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Complex microcolinearity among wheat, rice, and barley revealed by fine mapping of the genomic region harboring a major QTL for resistance to Fusarium head blight in wheat

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Abstract A major quantitative trait locus (QTL), *Qfhs.ndsu-3BS*, for resistance to Fusarium head blight (FHB) in wheat has been identified and verified by several research groups. The objectives of this study were to construct a fine genetic map of this QTL region and to examine microcolinearity in the QTL region among wheat, rice, and barley. Two simple sequence repeat (SSR) markers (*Xgwm533* and *Xgwm493*) flanking this QTL were used to screen for recombinants in a population of 3,156 plants derived from a single F_7 plant heterozygous for the *Qfhs.ndsu-3BS* region. A total of 382 recombinants were identified, and they were genotyped with two more SSR markers and eight sequence-tagged site (STS) markers. A fine genetic map of the *Qfhs.ndsu-3BS* region was constructed and spanned 6.3 cM. Based on replicated evaluations of homozygous recombinant lines for Type II FHB resistance, *Qfhs.ndsu-3BS*, redesignated as *Fhb1*, was placed into a 1.2-cM marker interval flanked by STS3B-189 and STS3B-206. Primers of STS markers were designed from wheat expressed sequence tags homologous to each of six barley genes expected to be located near this QTL region. A comparison of the wheat fine genetic map and physical maps of rice and barley revealed inversions and insertions/deletions. This suggests a complex microcolinearity among wheat, rice, and barley in this QTL region.

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Introduction

Fusarium head blight (FHB), also known as scab, caused mainly by *Fusarium graminearum* Schwabe [telomorph: *Gibberella zeae* Schw. (Petch)], is a devastating disease of wheat worldwide. A Chinese cultivar, Sumai 3, and its derivatives have been successfully used as FHB resistance sources throughout the world. A major quantitative trait locus (QTL) for FHB resistance derived from Sumai 3 was identified and designated as *Qfhs.ndsu-3BS* (Waldron et al. 1999). This QTL is flanked by two simple sequence repeat (SSR) marker loci, *Xgwm533* and *Xgwm493*, and has been verified in several mapping populations (Bai et al. 1999; Anderson et al. 2001; Buerstmayr et al. 2002; Zhou et al. 2002). On the basis of cytological-based physical mapping, this QTL is most likely located in the deletion bin 3BS 0.78–0.87 (Liu and Anderson 2003a). The identification of more DNA markers and the construction of a fine genetic map of this QTL region are needed for map-based cloning of this QTL.

Comparative mapping studies using common restriction fragment length polymorphism markers have revealed extensive conservation of gene content and order, termed synteny or colinearity, among the genomes of cereal crops such as rice, wheat, barley, rye, oat, maize, sorghum, and others (Devos and Gale 2000). Wheat chromosome 3BS and rice chromosome 1S are syntenous (Gallego et al. 1998; Kurata et al. 1994; Van Deynze et al. 1995). Using this syntenous relationship and the large number of wheat expressed sequence tags (ESTs), more than 20 sequence-tagged site (STS) markers located in the deletion bin 3BS 0.78–0.87 were developed from wheat ESTs (Liu and Anderson 2003b).

To use the rice genomic sequence for cross-species map-based cloning, microcolinearity in the region of interest should be examined. High microcolinearity between wheat and rice was found in the vernalization gene *Vrn1* region

(Yan et al. 2003) and in the *Hardness* locus region between *Triticum monococcum* and rice (Chantret et al. 2004). However, frequent interruptions of microcolinearity are common. For the barley stem rust resistance gene, *Rpg1*, region, one out of nine rice probes was mapped in a non-syntenic position in barley (Kilian et al. 1995). Chromosome walking in barley led to the isolation of the *Rpg1* gene (Brueggeman et al. 2002), but no homologous gene was found in the rice genome. The *shrunken2* (*sh2*)/*anthocyaninless1* (*a1*) region has been studied at the sequence level in maize, sorghum, rice, and wheat. Despite the excellent microcolinearity in the *sh2/a1* region among rice, sorghum, and maize, the synteny is interrupted in wheat (Li and Gill 2002). For the wheat grain protein content locus, *Gpc-6B1*, region, good microcolinearity was found between wheat and rice, but the synteny is broken for the region distal to gene *Gpc-6B1* (Distelfeld et al. 2004). Sequence analysis revealed a mosaic organization of orthologous sequences in rice, maize, and sorghum at a seed storage protein gene family region (Song et al. 2002). Large-scale EST mapping in wheat has revealed numerous chromosomal rearrangements between wheat and rice (La Rota and Sorrels 2004).

A recent study of microcolinearity between barley and rice has further stimulated our interest in microcolinearity at the *Qfhs.ndsu-3BS* region. Brunner et al. (2003) used rice ESTs on rice chromosome 1S to saturate a leaf rust resistance gene, *Rph7*, region on barley chromosome 3HS. A bacterial artificial chromosome (BAC) contig spanning the *Rph7* locus was established by chromosome walking in barley. Sequence comparison with the orthologous rice sequence revealed the complete conservation of five members of a *HGA* gene family. However, six additional genes located between the genes *HvHGA4* and *HvHGA1* were identified in barley, thus breaking the synteny between rice and barley in the *Rph7* region. In one of our previous studies, we developed two STS markers, STS3B-102 and STS3B-142, from wheat ESTs homologous to the rice genes orthologous to *HvHGA4* and *HvHGA1*, respectively, and they were placed in the *Qfhs.ndsu-3BS* region (Liu and Anderson 2003b). Our long-term goal is to achieve a map-based cloning of *Qfhs.ndsu-3BS*. The objectives of this study were to construct a fine wheat genetic map of the *Qfhs.ndsu-3BS* region and to examine microcolinearity in the QTL region among wheat, rice, and barley.

Materials and methods

An FHB-resistant recombinant inbred line, RI 63, derived from the cross Sumai 3 (resistant)/Stoa (susceptible) was hybridized with an FHB-susceptible line, MN97448 (Fig. 1). An F_7 plant, designated 260-1-1-8, heterozygous for the *Qfhs.ndsu-3BS* region, was identified using three SSR markers (Liu and Anderson 2003a), gwm533, BAR C133, and gwm493. Among the F_8 plants derived from 260-1-1-8, 22 heterozygous plants (genetically equivalent to F_1 plants for the region around the markers) were selected using the three SSR markers. The self-pollinated seeds (equivalent to F_2) from these 22 heterozygous plants were grown to identify recombinants.

DNA was extracted according to Riede and Anderson (1996) with modifications. The first leaf of the wheat plants at the two-leaf stage was harvested into 1.6-ml microcentrifuge tubes and frozen in liquid nitrogen. The leaf tissue was ground with a glass rod and was mixed with 700 µl extraction buffer. After a 30-min incubation at 65°C, 700 µl solution of 24:1 (v/v) chloroform/isoamyl alcohol was added, and the tube contents were mixed vigorously. Centrifugation was performed at 10 000 rpm for 12 min, and 600 µl of the upper phase solution was transferred to another 1.6-ml microcentrifuge tube. The DNA was precipitated with 1 ml of cold (−20°C) 95% ethanol and rinsed with 1 ml of 70% ethanol. The air-dried DNA was dissolved in 300 µl TE buffer.

Two SSR markers flanking *Qfhs.ndsu-3BS*, gwm533 and gwm493, were used to identify the recombinants. The PCR reactions for SSR markers were performed as described by Liu and Anderson (2003a), with the exception that fluorescence-labeled forward primers were used. The genomic DNA was diluted with water in a 1:10 ratio, and 3 µl of diluted DNA was used for PCR with a total reaction volume of 10 µl. The PCR products were analyzed using a LI-COR Global Edition IR^2 DNA analyzer following the manufacturer's instructions.

The sequences of the six additional genes at the *Rph7* locus in barley (Brunner et al. 2003) were used as queries for BLASTn searches to identify wheat ESTs homologous to the barley genes. One pair of primers was designed from the wheat EST with the highest BLASTn score for each barley gene. The wheat cultivar 'Chinese Spring' (CS) and CS aneuploid lines were used to assign STS markers to wheat chromosomes. The aneuploid lines included a complete set of 21 nullisomic-tetrasomic lines (Sears 1966); three ditelosomic lines, DT3AL, DT3BL, and DT3DL (Sears and Sears 1978); and two CS deletion lines, 3BS-3 (FL=0.87) and 3BS-8 (FL=0.78) (Endo and Gill 1996).

To construct a fine map of the QTL region, all the recombinants identified above were genotyped with two additional SSR markers, BARC133 and BARC147, and eight STS markers (Table 1). Of these eight STS markers, Marker STS3B-89 was derived from the sequence of a genomic clone, AF085169, located on wheat chromosome 3BS (Feuillet and Keller 1999). The other seven markers were derived from wheat ESTs homologous to the sequences of rice chromosome 1S (Liu and Anderson 2003b) or barley chromosome 3HS. The linkage map was constructed using MAPMAKER for Macintosh v. 2.0 (Lander et al. 1987) using the Haldane mapping function.

To place *Qfhs.ndsu-3BS* on the fine map, ten to 15 F_3 plants from each of 15 F_2 recombinants representing most marker intervals were genotyped with marker gwm533 or gwm493 to select homozygous recombinants (HR). Additional DNA markers on the fine genetic map were used to validate the HR plants. Seeds of the homozygous plants were increased for replicated evaluation of type II FHB resistance in greenhouses at the University of Minnesota (UMN) and Kansas State University (KSU). Pairs of near-

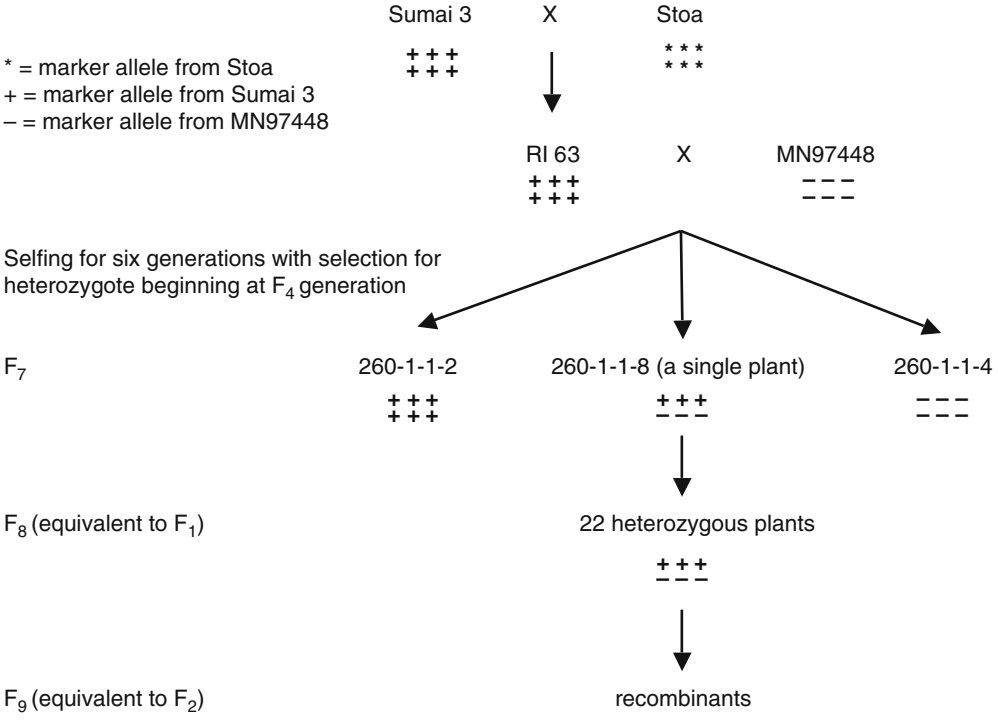

Fig. 1 Development of a population for fine mapping of the *Fhb1* region. Three SSR markers, gwm533, BARC133, and gwm493 (represented by *three symbols* in horizontal rows under each genotype name), were used to genotype the parental lines and to select plants heterozygous for all three markers

isogenic lines (NILs), 260-1-1-2 and 260-1-1-4 (Fig. 1), were used as controls for all experiments. Materials were planted on two dates at each location. For each planting date, each entry was planted into six pots, with four plants per pot, and all pots were completely randomized. At anthesis, the 11th spikelet from the bottom of each wheat head was inoculated with 10 µl of macroconidia suspension (1×10^5 ml^{-1}) of a single isolate of *F. graminearum*. The inoculated head was covered with a zip-loc bag for 48 h, and disease spread was recorded at 21 days postinoculation. Analysis of variance and least significant differences ($LSD_{0.05}$) were performed using Proc GLM of SAS v. 8.01. A line was classified as R (resistant) if its disease severity was significantly lower than the susceptible NIL, and a line was classified as S (susceptible) if its disease severity was significantly higher than the resistant NIL.

Results and discussion

Among the 3,156 plants (equivalent to F_2 plants for the region of interest) screened for recombinants with the two SSR marker loci, *Xgwm533* and *Xgwm493*, 382 recombinants were identified. Nine recombinants were homozygous for both of the two SSR markers. Thus, two recombination events occurred in these nine recombinants. All 382 recombinants were genotyped with two more SSR markers, BARC133 and BARC147, and eight STS markers (Table 1). A fine genetic map of the *Qfhs.ndsu-3BS* region was

Table 1 STS markers used for fine mapping of the *Qfhs.ndsu-3BS* region

Marker	Source[a]	Forward primer (5′→3′)	Reverse primer (5′→3′)	T_A[b] (°C)
STS3B-32	BE499148	GGACGAGTCCTCAGCCCTAT	CGGTGAAGATGAGCTTCCAT	55
STS3B-66[c]	TC269429	AGTCAGGCGAAGAGCGATAA	AGCACTGCACAATGAGCATC	55
STS3B-80[c]	TC251139	AGAAGAAGGAAGCCCCTCTG	GCCATGTCTTTTGTGCCTTT	55
STS3B-89	AF085169	TGTCGTCCGAGTTGAATGAA	CTCCATCCTCGAGCTGCTAC	60
STS3B-142[c]	TC273597	CGAGTACTACCTCGGCAAGC	CATAGAATGCCCCGAAACTG	50
STS3B-189	TC268917	GAAAAAGGGAGGAGGTGTCC	TTCAGTACCCACGGAGCTTT	50
STS3B-194	BE412128	ACAGTCATCGGCAAGATTCC	ACCCGGAATATCAATCACCA	55
STS3B-197[d]	TC257328	GACCTGAAACCAAGCAAGGA	GCGACTGCTTTGCTATAGGG	55
STS3B-206	TC272151	CCACGTCACCAACATCACC	GAAGACGGGGAGGAACTTG	55

[a]The GenBank accession number or the tentative consensus (TC) number of The Institute for Genomic Research (TIGR) *Triticum aestivum* gene index release 10.0 (January 14, 2005)
[b]Annealing temperature
[c]Markers reported in Liu and Anderson (2003) *Genome* 46:817–823
[d]Marker STS3B-197 was monomorphic in our mapping population

constructed (Fig. 2a). Except for two STS markers that cosegregate, the genetic distances between adjacent markers range from 0.2 to 1.6 cM.

To place the QTL on the fine map, it is necessary to limit the genetic and environmental factors affecting FHB evaluations. Because all the recombinants identified in this study were derived from a single F_7 plant heterozygous for the *Qfhs.ndsu-3BS* region, they are nearly genetically identical except for the *Qfhs.ndsu-3BS* region. This minimizes the effects of genetic background on FHB evaluations. The genetic background used to develop this population was chosen after testing more than 30 pairs of NILs for this QTL region. The NIL pair in the lineage used to select the F_7 plant, 260-1-1-8, showed the most consistent and significant differences for FHB resistance over several greenhouse-based evaluations (Pumphrey and Anderson 2003). This assured us that the genetic background of the recombinants has no negative effects on the expression of the QTL. Furthermore, HR lines were selected from the self-pollinated progeny of the recombinants, and replicated FHB evaluations of these HR lines were performed at multiple locations.

The FHB data of the HR lines and the two NILs evaluated for type II resistance at UMN and KSU are summarized in Fig. 2b. All HR lines can be classified unequivocally as R or S line by comparing them to the disease severity of the parental NILs. Based on the FHB phenotypes of three HR lines, HR37, HR45, and HR56, *Qfhs.ndsu-3BS* was placed into a 1.2-cM marker interval flanked by STS3B-189 and STS3B-206. This finding was also supported by the phenotypes of the other HR lines (Fig. 2b). More than 20 additional HR lines with recombination events between markers STS3B-189 and STS3B-206 were tested for FHB resistance at UMN, KSU, and North Dakota Sate University (data not shown), and all results indicated that *Qfhs.ndsu-3BS* is located in the marker interval between STS3B-189 and STS3B-206. Because all HR lines can be clearly classified as R or S line, this QTL can be mapped as a single Mendelian locus. We propose to redesignate *Qfhs.ndsu-3BS* as *Fhb1*.

An inversion was revealed after comparison of the order of the STS markers on the genetic map and the order of the homologous genes on the rice physical map (Fig. 3). Marker STS3B-189 is distal to marker STS3B-66 on the fine genetic map of the QTL region. However, the rice homologous genes of these two markers are in the opposite order on the rice physical map (Fig. 3). The positions of other markers between these two markers also support the presence of an inversion. Because we have made extensive use of the rice physical map and sequence data to find new wheat markers close to *Fhb1* (Liu and Anderson 2003b), the identification of this inversion was critical for the future success of this strategy. Markers derived from wheat ESTs homologous to the sequence of rice P1-derived artificial chromosome (PAC) clone AP002487 should be distal to markers derived from wheat ESTs homologous to the

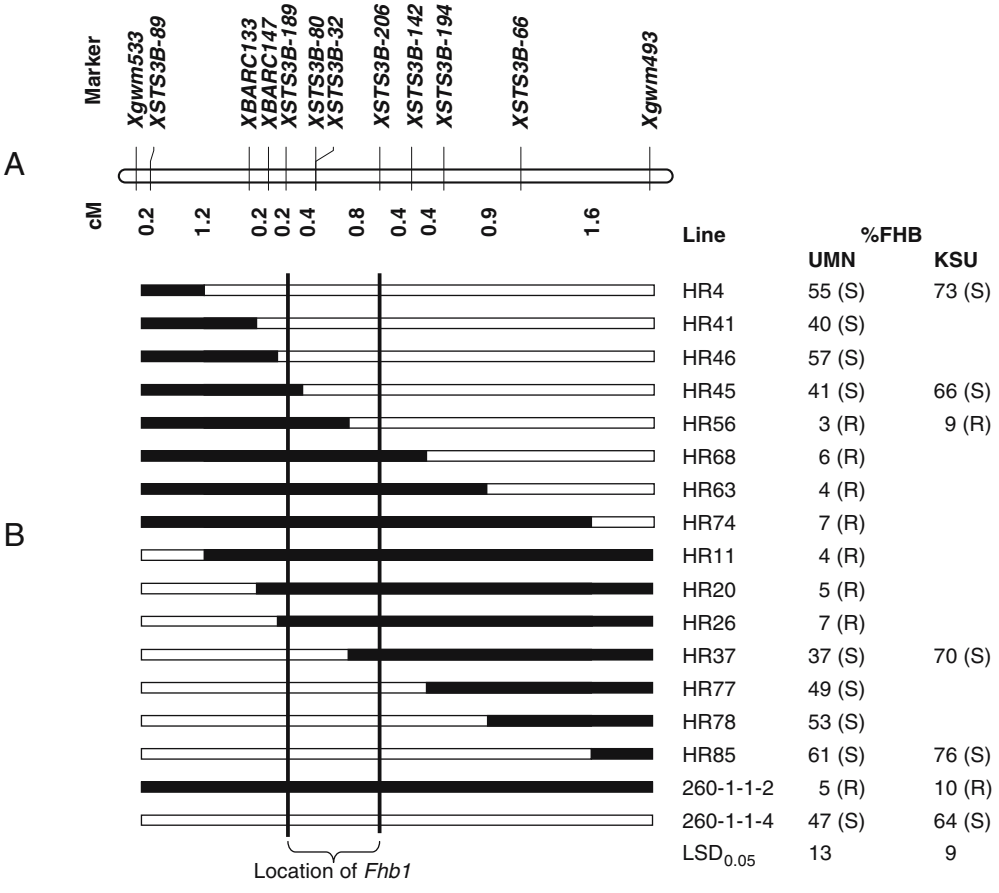

Fig. 2 Fine mapping of the *Fhb1* region. (**a**) A high-resolution map of the QTL region. (**b**) Graphical genotypes of homozygous recombinant lines and their disease severity (% diseased spikelets) of type II FHB resistance. The *black* and *open boxes* indicate homozygous alleles of Sumai 3 and MN97448, respectively. The break points of recombinations were assumed to be in the middle of the marker intervals. *Fhb1* was placed in a 1.2-cM marker interval between STS3B-189 and STS3B-206, illustrated by the *area between the two vertical lines*

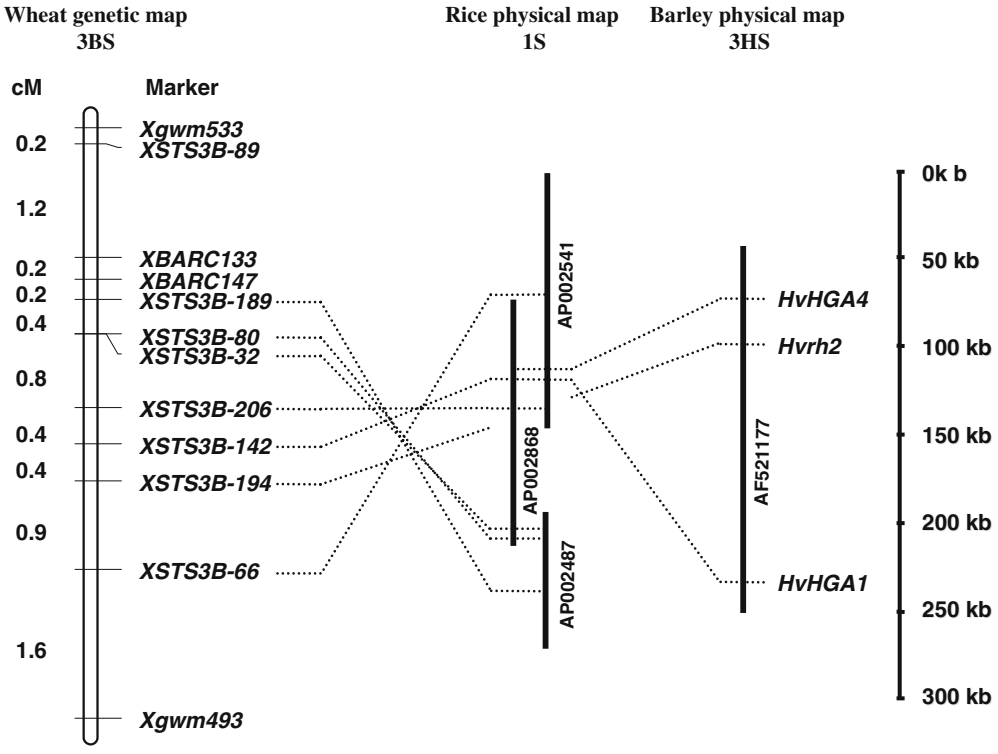

Fig. 3 Complex microcolinearity among wheat, rice, and barley in the *Fhb1* region. *Left* the fine wheat genetic map of the *Fhb1* region; *middle* PAC contig of the subdistal region of rice chromosome 1S (http://rgp.dna.affrc.go.jp/); *right* physical map of the subdistal region of barley chromosome 3HS (Brunner et al. 2003). The *top* of each map is towards the telomere and the *bottom* is towards the centromere. Orthologous genes among the three species are connected by *dotted lines*. Gene *Hvrh2* is present in a nonsyntenous location in rice

overlapping sequence of the two PAC clones AP002541 and AP002868. However, the boundaries of the inversion have not been clearly defined, and markers distal to STS 3B-189 or markers proximal to STS3B-66 may not fit the wheat/rice inversion described in this study.

Among the six pairs of STS primers (Table 2) derived from wheat ESTs homologous to the six additional genes on barley chromosome 3HS reported by Brunner et al. (2003), all except marker STS3B-196 amplified DNA fragments from the genomic DNA of CS. On the basis of aneuploid analysis, two STS markers, STS3B-194 and STS3B-197, were assigned to the deletion bin 3BS 0.78–0.87, where *Fhb1* is located (Liu and Anderson 2003a). Marker STS3B-197 was also assigned to chromosomes 3A and 3D using wheat aneuploid lines (data not shown). For the other three STS primer pairs, the PCR products could not be assigned to wheat chromosomes because all the 21 nullisomic–tetrasomic lines had the same banding patterns. By searching the database of mapped wheat ESTs (http://wheat.pw.usda.gov/wEST/blast/), BE404719, homologous to gene *Hvpg4*, was mapped to the most distal deletion bins of chromosomes 3AS, 3BS, and 3DS. Thus, at least three of the six counterparts of the barley genes are present in syntenous regions in wheat. This confirms the results of wheat aneuploid analysis using barley genes as probes in Southern hybridizations (Brunner et al. 2003).

Among the six STS markers corresponding to the barley genes, only marker STS3B-194 was polymorphic in the fine mapping population and was placed on the fine genetic map (Fig. 2). Two STS markers, STS3B-102 and STS3B-142, reported in our previous study (Liu and Anderson 2003b), were derived from wheat ESTs homologous to *HvHGA4* and *HvHGA1*, respectively. Only marker STS3B-142 was polymorphic and was 0.4 cM distal to marker STS3B-194 (Fig. 2). Therefore, the fine map revealed an inversion between wheat and barley because gene *Hvrh2* is distal to gene *HvHGA1* on the barley physical map (Fig. 3). Together with the comparison between wheat and rice described above, microcolinearity among wheat, rice, and barley at the *Fhb1* region is complicated by microrearrangements such as inversions and insertions/deletions.

Comparative analysis is a powerful tool used to study genome evolution. Based on the comparative maps shown

Table 2 STS markers developed from wheat ESTs homologous to genes at the *Rph7* locus in barley

Marker	EST/TC[a]	Gene[b]	Chromosome
STS3B-102[c]	BJ222861	*HvHGA4*	3BS 0.78–0.87
STS3B-194	BE412128	*Hvrh2*	3BS 0.78–0.87
STS3B-195	TC255680	*Hvpg3*	
STS3B-196	TC247082	*Hvgad1*	
STS3B-197	TC257328	*Hvpg1*	3BS 0.78–0.87, 3A, 3D
STS3B-198	BU100479[d]	*Hvpg4*	
STS3B-199	BJ304679	*Hvhel1*	
STS3B-142[c]	TC273597	*HvHGA1*	3BS 0.78–0.87

[a]The GenBank accession number or the TC number of the TIGR *T. aestivum* gene index release 10.0 (January 14, 2005)
[b]The six additional barley genes relative to the orthologous region on rice chromosome 1S are flanked by genes *HvHGA4* and *HvHGA1*, and the genes were listed in the order from telomere to centromere (Brunner et al. 2003)
[c]Markers reported in Liu and Anderson (2003b) *Genome* 46:817–823
[d]This EST is homologous to wheat EST BE404719, which has been mapped to 3AS, 3BS, and 3DS

in Fig. 3, we can speculate on genome evolution in this region. Because the additional genes (relative to rice) identified at the *Rph7* locus in barley are also present in the syntenic region of wheat, the existence of these genes in this region should predate the wheat and barley divergence from the last common ancestor. This is consistent with the results of the latest comparison of the *Rph7* orthologous loci in wheat, barley, rice, and sorghum (Scherrer et al. 2005). The inversion in this region may have happened in the wheat lineage because the marker order of wheat chromosome 3B in the *Fhb1* region is inverted in comparison with the gene order in rice and barley.

Genome synteny is much more complicated than previously thought (for a review, see Delseny 2004). Despite the macrosynteny between wheat group 3 chromosomes and rice chromosome 1 (Ahn et al. 1993; Kurata et al. 1994; Van Deynze et al. 1995) or barley chromosome 3H (Linde-Laursen et al. 1997), the microcolinearity among wheat, rice, and barley at the *Fhb1* region is interrupted by rearrangements such as inversions and insertions/deletions. Munkvold et al. (2004) reported the most detailed comparison to date between wheat group 3 chromosome and rice chromosome 1. Despite many rearrangements between wheat and rice, the deletion bin 3BS 0.78–1.00, harboring *Fhb1*, is one of the regions showing excellent synteny with rice chromosome 1S. However, this detailed comparison between wheat and rice was limited by the resolution of the chromosome deletion bin maps of wheat ESTs, and the comparison was based on the assumption that the EST order within the deletion bins is similar to the order in rice. Thus, it is not surprising that complex microcolinearity in the *Fhb1* region was revealed in this study. It is possible that the microcolinearity among wheat, rice, and barley is even more complex than that reported in this study. All the STS markers, except STS3B-89, used for the fine mapping of this QTL region were derived from wheat ESTs homologous to the genomic sequence of rice chromosome 1 or barley chromosome 3H. Genes homologous to other chromosomes of rice or barley and genes specific to the wheat genome were not detected by our methods.

The complex microcolinearity at the *Fhb1* region complicates but does not negate the use of rice and barley sequence information for fine mapping of this QTL region in wheat. As shown in Fig. 3, seven STS markers derived from wheat ESTs homologous to rice or barley genomic sequences have been mapped in this QTL region. More than 20 STS markers derived from wheat ESTs homologous to the sequences of rice chromosome 1 have been assigned to the deletion bin 3BS 0.78–0.87 (Liu and Anderson 2003b). However, the complex microcolinearity at the *Fhb1* region and the rapid cereal genome evolution of disease resistance genes (Leister et al. 1998) may limit the use of synteny-based cloning of this QTL. Three disease resistance genes have been cloned in wheat. No rice genes are homologous to *Lr10* (Feuillet et al. 2003) or *Lr21* (Huang et al. 2003) at the nucleotide level. Rice genes homologous to *Pm3* (Yahiaoui et al. 2004) are located in nonsyntenous regions. Therefore, we are simultaneously developing more DNA markers near this QTL based on synteny with rice and barley and screening a wheat BAC library to construct a physical map of this QTL region.

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