Comparative analyses of genomic locations and race specificities of loci for quantitative resistance to *Pyricularia grisea* in rice and barley

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Comparative genomic analyses have revealed extensive colinearity in gene orders in distantly related taxa in mammals and grasses, which opened new horizons for evolutionary study. The objective of our study was to assess syntenic relationships of quantitative trait loci (QTL) for disease resistance in cereals by using a model system in which rice and barley were used as the hosts and the blast fungus *Pyricularia grisea* Sacc. as the pathogen. In total, 12 QTL against three isolates were identified in rice; two had effects on all three isolates, and the other 10 had effects on only one or two of the three isolates. Twelve QTL for blast resistance were identified in barley; one had effect on all three isolates, and the other 11 had effects on only one or two of the three isolates. The observed isolate specificity led to a hypothesis about the durability of quantitative resistance commonly observed in many plant host-pathogen systems. Four pairs of the QTL showed corresponding map positions between rice and barley, two of the four QTL pairs had complete conserved isolate specificity, and another two QTL pairs had partial conserved isolate specificity. Such corresponding locations and conserved specificity suggested a common origin and conserved functionality of the genes underlying the QTL for quantitative resistance and may have utility in gene discovery, understanding the function of the genomes, and identifying the evolutionary forces that structured the organization of the grass genomes.

Recent molecular marker-based comparative genetic analyses have revealed extensive collinear relationship in gene orders, which is frequently referred to as synteny, among the genomes of mammalian species (1). In plants, it has been shown that the genomes of cereal grasses share colinearity in gene orders as detected by probes that hybridize with DNA from various members across the grass family (2, 3). It has also been reported that some of the genes affecting seed mass, seed dispersal, and flowering time reside in corresponding chromosomal locations among the genomes of rice, sorghum, and maize (4). Alignment of cereal genomes identified candidate genes affecting dormancy from maize and dormancy-related quantitative trait loci (QTL) of rice that may be related to wheat QTL for preharvest sprouting (5). Thus, identification of the syntenic relationships of important functional genes in different species may help gene discovery across species and help understanding the evolutionary processes that occurred to shape the genomes of the species.

Disease resistance of plants can be classified into two major types (6). Various terms have been used to describe the two types of resistance, such as vertical versus horizontal resistance (6), qualitative versus quantitative resistance (7), and complete versus partial resistance (8). Complete resistance modulated by the interaction between a disease resistance (*R*) gene and an avirulence gene is specific to pathogen race and lifetime limited in a particular cultivar because of the strong selection pressure against and the rapid evolution of the pathogen. Partial resistance conferred by QTL, on the other hand, is presumably race-nonspecific and durable (9).

The recent development of molecular marker techniques has generated considerable interests in identifying loci involved in quantitative disease resistance in cereals. In rice, for example, a large number of QTL for resistance to various diseases, such as blast, sheath blight, bacterial blight, and yellow mottle virus, have been identified (10–13). Studies were also conducted in barley to characterize quantitative resistance, which identified a large number of QTL for resistance to a number of barley diseases, including bacterial leaf streak, stripe rust, leaf rust, stem rust, powdery mildew, scald, and net blotch (14–16). However, it is not known whether genes controlling resistance to various diseases have any relationship in different members of the grass family.

Rice blast, caused by *Pyricularia grisea* Sacc., continues to be the most destructive disease despite decades of research efforts toward its control (17). The rice blast fungal pathogen is also infective to several grasses, including barley, and can cause epidemic in barley fields (18–20). More than 40 *R* genes against rice blast have been identified; >30 genes were mapped on the chromosomes, and two blast resistance genes, *Pib* and *Pita*, were recently isolated (21, 22). The detection of QTL to rice blast fungus in barley has been reported (23). Therefore, rice blast can be used as a model system for comparative study of quantitative resistance between rice and barley. Moreover, identification of syntenic QTL for resistance to blast in rice and barley should enhance the understanding of durable and wide spectrum resistance, which in turn may provide clues for formulating new strategies for improving disease resistance of the crops.

The objective of the present study is to find a possible syntenic relationship of loci for quantitative resistance to *P. grisea* in rice and barley. It is expected that the findings of the study may have general implications across the grass family.

Materials and Methods

Experimental Materials. Two populations were used for studying the QTL to rice fungal blast. The rice population consisted of 241 recombinant inbred lines (RILs) developed from a cross between Zhenshan 97 (*Oryza sativa* L.) and Minghui 63 (*O. sativa* L.) by single seed descent. A molecular linkage map containing 221 restriction fragment length polymorphisms and simple sequence repeat loci and covering the whole rice genome was developed with this population (24). The barley population, consisting of 150 doubled haploid lines (DHLs), was derived from a cross between Harrington (*Hordeum vulgare* L.) and TR306 (*H. vulgare* L.). A molecular linkage map based on this barley population contained 127 framework loci (D. E. Mather, online data set for the Harrington/TR306 base map, ftp://gnome.agrenv.mcgill.ca/data/basemaps, 1995).

Pathogen Inoculation and Disease Scoring. The plants used for inoculation were grown in 60 × 40 × 8-cm plastic trays. For rice

Abbreviations: QTL, quantitative trait locus or loci; RIL, recombinant inbred line; DHL, doubled haploid line; LOD, logarithm of odds; LN, lesion number; LL, lesion length; LA, lesion area; LD, lesion degree.

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Table 1. Performance of rice and barley populations for rice blast resistance

		Rice RILs		Rice parent		Barley DH lines		Barley parent	
Trait	Isolate	Range	Mean ± SE	Zhenshan 97	Minghui 63	Range	Mean ± SE	Harrington	TR306
LN	F1366	0–96	19 ± 19.3	91.8	11.8	1–70	22 ± 10.4	48.3	7.3
	F1814	0–59	9 ± 11.5	65.6	12.0	0–24	10 ± 5.0	21.5	7.7
	V86013	0–125	10 ± 13.3	47.4	3.0	3–87	31 ± 15.9	38.6	11.9
LL, mm	F1366	0–9	3 ± 1.9	3.9	0.3	1–4	3 ± 0.8	3.8	1.4
	F1814	0–9	2 ± 1.5	1.8	2.3	0–6	3 ± 1.1	3.7	3.2
	V86013	0–13	2 ± 2.6	2.6	1.2	1–8	3 ± 0.9	3.3	2.1
LA, %	F1366	0–71	11 ± 15.1	54.5	5.3	0–43	18 ± 10.4	34.5	4.9
	F1814	0–53	5 ± 9.0	12.0	5.8	0–53	13 ± 8.5	26.5	2.5
	V86013	0–52	6 ± 8.9	34.3	1.8	1–51	19 ± 11.2	25.3	7.3
LD, 0–5	F1366	0–5	3 ± 1.4	5	3	1–4	4 ± 0.8	4	2
	F1814	0–5	2 ± 1.3	4	3	0–5	3 ± 1.0	4	2
	V86013	0–5	2 ± 1.2	4	2	2–5	4 ± 0.6	4	3

inoculation, each tray contained 15 experimental materials, including 12 RILs, the highly susceptible rice cultivar CO39 (susceptible control), and the two parents of RIL population, with each material having at least 10 plants. For barley inoculation, each tray contained 14 materials, including 12 DHLs and the two parents of the DHL population. The entire inoculation experiment was replicated twice.

The blast inoculation was carried out as described (25). In brief, the blast conidial suspension was adjusted to $\approx 2 \times 10^5$ per ml with sterilized deionized water. Before inoculation, 0.05% Tween 20 was added to the suspension for increasing the adhesion of fungi to the plants. Rice seedlings of 3–4 leaf stage and 21-day-old barley seedlings were inoculated by spraying fresh preparation of conidial suspension at 80 ml per tray. The inoculated seedlings were placed in an air-conditioned greenhouse maintained at 25°C and covered with moist jute sacks to ensure >93% of relative humidity for 24 h in the dark. The seedlings were then kept at 24–28°C and sprayed with a mist of water four to five times during the day.

The plants were scored for disease infection 14 and 6 days after inoculation for rice and barley, respectively. Four important components of partial resistance, lesion number (LN), lesion length (LL), lesion area (LA), and lesion degree (LD) were investigated (26), which will be referred to as four traits for ease of description. The most seriously diseased leaves from five randomly chosen plants of each line were used for counting the LN and visually estimating the LA (percent of diseased area in the whole leaf area). Three of the largest lesions in the selected leaves were measured for LL (mm). The LD was determined based on the LL and LA by using the 0–5 scale rating system (27), in which ratings 0–3 indicated an incompatible (resistant) reaction and ratings 4 and 5 indicated a compatible (susceptible) reaction.

Data Analysis. The mean of the five plants of each line was used in the analysis. The QTL were determined by using the software QTLMAPPER that was developed based on the mixed linear model approach (28) to analyze main-effect QTL, digenic interactions, and their environmental interactions. For analyzing single-locus QTL, this analysis is approximately equivalent to the composite interval mapping method (29). The QTLMAPPER program first selected some important markers by stepwise regression for the genetic background control, and then estimated the QTL effects by the maximum-likelihood estimation method. A resampling technique, Jackknife test, was further used for posterior significance test of QTL effects and also for parameter estimation by omitting one line each round. QTL was determined with threshold $P \leq 0.005$.

For comparing the correspondence of QTL that are likely to be syntenic in rice and barley based on previous results, the locations for a number of barley markers in the rice map were determined by homology search of the barley probe sequences against rice genomic sequences with known chromosomal locations (http://rgp.dna.affrc.go.jp and www.genome.clemson.edu) by using BLAST analysis (30).

Results

Resistance of the Parents of the Rice and Barley Populations. We used 21 and 11 isolates of *P. grisea* in testing their infections on the rice and barley parents, respectively. Two Chinese isolates, F1366 and F1814 from our laboratory (25), and a Philippine isolate V86013, were chosen for inoculating the RIL and DHL populations. Each of the isolates produced compatible reactions (LD 4–5) with the rice parent Zhenshan 97 and barley parent Harrington, but incompatible reactions (LD 2–3) with Minghui 63 and TR306 (Table 1).

Resistance of Rice RIL and Barley DHL Populations. The disease measurements produced by the infection of the *P. grisea* isolates varied greatly in all four traits (LN, LL, LA, and LD) in both the rice RIL and barley DHL populations (Table 1). Transgressive segregations were observed for almost all of the trait/isolate combinations. Some of the rice RILs and barley DHLs showed less disease than their respective resistant parents, whereas other lines showed more disease than their susceptible parents (data not shown).

QTL for Resistance in the Rice Population. For the four traits (LN, LL, LA, and LD), effects on resistance to the three blast isolates were detected in 7-, 10-, 15-, and 10-marker intervals, respectively (Table 2). The phenotypic variations of resistance accounted for by the QTL varied greatly among different trait/isolate combinations, ranging from 1.6% to 44.2%. The logarithm of odds (LOD) peaks detected for the four attributes of resistance, or the four traits, to the same isolate were frequently located in the same marker intervals or nearby regions. Examination of these LOD peaks clearly showed that the 1-LOD support intervals of the QTL (data not shown) overlapped substantially with each other and hence the effects detected can be regarded as caused by the same QTL (31). Thus, overall 12 QTL were detected for resistance to the three isolates and the 12 QTL were distributed on six of the 12 rice chromosomes (Table 2, Fig. 1).

The resistance alleles at six (*rbr1a*, *rbr1b*, *rbr2*, *rbr8*, *rbr9a*, and *rbr9c*) of the 12 QTL were from resistant parent Minghui 63, and six (*rbr1c*, *rbr1d*, *rbr3*, *rbr7a*, *rbr7b*, and *rbr9b*) were from susceptible parent Zhenshan 97 (Table 2). Interestingly, the accumulation of resistant alleles of the various QTL resulted in several RILs with LDs ranging from 0 to 1 for all three isolate infections, which were more resistant than the resistant parent Minghui 63.

Table 2. Putative QTL identified for rice blast resistance in the rice RIL population

QTL	Trait	Isolate	Marker interval	LOD	*P*	A*	Var†
rbr1a	LL	F1366	C161-R753	2.0	0.0026	0.30	2.1
	LA	F1366	C161-R753	1.8	0.0039	2.21	1.6
	LA	V86013	C161-R753	1.8	0.0042	1.61	3.3
rbr1b	LN	F1366	RM259-RM243	2.3	0.0011	3.25	2.5
	LA	F1366	RM259-RM243	3.5	0.0001	3.25	3.5
	LD	F1366	RG532-RM259	2.6	0.0008	0.26	3.4
	LN	F1814	RM243-RG173	2.6	0.0005	2.24	3.7
	LL	F1814	RM243-RG173	2.2	0.0012	0.30	3.9
	LA	F1814	RM243-RG173	2.2	0.0025	1.74	3.4
rbr1c	LA	F1366	G393-R2201	7.0	0.0000	−4.41	6.5
	LA	V86013	G393-R2201	2.5	0.0008	−1.83	4.2
rbr1d	LL	F1366	RM212-C547	10.4	0.0000	−0.71	11.7
	LL	F1814	RM212-C547	3.6	0.0000	−0.37	6.0
	LD	F1814	RM212-C547	2.0	0.0026	−0.23	2.8
	LD	F1366	C547-C2340	3.7	0.0000	−0.29	3.9
	LD	V86013	C547-C2340	3.1	0.0002	−0.26	4.3
	LA	F1814	C2340-C86	1.9	0.0030	−1.64	3.1
rbr2	LN	F1366	RM213-RM208	27.8	0.0000	13.42	42.7
	LL	F1366	RM213-RM208	19.7	0.0000	1.13	29.5
	LA	F1366	RM213-RM208	22.3	0.0000	9.41	29.2
	LD	F1366	RM213-RM208	27.8	0.0000	0.96	44.2
	LN	F1814	RM213-RM208	10.6	0.0000	5.29	20.8
	LL	F1814	RM213-RM208	2.3	0.0015	0.34	5.0
	LA	F1814	RM213-RM208	6.9	0.0000	3.54	14.3
	LD	F1814	RM213-RM208	7.7	0.0000	0.53	15.2
	LN	V86013	RM213-RM208	7.9	0.0000	5.50	17.1
	LA	V86013	RM213-RM208	5.4	0.0000	2.71	9.3
	LD	V86013	RM213-RM208	12.3	0.0000	0.59	22.3
rbr3	LN	F1814	RZ403-R19	1.9	0.0050	−2.08	3.2
rbr7a	LN	F1366	RG528-RG128	2.7	0.0007	−3.54	3.0
	LL	F1366	RG128-C1023	2.8	0.0005	−0.36	3.0
	LA	F1366	RG128-C1023	2.6	0.0009	−2.66	2.3
rbr7b	LL	F1366	RM234-R1789	2.0	0.0003	−0.30	2.1
rbr8	LL	F1366	RG333-RM25	3.0	0.0003	0.38	3.4
	LA	F1366	RM25-R1629	4.3	0.0000	3.87	4.9
	LA	V86013	RM25-R1629	2.9	0.0002	1.95	4.8
	LD	V86013	RM25-R1629	3.9	0.0000	0.29	5.4
rbr9a	LA	F1366	RM201-C472	2.0	0.0040	3.00	3.0
	LD	F1814	RM201-C472	3.3	0.0000	0.33	6.1
rbr9b	LD	F1814	RM257-RM242	2.4	0.0004	−0.30	5.1
rbr9c	LA	F1366	RG570-RG667	2.4	0.0009	4.00	5.3
	LL	V86013	RM215-R1952	1.9	0.0012	0.51	3.7

*Additive effect. The positive or negative value indicates that allele from Minghui 63 or Zhenshan 97 decreases the trait score, respectively.

†Variation explained by the putative QTL.

The identified QTL showed certain degrees of isolate specificity. Of the 12 QTL, only two were detected as showing resistance to all three isolates, six QTL showed resistance to two isolates, and the remaining four QTL showed resistance to only one isolate (Table 2, Fig. 1). Altogether, 10 QTL had effects on F1366, six QTL had effects on F1814, and six QTL had effects on V86013.

The QTL *rbr2* showed the largest effect on resistance to all three isolates (Table 2); Minghui 63 allele expressed strong resistant reaction in the all cases. In the extreme case of LN and LD after F1366 infection, this QTL explained 43% and 44% of the phenotype variation (Table 2), respectively, which apparently represented the effect of a major gene for resistance. The genomic location of this QTL coincided with the blast resistance gene *Pib* (21) (Fig. 1). Whether this is the *Pib* gene or an allele of this locus, or a tightly linked gene, remains to be determined. It is nonetheless clear that this gene had a large effect on resistance to one of the isolates, and relatively small effect on resistance to other two isolates.

Although *rb2* had a major effect on resistance to F1366, it appeared that the QTL with small effects collectively had about the same amount of effect as *rbr2* on resistance to F1366 in this population. For example, the RILs R140, R159, and R193 had the resistant allele of *rbr2* and the susceptible alleles at most of the other QTL and exhibited resistance reaction to F1366 with LDs 2–3, which was about the same level as their resistant parent, Minghui 63. On the other hand, lines R15, R123, R124, and R151 having the susceptible allele of *rbr2* but resistant alleles at most of the other QTL also showed about the same level of resistance to F1366 as did R140, R159, and R193.

QTL for Resistance in the Barley Population. Effects on resistance to the three blast isolates were detected in 7-, 9-, 10-, and 10-marker intervals for the four traits (LN, LL, LA, and LD), respectively (Table 3). These effects accounted for from 3.4% to 32.6% of the phenotypic variation of the resistance. Examination of 1-LOD support intervals of the LOD peaks (data not shown) indicated that

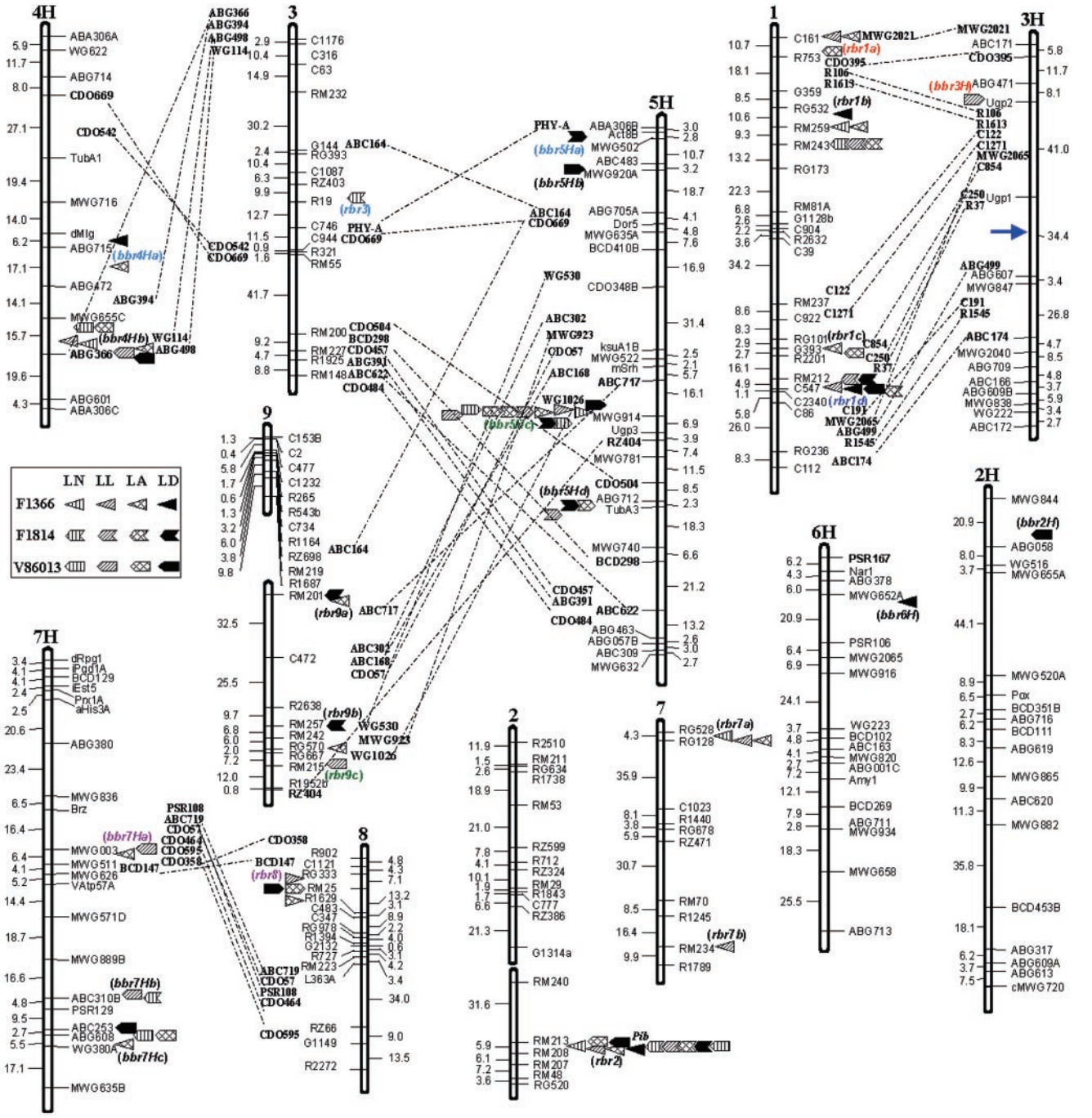

Fig. 1. Locations of QTL for resistance to rice blast in rice and barley. The QTL names are in parentheses. Each triangle indicates the LOD peak of the resistance effect evaluated by using LN, LL, LA, or LD. The location of *Pib* on rice chromosome 2 is deduced by using the mapping information of Wang *et al.* (21). The arrow on barley chromosome 3H indicates the location of a QTL against net blotch (15). The barley markers in bold on both sides of the chromosomes were placed according to published mapping information (refs. 34 and 35; www.ncbi.nlm.nih.gov/Entrez). Thirteen barley markers, ABG394, ABG366, CDO669, BCD147, ABG391, CDO457, ABC622, BCD298, CDO504, ABG395, CDO669, CDO358, and PRS108, were mapped on rice chromosomes by BLAST search (30) of the barley probe sequences against rice genomic sequences with known chromosomal locations (http://rgp.dna.affrc.go.jp and www.genome.clemson.edu), with the *E* values of identified sequence homology ranging from 0.0 to 3e-08. The probe ABG391, showing the least sequence homology (*E* value = 3e-08) with the rice sequence, had 72 bp overlap with 86% sequence identify. The remaining barley markers were placed on rice linkage maps according to published mapping information (refs. 32–36; www.ncbi.nlm.nih.gov/Entrez). QTL pairs showing syntenic map positions in rice and barley are labeled with the same colors.

the effects on resistance detected were caused by 12 QTL located on six of the seven chromosomes (Table 3, Fig. 1).

The resistance alleles at nine (*bbr2H*, *bbr3H*, *bbr4Ha*, *bbr4Hb*, *bbr5Hc*, *bbr5Hd*, *bbr7Ha*, *bbr7Hb*, and *bb7Hc*) of the 12 QTL were from resistant parent TR306, and three (*bbr5Ha*, *bbr5Hb*, and *bbr6H*) were from susceptible parent Harrington. Some of the DHLs (e.g., 14, 71, and 111) showed higher resistance than TR306, as a result of the accumulation of QTL alleles for resistance. Conversely, some of the DHLs (e.g., 18, 20, and 76) were more susceptible to rice blast than the susceptible parent Harrington, because of the accumulation of QTL alleles for susceptibility.

Of the 12 QTL, *bb5Hc* expressed the largest effect on resistance

Table 3. Putative QTL identified for rice blast resistance in the barley DHL population

QTL	Trait	Isolate	Marker interval	LOD	*P*	A*	Var†
bbr2H	LD	V86013	MWG844-ABG058	2.3	0.0012	0.15	4.7
bbr3H	LL	V86013	ABG471-Ugp2	2.5	0.0002	0.24	5.7
bbr4Ha	LD	F1366	dMlg-ABG715	2.6	0.0002	0.20	7.5
	LA	F1366	ABG715-ABG472	3.5	0.0004	2.96	6.6
bbr4Hb	LN	F1366	MWG655C-ABG366	5.1	0.0000	4.42	15.0
	LL	F1366	MWG655C-ABG366	2.6	0.0004	0.25	9.3
	LA	F1366	MWG655C-ABG366	2.8	0.0014	2.82	6.0
	LN	V86013	MWG655C-ABG366	2.7	0.0007	4.08	6.1
	LA	V86013	MWG655C-ABG366	4.4	0.0000	3.46	8.9
	LL	V86013	ABG366-ABG601	2.8	0.0010	0.27	7.0
	LD	V86013	ABG366-ABG601	5.1	0.0000	0.23	11.4
bbr5Ha	LD	F1814	Act8B-MWG502	2.0	0.0030	−0.20	3.5
bbr5Hb	LD	V86013	ABC483-MWG920A	2.3	0.0014	−0.15	4.8
bbr5Hc	LN	F1366	ABC717-MWG914	8.1	0.0000	5.04	19.6
	LL	F1366	ABC717-MWG914	5.0	0.0000	0.31	14.5
	LA	F1366	ABC717-MWG914	15.3	0.0000	6.50	31.9
	LL	F1814	ABC717-MWG914	5.7	0.0000	0.46	9.4
	LA	F1814	ABC717-MWG914	9.4	0.0000	4.42	21.5
	LN	V86013	ABC717-MWG914	12.4	0.0000	9.23	31.3
	LA	V86013	ABC717-MWG914	13.8	0.0000	6.62	32.6
	LD	V86013	ABC717-MWG914	10.6	0.0000	0.33	22.6
	LN	F1814	MWG914-Ugp3	6.9	0.0000	2.38	21.9
	LD	F1814	MWG914-Ugp3	8.3	0.0000	0.48	20.0
	LL	V86013	MWG914-Ugp3	4.8	0.0000	0.32	9.7
bbr5Hd	LA	F1814	ABG712-TubA3	2.6	0.0012	2.76	8.4
	LD	F1814	ABG712-TubA3	4.0	0.0007	0.40	13.3
	LL	F1814	TubA3-MWG740	2.2	0.0025	0.38	6.3
bbr6H	LD	F1366	MWG652A-PSR106	2.1	0.0024	−0.20	6.8
bbr7Ha	LA	F1366	MWG003-MWG511	1.8	0.0012	2.11	3.4
	LL	V86013	MWG003-MWG511	2.6	0.0007	0.27	6.9
bbr7Hb	LL	V86013	MWG889B-ABC310B	2.9	0.0003	0.28	7.4
	LN	F1814	ABC310B-PSR129	1.9	0.0034	1.12	4.8
bbr7Hc	LD	V86013	PSR129-ABC253	5.0	0.0000	0.21	9.3
	LA	F1366	ABG608-WG380A	2.2	0.0021	2.15	3.6
	LN	V86013	ABG608-WG380A	2.4	0.0015	3.60	4.7
	LA	V86013	ABG608-WG380A	3.3	0.0002	2.83	5.9

*Additive effect. The positive or negative value indicates that allele from TR306 or Harrington decreases the trait score, respectively.

†Variation (%) explained by the putative QTL.

to all three isolates, four QTL showed resistance to two isolates, and the remaining seven QTL were detected as showing resistance to only one isolate (Table 3, Fig. 1). Overall, six QTL had effects on F1366, four QTL had effects on F1814, and eight QTL had effects on V86013.

Comparison of Rice and Barley QTL. Although comparative mapping of common molecular markers in the rice RIL and barley DHL populations was not conducted in this study, the collinear relationship of the two maps can be deduced on the basis of the information from various sources. This includes the published rice (32, 33) and barley (ref. 34 and www.ncbi.nlm.nih.gov/Entrez) molecular linkage maps, the comparative linkage maps of rice and barley (35, 36), and the results from a homology search of the barley probe sequences against the rice genomic sequences. Four rice QTL and four barley QTL identified in this study that comprised four pairs, *rbr1a* with *bbr3H*, *rbr3* with *bbr5Ha*, *rbr8* with *bbr7Ha*, and *rbr9c* with *bbr5Hc*, had corresponding map positions in the rice and barley genomes, as inferred on the basis of flanking molecular markers (Fig. 1). Likely positional correspondence may also exist between *rbr3* and *bb4Ha*.

Interestingly, the two corresponding QTL in two of the four pairs (*rbr3* with *bbr5Ha* and *rbr8* with *bbr7Ha*) identified above had the same isolate specificity and the two corresponding QTL in another two pairs (*rbr1a* with *bbr3H* and *rbr9c* with *bbr5Hc*) had partial isolate identity (Tables 2 and 3).

Discussion

Colinearity in gene orders has been detected by comparative mapping among distantly related taxa of mammals (1) and members of the grass family (3). Syntenic relationship has also been reported for genes controlling traits such as seed mass, seed dispersal, flowering time, preharvest sprouting, and dormancy among several members of the grass family (4, 5). The present study expands the analysis to the identification of syntenic relationship of genes for quantitative resistance to *P. grisea* in the genomes of rice and barley and identified a number of QTL that reside in corresponding locations of the two genomes. An even more striking feature revealed by this dataset is that the race specificity has been completely or partially conserved for four pairs of QTL showing corresponding map positions in the two cereal plants. Such likely syntenic relationships and conserved specificity suggested a common origin and conserved functionality of the genes underlying the QTL for quantitative resistance. In addition, a rice QTL (*rbr1d*) identified in this study seems to have a corresponding chromosomal location with a QTL against

net blotch detected in the same barley population as the one used in this study (15) (Fig. 1). Thus, the actual numbers of syntenic QTL in the rice and barley genomes may be larger than that detected in this study if QTL for resistance to more pathogens are compared. Such likely syntenic distributions of QTL seem to be different from that of *R*-gene homologues that were reported to occur frequently in nonsyntenic map locations in rice and barley (37), although the causes for such differences can only be speculated on at present.

When the locations of the QTL detected in the present study were compared with previous mapping results of other diseases, it is interesting to note that many of the QTL, including two isolate-specific QTL (*rbr3* and *rbr7b*), appeared to reside in the same genomic regions as the ones detected in previous studies. For example, four QTL, *rbr1a*, *rbr1c*, *rbr7b*, and *rbr8*, had similar locations with four of the 10 QTL against the *P. grisea* isolate PO6–6 in rice (10). Two QTL, *rbr2* and *rbr8*, coincided with two of the seven QTL against rice sheath blight in chromosomal locations (11). The locations of two QTL, *rbr1d* and *rbr9c*, corresponded well with two of the seven QTL against rice yellow mottle virus (12). Four QTL, *rbr2*, *rbr3*, *rbr8*, and *rbr9c*, showed location coincidence with four of the 10 QTL for bacterial blight resistance (13). Similar situation also occurred in barley. For example, three of the QTL identified in the present study, *bbr4Ha*, *bbr4Hb*, and *bbr5Hb*, appeared to have the same chromosomal locations as three of the four QTL against isolate Ken 54-20 of *P. grisea* identified by Sato *et al.* (23) using the same barley population. Three of the QTL identified in the present study also had corresponding chromosomal locations with some of the QTL identified by Spaner *et al.* (15) who mapped QTL for resistance to five barley diseases also using this population. For instance, *bbr2H* coincided with one of the three QTL against leaf rust, *bbr4Ha* coincided with one of the two QTL against powdery mildew, and *bbr5Hb* coincided with one of the three QTL against leaf rust and one of the five QTL against net blotch. In addition, one QTL, *bbr7Hc*, identified in this study also had corresponding chromosomal location with one of the QTL against leaf stripe detected in a different barley population (38). The location correspondence of QTL detected for resistance to various diseases suggest that some of the genes underlying QTL are commonly involved in the defense response again pathogens. This is consistent with the finding that monocots share at least certain common pathways in systemic acquired resistance, as in the case of inducing systemic acquired resistance to powdery mildew in barley (39) and blast in rice (40) by the inducing compound, benzothiadiazole.

The results also shed light on the mechanism of partial resistance commonly occurring in plant response to pathogens. For long, it has been believed that complete resistance governed by major genes is race specific, whereas partial resistance acts in race-nonspecific manner. However, results from the present study showed that about half of the QTL detected in the rice population and more than half of the QTL detected in barley population were effective to only one of the three blast isolates, clearly indicating race specificity of the QTL. Similar results were also reported in other host-pathogen systems. For example, Geffroy *et al.* (41) reported that eight of 10 QTL detected for resistance to anthracnose in common bean showed race specificity. Thus, clearly a different explanation for the apparent race nonspecificity of quantitative resistance is indicated, and a hypothesis concerning the durability of the quantitative resistance can be tentatively formulated as follows based on the results of QTL analyses: The overall resistance to a pathogen involved a large number of QTL. For each of the races (isolates) there is a subset of QTL that is active against the infection. Therefore, for most, if not all, of the host-pathogen systems, there would be certain degrees of quantitative resistance caused by the effects conferred by the subsets of QTL.

In summary, the results revealed several important features of quantitative resistance against *P. grisea* between rice and barley. Some of the genes for quantitative resistance appear to locate in syntenic positions between the two grasses. Some of the genes underlying QTL may be commonly involved in the defense responses against a broad range of pathogen infections and others may be only involved in limited defense responses thus showing certain degrees of race specificity. The syntenic relations may have utility in gene discovery, understanding the function of the genomes, and identifying the evolutionary forces that structured the organization of the grass genomes.

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