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ORIGINAL PAPER

Microsatellite mapping of genes that determine supernumerary spikelets in wheat (*T. aestivum*) and rye (*S. cereale*)

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Abstract The wheat and rye spike normally bears one spikelet per rachis node, and the appearance of supernumerary spikelets is rare. The loci responsible for the 'multirow spike' or MRS trait in wheat, and the 'monstrosum spike' trait in rye were mapped by genotyping F_2 populations with microsatellite markers. Both MRS and the 'monstrosum' trait are under the control of a recessive allele at a single locus. The *Mrs1* locus is located on chromosome 2DS, co-segregating with the microsatellite locus *Xwmc453*. The placement of flanking microsatellite loci into chromosome deletion bin 2DS-5 (FL 0.47–1.0) delimited the physical location of *Mrs1* to the distal half of chromosome arm 2DS, within the gene rich region 2S0.8. The *Mo1* locus maps about 10 cM from the centromere on chromosome arm 2RS. The similar effect on phenotype of *mo1* and *mrs1*, together with their presence in regions of conserved synteny, suggest that they may well be members of an orthologous set of *Triticeae* genes governing spike branching. The practical importance of the MRS spike is that it produces more spikelets per spike, and thereby enhances the sink capacity of wheat, which is believed to limit the yield potential of the crop.

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Introduction

The inflorescence of wheat and its close relatives, barley and rye, is referred to as a spike, and variation in spike morphology is one of the most widely used criteria used in grass taxonomy. The *Triticum compactum* (club wheat) group is distinguished from other hexaploid wheats by its compact spike, while spelt wheats (*T. aestivum* ssp. *spelta*) produce a lax spike. Although spike length and density can vary intraspecifically, the number of spikelets at each rachis node is usually constant. Wheat and rye spikes normally bear one spikelet per rachis node, and the formation of supernumerary spikelets (SS) is rare. The term SS includes sessile additional spikelets at a rachis node, additional spikelets on an extended rachilla, and the ramified spike (RS) seen in some tetraploid and hexaploid wheats. A synonym of RS is "branched spike", while a strongly branched spike in rye is referred to as a "monstrosum ear".

The spikelet is the basal unit of the grass inflorescence, and first develops as a lateral or a terminal meristem on the wheat, rye, and barley spike, later differentiating into the floral meristem. In maize and rice, the spikelet primordia appear on inflorescence branches, and the analysis of mutants, such as *barren stalk1* (*ba1*) in maize (Gallavotti et al. 2004) and *LAX PANICLE* (*LAX*) in rice (Komatsu et al. 2003a), in which the pattern of spikelet formation is altered, has shown that they affect meristem initiation.

The transition from spikelet to floral meristem identity has also been investigated by the characterisation of mutants, such as *branched silkless1* (*bd1*) in maize (Chuck et al. 2002) and *frizzy panicle* (*fzp*) in rice (Komatsu et al. 2003b). The determinacy of the spikelet meristem is governed in maize by the action of the *indeterminate spikelet1* gene *ids1* (Chuck et al. 1998). Functional analysis of some of these genes has revealed that many are regulatory elements; in particular helix-loop-helix transcription factors, ERF transcription factors, and AP2-like MADS box transcription factors (Gallavotti et al. 2004; Komatsu et al. 2003a, b; Chuck et al. 1998).

Both in wheat and in rye, SS is a recessive trait (Pennell and Halloran 1983; Klindworth et al. 1990a; Peng et al. 1998; Martinek and Bednar 2001; De Vries and Sybenga 1984; Benito et al. 1991). The expression of the trait is modulated by a number of environmental factors (Sharman 1944; Pennell and Halloran 1983). The number of genes underlying SS in hexaploid wheat has been suggested to be two (Pennell and Halloran 1983) or three (Koric 1973, 1980). The latter identified the three genes *Rm*, *Ts*, and *Nr*, where *Nr* acts as a dominant inhibitor of SS expression. A similar gene complex is thought to be present in tetraploid wheat. Klindworth et al. (1990a) suggested that in tetraploid wheat, SS was quantitatively inherited, conditioned by a single major gene acting in concert with an unknown number of minor genes. The RS trait in hexaploid wheat is induced by the absence of the complete chromosome or by a deletion of a chromosome (Swaminathan et al. 1966; Košner and Foltýn 1989). Hexaploid wheat plants nullisomic for chromosomes 2A or 2D produce twin spikelets (Sears 1954) and the chromosome arm locations of the genes responsible for suppressing this trait are 2AL and 2DS. The involvement of the homoeologous group 2 chromosomes in the control of SS has been noted in both tetraploid and hexaploid wheat (Klindworth et al. 1997, 1990a, b; Peng et al. 1998; Laykova et al. 2005), while Peng et al. (1998) has also implicated gene(s) on chromosome 4A. A 'triple-spikelet wheat' has been reported recently in a Tibetan landrace of bread wheat; this phenotype is genetically determined by the action of two recessive, as yet unmapped genes (Yang et al. 2005). In rye, the monstrosum ear is governed by a recessive allele at the major gene locus *Mo1*, localised on chromosome 2R (De Vries and Sybenga 1984; Benito et al. 1991).

Since spike morphology can affect grain yield, it attracts the attention of breeders. Martinek and Bednar (2001) have developed winter wheat germplasm characterised by its genetically stable multirow spike (MRS) appearance (Fig. 1a). The feature of this material is the large number of (up to 10) spikelets emerging from each rachis node. The lower third of the spike is most affected, although some of the SS in this part of the spike do not develop fully probably due to limited space. In the central and upper thirds of the spike, there are generally only three spikelets per node, similar to the spike architecture of six-row barley. Most of these SS carry three fertile florets. The apex of the MRS spike resembles a conventional spike. Overall, the number of functional spikelets per unit cropping area is approximately twice that of a conventional wheat crop. The MRS trait was transferred from the hexaploid wheat gene resource 'Ra1', a mutant that was produced through chemical

Fig. 1 Spikes with supernumerary spikelets in **a** bread wheat, determined by *mrs1* and **b** in rye, determined by *mo1*

mutagenesis and provided by the N. I. Vavilov Research Institute of Plant Industry (St. Petersburg, Russia). The trait is controlled by a single recessive gene (Martinek and Bednar 2001). The aim of the present study was to genetically and physically map this gene, along with the gene underlying the 'monstrosum ear' in rye.

Materials and methods

Plant material and mapping populations

Wheat

Mapping the MRS trait was achieved using two F_2 populations bred from the crosses Rŭc163-1-02 × So149-1-02 (population I) and Rŭc167-1-02 × So149-1-02 (population II). The two Rŭc accessions are related MRS types, and So149-1-02 has the conventional spike type. The pedigrees of these lines are: Rŭc163-1-02: OY 2912-1/KM 4823-92 (OY 2912-1 was an MRS selection from Ra1/ZG K 242-81; KM 4823-92 was a conventional spike type breeding line); Rŭc167-1-02: Alana/3/Ra1/ZG K 242-82//Ra1; and So 149-02: ZG K 171-1-82/Sparta. Both cv. Sparta and cv. Alana were commercial winter wheats grown in the Czech Republic, while ZG K 242-82 originates from Croatia. Population I consisted of 106 plants, and population II of 100. The nullisomic–tetrasomic stocks N2AT2B, N2BT2D, and N2DT2B, ditelosomic stocks Dt2DS and Dt2DL, and the four chromosome 2DS deletion lines 2DS-1, -3, -4, and -5 were used for the chromosome and deletion bin mapping of microsatellite (SSR) markers linked to the MRS gene. All these cytogenetic stocks were developed in the background of cv. Chinese Spring (Sears 1954; Sears and Sears 1978; Endo and Gill 1996). The fraction lengths (FL) of the deletion lines are, respectively, 0.33, 0.36, 0.41, and 0.47 (Endo and Gill 1996). All plants were greenhouse grown and F_2 plants were scored for spike type after heading. Segregants which produced some MRS and some conventional type spikes were scored as MRS types.

Rye

The rye inbred line S11 (conventional spike morphology, ligules present) was crossed with self-incompatible line D40 (monstrosum ear, ligules absent) from the Peterhof rye stock collection (St. Petersburg, Russia) (Fig. 1b). A single F_1 plant was self-fertilised to generate an F_2 population of 75 plants. The F_2 plants were grown in a greenhouse, and the spike type was assessed after heading. The presence/absence of ligules, which is under control of the *el* gene (De Vries and Sybenga 1984; Benito et al. 1991), was evaluated at the seedling stage.

DNA isolation, marker analysis, and map construction

Total genomic DNA was isolated from leaf material of individual F_2 plants and parental lines according to Plaschke et al. (1995). A set of SSR assays defining loci on wheat homoeologous group 2 chromosomes and chromosome 4A was selected for mapping in wheat; these included both genomic (gSSRs) and EST-derived (eSSRs) SSRs carrying the prefixes GWM (Röder et al. 1998; Ganal and Röder 2007), GDM (Pestsova et al. 2000), WMC and BARC (Somers et al. 2004), CFE (Zhang et al. 2005), and KSUM (Yu et al. 2004). The position of the centromere was determined using cv. Chinese Spring aneuploid stocks. The chromosome 2R map was constructed using GWM (Khlestkina et al. 2004), RMS and SCM (Korzun et al. 2001) gSSRs, along with a number of eSSRs recognising loci on wheat homologous group 2 chromosomes which have been tested for functionality in rye (Zhang et al. 2005; Zhang 2006). Unpublished primer sequences are available upon request. PCR analysis and fragment detection were performed as described by Röder et al. (1998). Genetic maps were constructed using MAP-MAKER/EXP v3.0b software (Lander et al. 1987) with the Kosambi (1944) mapping function and a LOD threshold of 3.00. A consensus map was constructed with the help of the BioMercator version 2.1 software (Arcade et al. 2004). The computation was based on loci position data from four 2DS genetic maps, the community ITMI map (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical), the Ganal and Röder (2007) map, and two 2DS genetic maps constructed in the course of the present work, 2D (I) and 2D (II). Automated compilation of these maps was performed and a consensus map was built from the individual maps by projection of the RFLP, SSR, and gene (*Mrs1*) loci as described (Arcade et al. 2004). The projection process was started with ITMI maps, where the community ITMI map was a map to project on.

Results

Mapping of the locus determining MRS in wheat

Under greenhouse conditions, all of the Rŭc163-1-02 and Rŭc167-1-02 spikes had the MRS trait. Several Rŭc167-1-02 spikes also showed genuine spike rachis branching. Spikes of both So149-1-02 and the two F_1 hybrids were of the conventional type. The F_2 progeny showing either MRS or conventional type spike were represented in both population I and II (Fig. 1). The segregation ratio in both populations was consistent with three conventional to one MRS (Table 1), confirming the monogenic inheritance reported by Martinek and Bednar (2001). Initially 21, 26, 28, and 25 SSR markers mapping to, respectively, chromosomes 2A,

Table 1 Segregation for spike type in F_2 populations of wheat and rye

	Total	Observed segregation		Expected segregation		χ^2	*P*
		Normal spike	SS	Normal spike	SS		
Ruc167-1-02 × So149 (wheat)	106	80	26	79.5	26.5	0.013	0.90–0.95
Ruc163-1-02 × So149 (wheat)	100	78	22	75	25	0.48	0.25–0.50
S11 × D40 (rye)	75	54	21	56.25	18.75	0.36	0.50–0.75

SS supernumerary spikelets

2B, 2D, and 4A were tested for informativeness in the two populations, resulting in the selection of 12, 19, 19, and 20 markers for mapping population I, and 13, 20, 19, and 21 for population II. Linkage between the MRS locus and 12 (population I) and 11 (population II) chromosome 2D SSR markers was detected. All these microsatellite loci (except for the dominant SSR *Xgdm19*) segregated consistently in the ratio 1:2:1, as expected, while *Xgdm19* segregated in 3:1. A further set of 18 chromosome 2D SSR markers (Guyomarc'h et al. 2002; Somers et al. 2004; Yu et al. 2004; Zhang et al. 2005) was then tested, and five of these proved informative in the populations. Three out of the five were linked to the MRS locus, and all three were co-dominant with a segregation ratio consistent with 1:2:1. The resulting two genetic maps (Fig. 2a) show that marker order was consistent in the two populations, and both this order and the inter-marker distances agree with the established chromosome 2D SSR map (Ganal and Röder 2007). The primer pair GWM448 amplified one locus on chromosome 2A and a second one on 2D. Although the map location of the former is well known (Röder et al. 1998), this represents the first report of a location for *Xgwm448-2D*. Because the MRS trait is monogenically inherited as a recessive allele, we have denoted the mutant allele *mrs1*

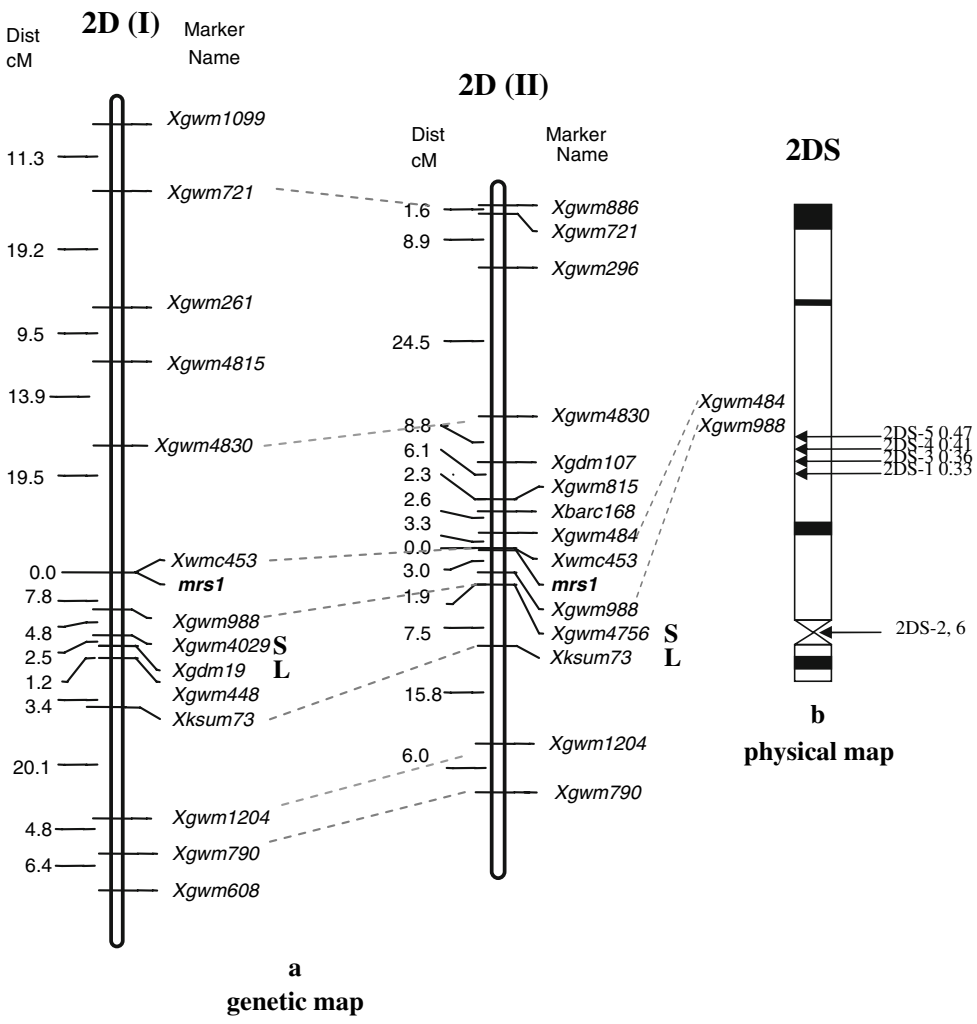

Fig. 2 **a** Genetic linkage maps of chromosomes 2D, in reference to **b** the physical deletion map of chromosome arm 2DS. Kosambi map distances (cM) are shown on the left hand side. S = short arm, L = long arm. *Arrows* indicate deletion breakpoints. *Dark bands* on the chromosome indicate the location of C-bands (Gill et al. 1991). *Dotted horizontal lines* connect common loci

and the wild-type allele *Mrs1*. The *Mrs1* locus, therefore, is present on the short arm of chromosome 2D, closely linked to *Xgwm988* (in both populations) and to *Xgwm484* (in population II). It co-segregated with *Xwmc453* in both mapping population (Fig. 2a).

The deletion bin locations of the flanking markers *Xgwm484* and *Xgwm988* (as determined by the SSR genotype of the 2DS-1, 2DS-3, 2DS-4, and 2DS-5 deletion lines) revealed that *Mrs1* maps in the chromosome deletion bin 2DS-5 (FL 0.47–1.0) that spans the distal 53% of chromosome arm 2DS (Fig. 2b). A consensus map of the 2DS region containing *Mrs1* was constructed by combining the two *Mrs1* maps with the community wheat (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical) and the Ganal and Röder (2007) genetic maps. The consensus map contains SSRs, RFLPs (source of RFLPs—ITMI maps), and the *Mrs1* locus. Since the RFLP loci flanking *Mrs1* (namely *Xcdo1379*, *Xbcd262*, *Xfbb279*, and *Xcdo405*) have been allocated to gene rich region 2S0.8 by Erayman et al. (2004) (Fig. 3a), we conclude that *Mrs1* also lies within this consensus gene rich region, which spans a physical segment of 7 Mbp with a recombination frequency of 215 Kb/cM (Erayman et al. 2004).

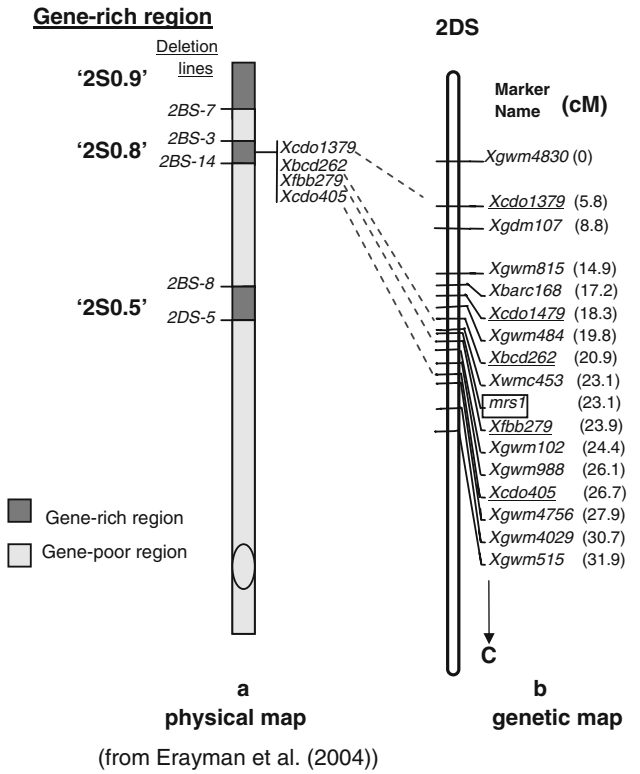

Fig. 3 **a** Physical map of the consensus group 2S chromosome arm, showing the location of gene rich regions (from Erayman et al. 2004). **b** A partial consensus genetic map of chromosome 2D involving *mrs1* (*boxed*). Kosambi map distances (cM) are shown on the right hand side. RFLP loci are *underlined*. *Horizontal dotted lines* connect common loci

Mapping *Mo1* in rye

The F_2 population segregated into 54 with the conventional spike type and 21 with the monstrosum spike type, fitting the expected monogenic pattern for a fully dominant gene (Table 1). Among the 16 chromosome 2R gSSRs and 14 eSSRs surveyed for informativeness between the mapping parents, 9 (seven gSSRs and two eSSRs) were useful for map construction. Eight of these generated a co-dominant pattern and the remaining one a dominant pattern. The significant deviation from the expected 1:2:1 segregation observed for *Xgwm877*, *Xrms5a*, and *Xgwm526* and for the *el* locus that controls the absence of ligule trait (De Vries and Sybenga 1984; Benito et al. 1991) is thought to result from linkage to the *Z* locus, which determines self-incompatibility in line S11. The resulting genetic map (Fig. 4) showed that *Mo1* is flanked proximally by *Xrms5b* (15.7 cM) and distally by *Xcfe209* (10.7 cM). *el* co-segregated with *Xrms5a*. The genetic distance between the *el* and *Mo1* was about 40 cM. Since *Mo1* maps distal to *Xscm43*, which lies near the centromere of the short arm of chromosome 2R (Korzun et al. 2001; Malyshev et al. 2007), the gene can be placed on the short arm of chromosome 2R.

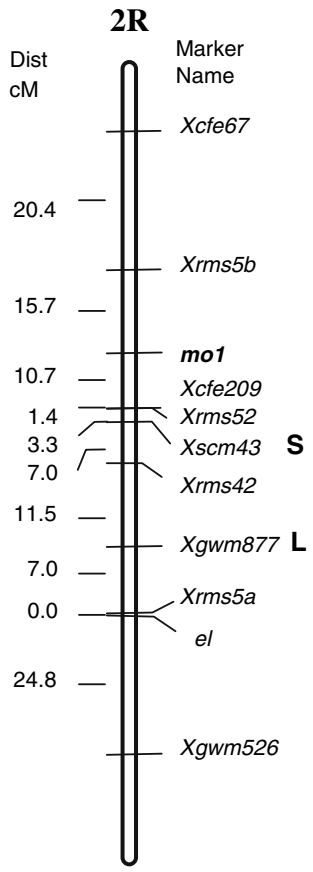

Fig. 4 An SSR-based linkage map of chromosome 2R. Kosambi map distances (cM) are shown on the left hand side. S = short arm, L = long arm

The genetic distance between *Mo1* and the centromere was approximately 10 cM.

Discussion

According to our current study, the segregation behaviour of the MRS trait shows that it is controlled by a single major gene. Our conclusion is in agreement with that of Laykova et al. (2005) for two mutant lines of common wheat in which the SS trait is effected by a recessive gene localised on chromosome 2D by monosomic analysis. The conclusion of Pennell and Holloran (1983) and Koric (1973, 1980), who have suggested that spike branching in hexaploid wheat is controlled by either two or three genes, was not confirmed in the current study. The disagreement may possibly result from the different genotypes used in these studies. The number of identified loci may depend on the crosses analysed, reflecting genetic differences between parents. If these analyses are correct, then the mutant alleles studied by these researchers must have involved loci in addition to (or even not including) *Mrs1*. One of these may have been related to the *bh* gene, which produces SS in tetraploid wheat, and was mapped close to the centromere on the short arm of chromosome 2A by Klindworth et al. (1997). This location is suggestive that *bh* and *Mrs1* are in fact orthologous loci.

Ullmannová et al. (2006) have compared apex formation between a conventional spike line and the MRS line KM 823-4-01 (closely related to Rŭc163-1-02 and Rŭc167-1-02). The earliest observable difference occurred at the beginning of the V stage of development (Kuperman 1968). At this stage, spikelets begin to differentiate, and MRS types can be distinguished from the wild type by the presence of horizontally positioned SS. Thus, the *mrs1* mutant allele causes changes in the spike development at the V stage of development.

Branched spikes also occur in barley (Castiglioni et al. 1998; Rossini et al. 2006) and rye (De Vries and Sybenga 1984; Benito et al. 1991). The *mo1* mutation in rye is present on chromosome 2R (De Vries and Sybenga 1984; Benito et al. 1991), a location which the current experiments was able to both confirm and extend, defining its location to 2RS. Although most of the wheat-derived eSSRs mapped on chromosome 2R were non-informative in the two wheat mapping populations, *Xcfe67* is known to map on chromosome arm 2DS distally to the *Xgwm484* and *Xgwm261* loci (Zhang 2006). Hence, *Mo1* lies in a region of 2RS which is colinear with 2DS (Devos et al. 1993). The similar effect on phenotype of *mo1* and *mrs1*, together with their presence in a region of conserved synteny suggest that they may well be members of an orthologous set of *Triticeae* genes governing spike branching. Moreover, mutant genes for spike branching have also been mapped on the short arm of barley chromosome 2H (Scholz and Lehmann 1958; Castiglioni et al. 1998; Rossini et al. 2006). The *brc1* (*branched 1*) barley mutants have ramified spikes with genuine spike rachis branching. The morphological similarities of the *brc1* mutants, along with the *brc1* mapping position on the short arm of barley chromosome 2H colinear with the wheat group 2 chromosomes (Devos et al. 1993), may suggest that *Brc1* also belong to a series of orthologous genes including *Mrs1* and *Mo1*. By comparative mapping of the RFLPs linked to the *Brc1* locus, Rossini et al. (2006) defined a rice region of shared synteny on the rice chromosome 7 and showed that the barley region hosting the *Brc1* locus is colinear with the rice region containing the *Fzp* (*FRIZZY PANICLE*) locus. The *Fzp* gene in rice and its maize orthologue *Bd1* (*BRANCHED SILKLESS1*) encode the ERF transcription factors that are required for the transition from spikelet to floral meristem identity (Chuck et al. 2002; Komatsu et al. 2003a, b). The *fzp* and *bd1* mutations altered the identity of the spikelet meristem, causing inflorescence branching. All the *mrs1*, *mo1*, *brc1*, and *bd1/fzp* mutants show certain phenotypic similarities and the genes that affect these traits may well be orthologues. Further saturation of the 2DS and 2RS maps with EST-derived markers that are transferable across the wheat, rye, and barley genomes and suitable for in silico mapping in the rice genome will make possible an accurate map-based comparative analysis.

Physical mapping of *Mrs1* defined its location in chromosome deletion bin 2DS-5, which spans the distal half of the chromosome arm. Numerous ESTs have been physically mapped into this deletion bin (http://wheat.pw.usda.gov/cgi-bin/westsql/bin_candidates.cgi?bin=2DS5-0.47-1.00) and can be used together with comparative genomic tools, such as colinearity between rice and wheat (Sorrells et al. 2003) to enrich the marker content around *mrs1* and fine map this locus or to isolate a candidate gene of *mrs1* from the syntenic BACs of the rice genome sequence. Erayman et al. (2004) have identified 18 major and 30 minor gene rich regions in wheat, and the *Mrs1* locus lies in one of these (2S0.8) which encompasses a physical length of 7 Mbp with a recombination frequency of 215 kb/cM. Thus, the gene clearly is located in a high recombination region of the wheat genome.

Spike architecture is influential in the processes of pollination and seed formation, and thus plays a role in the determination of grain yield. Thus, the MRS trait is potentially important, since it allows the formation of more spikelets in spike, thereby increasing the sink capacity of the plant. This is of particular significance for enhancing the yield potential of the crop, since wheat yield is generally thought to be sink limited (Wang et al. 1998), making genetic resources which increase the number of reproduction organs particularly desirable (Miralles and Slafer 2007;

Reynolds et al. 2005). Preliminary comparisons of yield between MRS and conventional spike cultivars have shown that the former respond particularly well to the application of high rates of mineral fertilizer.

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