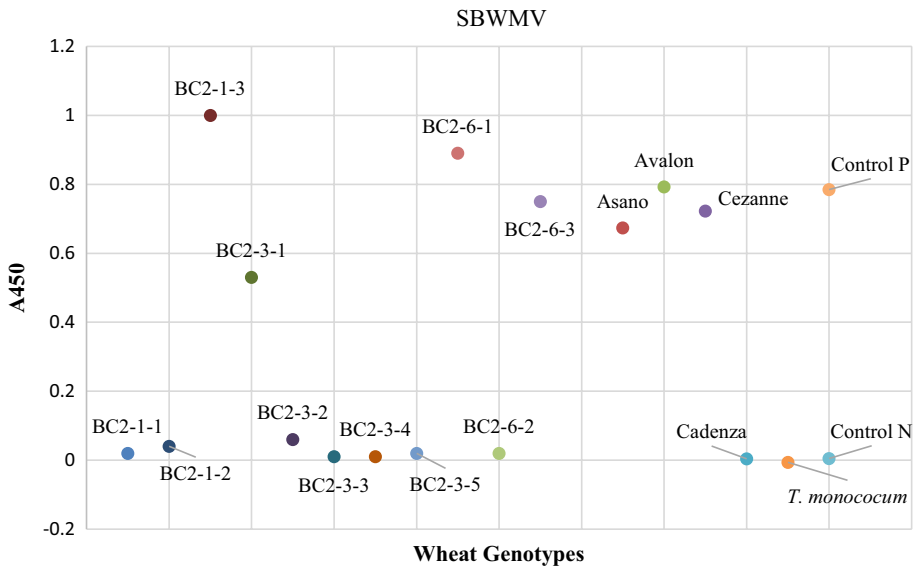

Fig. 7 Absorbance values in SBWMV ELISA tests for F1BC2 plants from a cross of [*Triticum aestivum* var. "Chinese Spring" x *T. monococcum* (PC2205)] // "Asano". Values for parental lines (susceptible "Asano" and resistant *T. monococum* (PC2205), two susceptible lines ("Avalon" and "Cezanne") and one resistant line ("Cadenza") are also presented. Plants were grown in naturally infested soil in the greenhouse. Absorbance values are means from two replicate plant samples (4-5 plants per bulk) in case of lines. In case of plants from back cross, absorbance values were means from two replicates, from the same plant. Values for F1BC2-1–3, F1BC2-3–1, F1BC2-6–1, "Asano", "Avalon", and "Cezanne" are significantly different ($P < 0{\cdot}001$) from the negative control (SED = 0.0749,-48 df). Negative control–"Alcedo" grown in virus-free soil. Positive control–"Alcedo" mechanically inoculated with SBWMV

of einkorn [*Lr10*, (leaf rust resistance); *Sr21*, *Sr22*, and *Sr35* (stem rust resistance); and *Pm25* and *Pm26* (powdery mildew resistance)] have been mapped and transferred to bread wheat (Zaharieva and Monneveux 2014).

Moreover, the A genome of *T. monocccum* is related to the A genome of modern wheats and the crossability with hexaploid wheat is possible. Since Kanyuka et al. (2004) already indicated resistance to SBCMV in *T. monococcum*, we have focussed on the *Triticum monococcum* landrace, segregating for resistance to soil-borne viruses, and developed resistant homozygous line (PC2205), which was used for the initial crossing.

Unfortunately, the crosses with two bread wheats turned out to be very difficult. One seed of about 10,000 florets pollinated is a result of extremely low crossability. Even variations of crossing and growth synchronization did not improve the result. Other authors were much more successful (The and Baker 1975; Miller and Reader 1980; Chapman et al. 1976; Gonzalez et al. 1993). Obviously, the PC2005 line has genes that complicate the crossing with hexaploid wheat, but also with other diploid *T. monococcum* genotypes (Mettin et al. 1984, Schlegel, unpub.) by low progamous and also postgamous compatibility. Nevertheless, the approach succeeded.

Chromosome pairing

As can be seen from Table 1 the F1 hybrid between "Chinese Spring" and "PC2205" exhibited quite a high degree of chromosome pairing. In some PMCs up to seven bivalents were formed. This resulted in a mean of about 6 chiasmata per PMC. It can be assumed that the pairing occurs mainly between the homoeologous chromosomes of the A genome of "Chinese Spring" and the A' genome of *T. monococcum* because these two genomes are closely related. Genetic recombination is most likely between these two genomes being, a good prerequisite for transferring the resistance gene(s) from *T. monococcum* to the hexaploid wheat by recombination. The detection of resistant genotypes in the F1BC2 generation confirms this assumption (cf. Figure 7). Further backcrossing will lead to karyotype stabilization and replacement of the "Chinese Spring" by "Asano" genome. This is continued. In order to produce a homozygous introgression line a final selfing of a resistant plant is necessary resulting in 25% homozygous susceptible, 50% heterozygous resistant, and 25% homozygous resistant genotypes, respectively (cf. Figure 1).

The extent of chromosome pairing of the F1 hybrid (K16-100–1) largely agrees with the results of earlier experiments (The and Baker 1975; Chapman et al. 1976; Miller and Reader 1980; Gonzalez et al. 1993). The paring behaviour of the *T. monococcum* genotype used thus corresponds to that of other *T. monocccum* genotypes.

SBWMV resistance

The results of resistance test to SMWMV of the parents of the introgression lines ("Asano" and "PC2205") were highly informative. The inoculation efficiency for the susceptible variety "Asano" was 100%, and all plants of the donor line "PC2205″ were resistant. In case of susceptible varieties "Avalon" and "Cezanne" 80% of plants were infected, indicating good control of environmental/experimental conditions providing high efficiency of the test for resistance to SBWMV.

Based on these data, the 11 F1BC2 plants were examined (Fig. 7). A clear distinction between infected and non-infected offspring can be seen within the three single plant progeny. A segregation of seven resistant to four infected offspring was observed. Both, the infected and non-infected plants show a largely homogeneous reaction.

The expression of the resistance of these plants can also be demonstrated not only in the alien genetic background of hexaploid wheat but also in the hemizygous chromosome constitution. The hemizygosity results from constant backcrossing the resistant line with the susceptible male parent "Asano". Therefore, a dominant inheritance of a locus from *T. monococcum* can be assumed which causes the resistance resulting from a single cross event. According to Kanyuka et al. (2004), Perovic et al. (2009), and Maccaferri et al. (2011) it is proposed to describe this locus as *Sbm3* within the A genome. For this genome, no resistance loci to SBWMV were reported so far.

Detailed investigations on the inheritance of this locus, its location within the A genome as well as the introgression site within hexaploid wheat, and the identification of molecular markers that are linked to this locus are already in progress.

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