

Syntenic Relationship of Loci for Quantitative Resistance to *Pyricularia grisea* in Rice and Barley

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ABSTRACT

Rice blast (*Pyricularia grisea*) is one of the most severe diseases of rice. A Baronesse/BCD47 DH barley population was used to determine the location of the blast resistance quantitative trait loci (QTL) with different sources of blast pathogens (TH16, THL80, THL142 and THL222). Baronesse was highly resistant, whereas BCD47 was susceptible. The QTL mapped to the same linkage map position on chromosome 1H as the powdery mildew resistance locus *Mla* and an Expressed Sequence Tag (EST) k04320 corresponding to the barley gene 711N16.16 was obtained. Syntenic analysis corresponded to a region on rice chromosome 5. This region, including the bacterial blight resistance gene *xa5*, was demonstrated. These results indicated that a defined region on the short arm of the barley chromosome 1H contains genes conferring quantitative resistance to multiple pathogen isolates.

Keywords: *Pyricularia grisea*, quantitative, syteny, barley, blast

INTRODUCTION

Rice blast, caused by *Pyricularia grisea* Sacc. (Chen *et al.*, 2003), is one of the most severe diseases of rice (*Oryza sativa*). The blast fungal pathogen is also infective to several grasses including barley (*Hordeum vulgare*) (Matsumoto and Mogi, 1979; Kawai *et al.*, 1997; Sato *et al.*, 2001; Inukai *et al.*, 2006), wheat (*Triticum aestivum*) (Urashima *et al.*, 2004) and ryegrass (*Lolium perene*, and *L. multiflorum*) (Williams *et al.*, 2001; Miura *et al.*, 2005). Although reports on blast resistance in these grass species are

limited, it appears that some of these species possess qualitative and/or quantitative resistance genes to the blast fungus.

In barley, Yaegashi (1988) identified a single dominant gene (*PHR-1*) conferring resistance to a barley blast fungus in the F₂ progenies of the resistant cultivars ('Daisen Gold' and 'Miho Golden') crossed with susceptible varieties. Recent studies have indicated that the barley experimental line TR306 carried quantitative trait loci (QTL) alleles for resistance to rice blast (Sato *et al.*, 2001; Chen *et al.*, 2003). Inukai *et al.* (2006) also reported that the barley

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cv. Baronesse was completely resistant to a rice blast pathogen isolate (Ken 54-20) and the resistance was controlled by a single dominant gene *RM01*.

Plant disease-resistant genes often belong to a large cluster that occurs in particular chromosomal regions. Recently, the development of molecular marker techniques has generated considerable interest in identifying loci involved in quantitative disease resistance in cereals. In rice, a large number of QTL for resistance to various diseases (such as blast, sheath blight, bacterial blight and yellow mottle virus) have been identified (Wang *et al.*, 1994; Li *et al.*, 1995; 1999). However, it is not known if the genes controlling resistance to various diseases have any relationship with different members of the grass family. Wisser *et al.* (2005) identified several chromosomal segments associated with both qualitative and quantitative resistance to multiple pathogens. According to the integrated map of these disease resistance genes in rice, blast resistance QTL are often co-localized with blast resistance *Pi* loci and/or QTL for resistance to other pathogens causing diseases (such as sheath rot, sheath blight and bacterial blight). Resistance gene analogs (RGAs) of the nucleotide-binding site-leucine-rich repeat (NBS-LRR) class have been known also to co-localize with the cluster of *Pi* loci and blast resistance QTL. In barley, clustering of major resistance genes and resistance QTL has been reported (Williams, 2003) also. This suggests that these R (resistance) genes could be candidates for major genes and QTL (Wisser *et al.*, 2005).

Vales *et al.* (2005) and Rossi *et al.* (2006) have mapped quantitative and qualitative genes conferring resistance to multiple pathogens in a doubled haploid (DH) mapping population of barley derived from the cross of Baronesse/BCD47. In an ongoing screen of barley germplasm for blast resistance, Inukai *et al.* (2006) found Baronesse and BCD47 varieties showed qualitative and/or quantitative resistance to two

Japanese rice blast isolates. In order to identify these blast resistance genes and to determine their linkage relationships with previously mapped resistance genes, the same population was used to determine the location of the blast resistance genes in Baronesse and BCD47 varieties with different sources of the blast pathogens. By using the available mapped barley Expressed Sequence Tag (EST) markers, mapping would be extended to rice in order to determine if there is synteny between blast resistance genes in the two species in this study, in which four blast fungal isolates were used in blast disease inoculation. The objective of the present study was 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

Plant materials

The barley Oregon Resistance Opportunity (ORO) mapping population (Baronesse/BCD47 DH population) consisted of 94 doubled-haploid (DH) lines developed from the F₁ of the cross between Baronesse and BCD47. BCD47 is a two-rowed, spring growth habit DH line, developed via marker-assisted selection for barley stripe rust resistance alleles at QTL on chromosome 4H and 5H (Castro *et al.*, 2003). Baronesse is a two-rowed, spring growth habit cultivar developed by Nordsaat and released in Germany in 1989. The cultivar is grown extensively in the Pacific Northwest of the USA. IR64 and Azucena, used as susceptible controls or check cultivars of rice, were obtained from the Philippines. The seedlings of the barley DH lines, their parents and two blast susceptible rice cultivars were used in the inoculation of four blast pathogen isolates.

Blast pathogen (*Pyricularia grisea*) isolates

Four fungal isolates (TH16 and THL80, from Khon Kaen, Thailand; and THL142 and THL222, from Chiang Mai, Thailand) were used. TH16 and THL80 were obtained from barley, and THL142 and THL222 were obtained from rice. Additional detail on these isolates may be obtained from Dr Pattama Sirithunya, Lampang Agriculture Research and Training Center (LARTC), Muang Lampang 52000, Thailand. The isolates were grown on polished rice agar medium (20 g of polished rice, 2 g of yeast extract and 20 g of agar/L distilled water) at 24-25°C and a 12-hour photoperiod for 7-8 d. Spores were harvested by flooding the culture plates with 8 mL of sterile water.

Pathogen (disease) inoculation and disease scoring (DS)

For disease phenotyping in the ORO mapping population, barley plants (seedlings) and related plants for testing reaction to fungal isolates were grown in a greenhouse (25-30°C continuous temperature and natural light) in 72-well plastic trays with dimensions of 25.4 × 50.8 cm. In each well, three seeds of each DH line were sown. Two trays were needed to test the entire set of 94 DH lines, 50 in one tray and 44 in the other. Each tray also included three replicates for each of the two parents (BCD47 and Baronesse) and the two susceptible check cultivars of rice (IR64 and Azucena). Four sets of experiments were performed to test the response to the four pathogen isolates (TH16, THL80, THL142 and THL222). Each experiment was replicated four times. A commercial liquid fertilizer (16-16-16 of N-P₂O₅-K₂O) at the rate of 20 g/tray was applied weekly. Additional nitrogen in the form of urea was applied at the rate of 10 g/tray for the mapping population at 10, 3 and 1 d prior to disease or pathogen inoculation in order to increase host susceptibility to blast.

Seedlings were inoculated at the 1-2 leaf

stage with each of the four isolates using 50 ml of 50,000 spore mL⁻¹ suspension supplemented with 0.5% gelatin. Each tray of inoculated plants was then kept for one night in a controlled environment chamber at 24°C with near-saturation conditions for relative humidity. Trays were then returned to the greenhouse, which was kept at a continuous temperature of 25-30°C with natural light. Then, 3, 5 and 7 d after pathogen inoculation, plant reaction or disease lesion types were scored using the seven lesion-type categories or scaling (0 = resistant, 1- 3 = intermediate and 4 - 6 = susceptible) described by Roumen *et al.* (1992). Disease severity was scored at 7 d on a per-well basis after inoculation and used as a phenotypic value for subsequent analyses.

Statistical, QTL and sequence analysis

Statistics

Pearson correlation coefficients between traits and the significance of these correlations were estimated, using the CORR procedure of SAS V9.1 (SAS Institute, Cary, NC, USA). The variance components were estimated using the VARCOMP procedure of SAS V9.1, with the restricted maximum likelihood method according to the model (Equation 1):

$$Y_{ij} = \mu + E_i + R_{j(i)} + G_k + GE_{ik} + \varepsilon_{ijk} \quad (1)$$

where Y_{ij} = the infection score of the k th genotype (G) in the j th replicate (R) within the i th experiment or set of pathogen (E); GE_{ik} = the interaction (or deviation of G_i in E_j) between G and E; μ = the overall mean; and ε_{ijk} = the residual error.

Experiments were considered as fixed effects; genotype and replicates were considered as random effects. Heritabilities (h^2) were calculated using the formula (Equation 2):

$$h^2 = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2 / e + \sigma_e^2 / re} \quad (2)$$

where σ_G^2 = the genotypic variance; σ_{GE}^2 = the genotype-by-experiment or set of pathogen

variance; σ_e^2 = the error variance; e = the number of experiments or pathogens; and r = the number of replicates.

Broad sense heritability on an entry mean basis was calculated with $e=4$ and $r=8$.

Linkage map

The genotypic data for the Baronesse/BCD47 DH lines has been evaluated and reported by Rossi *et al.* (2006) for resistance genes in Peru. Linkage map construction was performed using JoinMap 3.0 (Van Ooijen and Voorrips, 2001) with a Kosambi mapping function (Kosambi, 1994). The linkage map had 70 markers, comprising eleven linkage groups at a logarithm of the odds (LOD) threshold grouping value of 4.0. Linkage groups were assigned to barley chromosomes by Rossi *et al.* (2006). The map covered 611.8 centimorgan (cM), corresponding to an average density of 8.7 cM per marker.

QTL

QTL analysis was performed using composite interval mapping (CIM) (Zeng, 1994) implemented in Windows QTL Cartographer 2.5 (Wang *et al.*, 2005). Cofactors for CIM were chosen, using a forward-selection and backward-elimination stepwise regression procedure with a significance threshold of 0.10 ($\alpha = 0.001$). The maximum number of cofactors used was six. The scan window was set at 10 cM. Set or experiment-wise significance ($\alpha = 0.05$) likelihood ratio test (LR) thresholds for QTL identification were determined with 1,000 permutations and expressed as a logarithm (base 10) of odds (LOD) (LOD = 0.217 LR). For every significant QTL, the individual R^2 (proportion of phenotypic variance explained by the individual QTL) and additive effect (expressed as one-half of the difference between the two allelic classes) were calculated. Negative values indicated that the parent line contributing the resistance allele was Baronesse. Epistatic interactions between QTL were tested by means of multiple interval mapping (MIM) (Zeng

et al., 1999) using QTL Cartographer and the Bayesian Information Criteria (BIC-M0). In each experiment or set, the R^2 was also calculated for the multilocus model that included the QTL detected using CIM and their significant interactions detected using MIM. The average TR^2 (the proportion of the variance explained by the QTL conditioned on the cofactors in CIM obtained with EQTL (QTL Cartographer v. 2.5)) was also calculated.

RESULTS AND DISCUSSION

Pyricularia grisea phenotyping

The parents, Baronesse and BCD47 varieties, had contrasting disease reactions to blast disease or pathogen inoculation with each of the four pathogen isolates used. Overall, Baronesse varied from high to intermediate levels of resistance, whereas BCD47 was susceptible (Figure 1.) (Kongprakhon *et al.*, 2009). The phenotypic or disease score frequency distributions did not provide evidence for Mendelian inheritance of resistance. The lack of discrete classes was not due to errors in scoring; the h^2 of disease severities or scores was 86%. Significant positive and negative phenotypic transgressive segregation was more prevalent. Inoculation with THL222 (from rice in Chiang Mai, Thailand) gave somewhat different results from inoculation with the other isolates. Based on phenotype, if the same or different genes determined resistance to the four isolates, correlation coefficients between any two sets/experiments of disease severities (DS) in response to inoculation with the four isolates would indicate good correlation of DS sets or experiments (Table 1). The correlation coefficients for pair-wise comparisons were significant and high with P-values mostly at 0.1% ($\alpha = 0.001$). This implies multiple resistances of the tested Baronesse/BCD47 DH population or DH lines to the four blast pathogen isolates used.

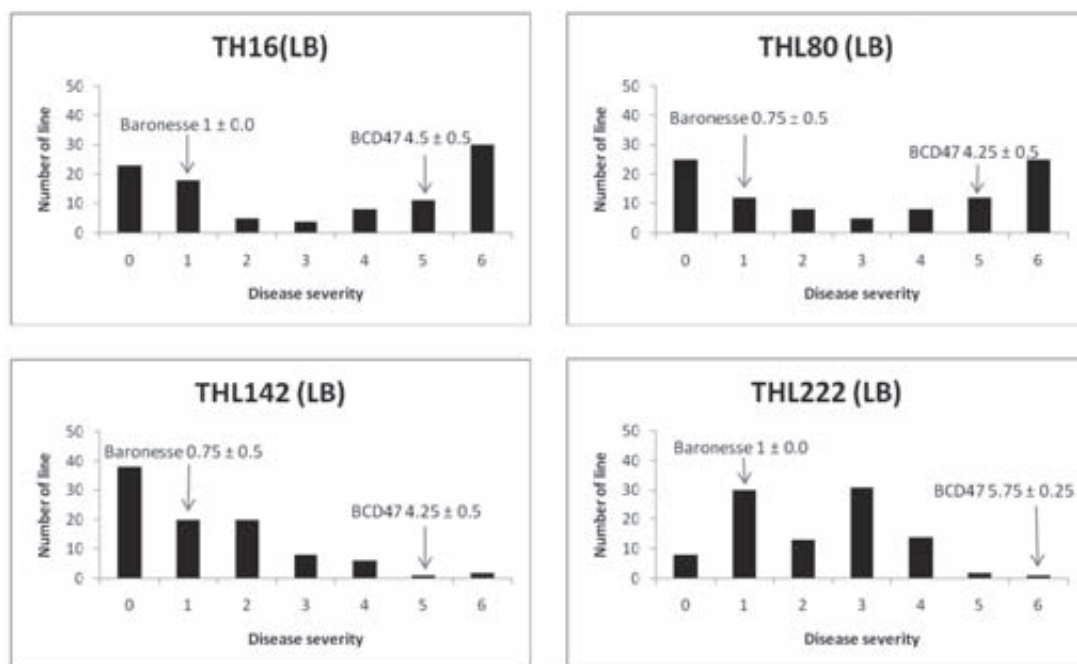


Figure 1 Phenotypic frequency distributions of disease severity (DS) for the reaction to four blast isolates [TH16(LB), THL80(LB), THL142(LB) and THL222(LB)]. (0 = resistant, 1- 3 = intermediate and 4 - 6 = susceptible) (Kongprakhon *et al.*, 2009).

Table 1 Pearson phenotypic correlation coefficients between disease scores observed in the ORO (Baronesse/BCD47 DH) mapping population inoculated with four blast isolates (TH16, THL80, THL142, and THL222) (Kongprakhon *et al.*, 2009).

	THL80	THL142	THL222
TH16	0.87 ***	0.64 ***	0.68 ***
THL80		0.68 ***	0.73 ***
THL142			0.73 ***

*** Significant at 0.1% level

QTL for resistance in Baronesse and ORO population

The number, allele phase and interaction of the leaf blast (LB) resistance QTL identified in response to inoculation with each of the four isolates are presented in Table 2 and Figure 2. The QTL on barley chromosomes 1H and 4H had LOD scores ranging from 2.9 to 27.0 (Table 2). Baronesse contributed resistance alleles at the QTL on the chromosome 1H. BCD47 contributed the resistance allele at the QTL on chromosome 4H.

The QTL on barley chromosome 1H (k04435 – Bmac399) was associated with resistance to all four blast pathogen isolates (Figure 2). Alleles at this QTL determined 65%, 69%, 51% and 71% of the phenotypic variance in resistance to TH16, THL80, THL142 and THL222, respectively. For each isolate, the QTL peak was located on marker M1ax (Figure 3). This marker was designed, based on the published sequence of *Mla7*, a gene that confers resistance to powdery mildew (*Blumeria graminis* f. sp. *hordei*) (Inukai

Table 2 Resistance QTL to blast isolates (TH16, THL80, THL142 and THL222) were QTL number 1 located on chromosome 1H and QTL numbers 2 and 3 located on chromosome 4H detected in the Baronesse/BCD47 DH population using composite interval mapping (Kongprakhon *et al.*, 2009).

QTL No.	Chromosome	Peak position (2 LOD conf. interval)	Closet marker	LOD	Additive effect	R ²	LOD threshold
TH16 (LB)							
1	1H	9.1 (0.2-48.8)	GMS21	22.4	1.7	0.65	2.5
THL80 (LB)							
1	1H	9.1 (0.1-50.6)	GMS21	26.5	2.0	0.69	2.6
THL142 (LB)							
1	1H	9.1 (2.0-44.9)	GMS21	15.8	1.1	0.51	2.4
THL222 (LB)							
1	1H	9.1 (1.4-50.6)	GMS21	27.0	1.2	0.71	
2	4H	44.6 (36.6-54.6)	Bmac030B	5.6	-0.4	0.06	
3	4H	105.3 (89.6-116.9)	k03352	2.9	-0.2	0.03	2.5

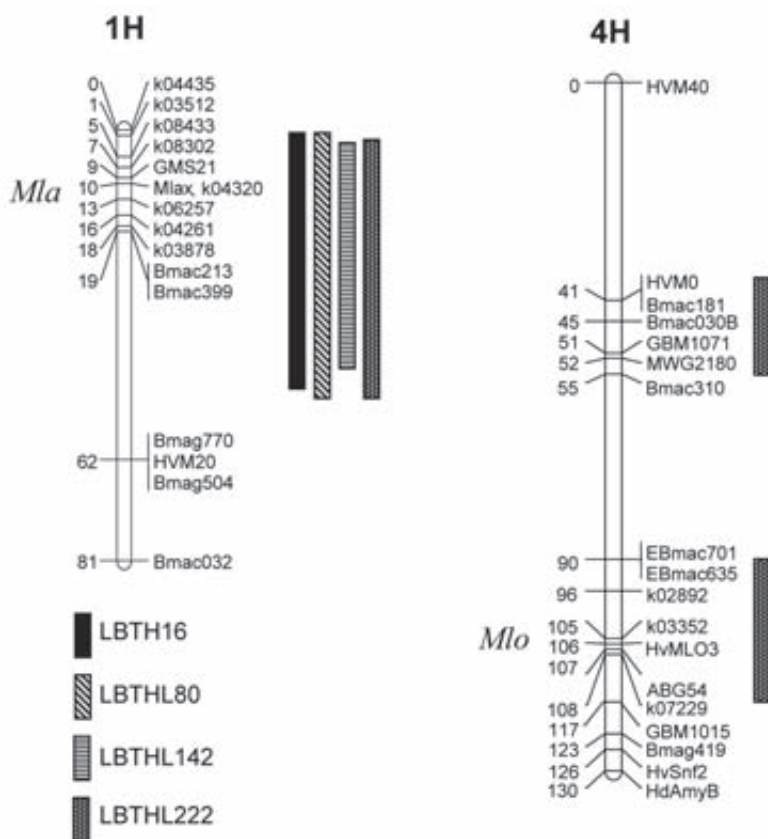


Figure 2 Linkage maps of barley chromosomes 1H and 4H in the Baronesse/ BCD47 mapping population. Distances are in Kosambi cM. The bars to the right of each linkage group indicate the 2-LOD confidence intervals for the blast resistance QTL detected in response to inoculation with each of four isolates (TH16, THL80, THL142, and THL222).

et al., 2006). Mlax also co-segregated with the EST marker, k04320. Inukai *et al.* (2006) designated the race-specific resistance gene in Baronesse to rice blast isolates, which co-segregated with Mlax and k04320 as *RMo1* (Resistance to *Magnaporthe oryzae* 1). A blast homology search of the marker k04320 displayed a similarity to the barley gene 711N16.16 (e-value = 0), which was reported to be 190 kb from *Mla* (Wei *et al.*, 2002). This established the position of Mlax and k04320 as

lying within, or near, the *Mla* - 711N16.16 interval. Baronesse was also reported to carry the *Mla3* resistance gene, based on its reaction to inoculation with differential isolates (Hovmøller *et al.*, 2000; Dreiseitl, 2003). *Mla7* and *Mla3* are members of the *Mla* complex locus, and *RMo1* co-segregates with *Mla*, based on linkage data (Inukai *et al.*, 2006). Two resistance QTL on barley chromosome 4H (HVMO-Bmac030B and EBmac701-k07229) were identified with isolate THL222 (Table 2 and

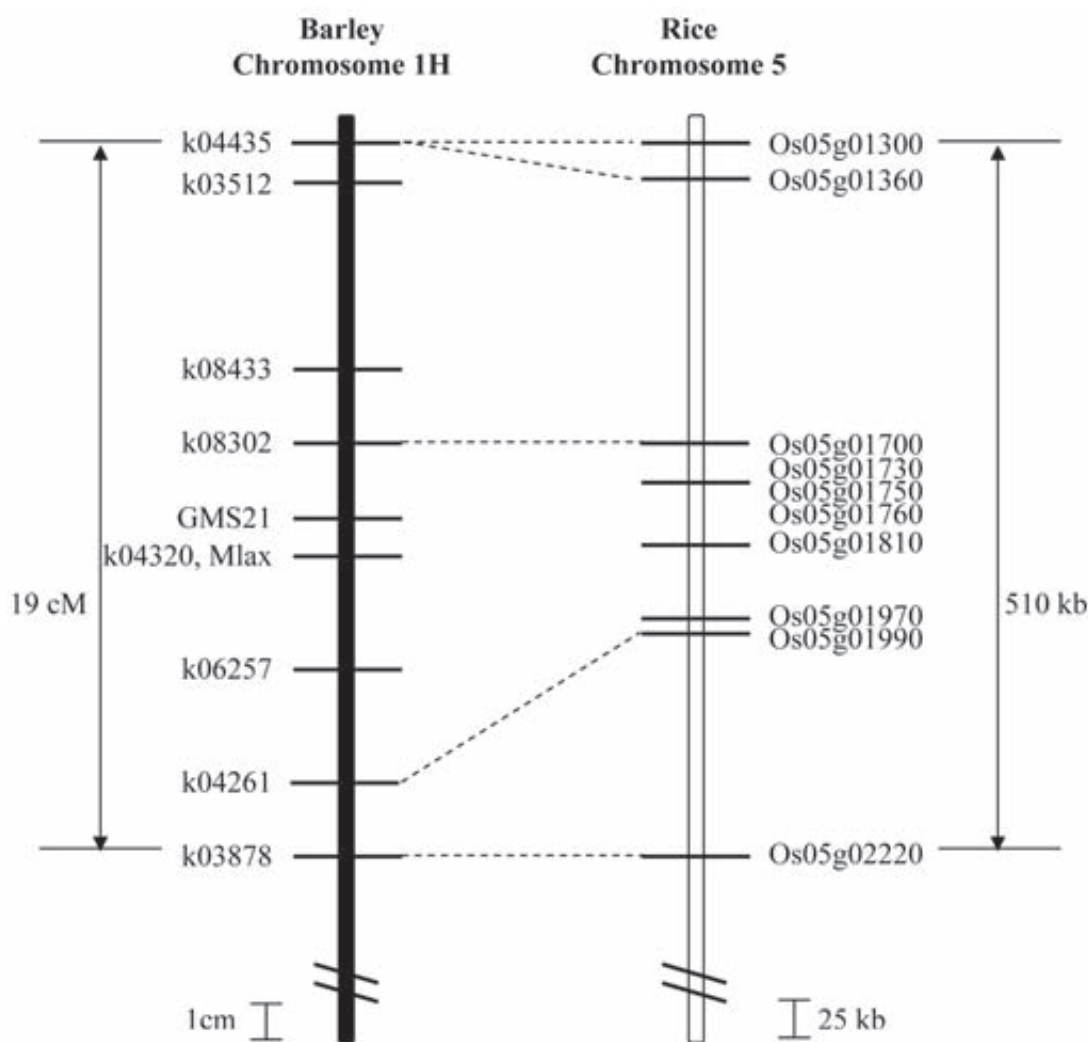


Figure 3 Schematic drawing of barley chromosome 1H and the subtelomeric region of rice chromosome 5 indicating the syntenic region. The genetic map of barley chromosome 1H and the physical map of rice chromosome 5 are aligned. In the barley genetic map, the k-loci are barley EST-based markers.

Table 3 Candidate NBS-LRR and defense genes in the syntenous regions in rice (summarized from the TIGR rice genome database).

Gene	Protein
LOC_Os05g01300	CHCH domain containing protein, expressed
LOC_Os05g01360	Expressed protein
LOC_Os05g01700	PXA1, putative, expressed
LOC_Os05g01710	TFIIA gamma chain, putative, expressed
LOC_Os05g01720	Hypothetical protein
LOC_Os05g01730	Drought induced 19 protein (Di19)
LOC_Os05g01750	tRNA pseudouridine synthase B
LOC_Os05g01990	ATP binding protein, putative, expressed
LOC_Os05g02220	Amino acid binding protein, putative, expressed

Figure 2). These two QTL accounted for 6 and 3% of the phenotypic variance in DS, respectively. BCD47 contributed a moderate resistance allele at both QTL. As observed in prior reports, at each of the genomic regions where LB and/or NB QTL were observed, there have been prior reports of *R* genes and/or QTL forming resistance gene clusters at each of the four genomic regions (Sato *et al.*, 2001; Chen *et al.*, 2003; Inukai *et al.*, 2006; Kongprakhon *et al.*, 2009).

Synteny

In order to establish a basis for the comparison of synteny with rice, based on the TIGR Rice Genome Annotation database, the above mentioned information on QTL was used to explore the syntenous region in rice. Four barley EST markers in the vicinity of M_{lax} (on barley chromosome 1H) had high homology to sequences on rice chromosome 5 (Figure 3). There was co-linearity of gene order between the 19 cM region extending from k04435 to k03878 in barley chromosome 1H and the 510 kb region from the gene Os05g01300 to Os05g02220 at the end of short arm of rice chromosome 5 (Figure 3). According to the annotation data in the TIGR rice genome database, this region contains one NBS-LRR gene and eight genes for proteins commonly induced in defense reactions (Table 3): a bacterial blight resistance gene *xa5* (Os05g01710), which

encodes the gamma subunit of transcription factor IIA (TFIIA γ) (Iyer and McCouch, 2004). TFIIA, a component of the RNA polymerase II holoenzyme complex, facilitates binding of the polymerase to the TATA-box binding protein (Gill, 2001). Although none of the basal transcription factors (such as TFIIa) is known to be involved in disease response, they have been shown to be targets of signal transduction pathways that regulate genome expression in other eukaryotic organisms.

The results of the current study should validate those of Inukai *et al.* (2006) in terms of location and effects of leaf blast resistance QTL in the barley Baronesse/BCD 47 DH population. The results should be extended to show that these QTL conferring resistance to blast pathogen isolates were obtained from rice and barley in Thailand. The barley cultivar Baronesse showed nearly complete and race-specific resistance to the rice blast fungus. The resistance QTL co-segregates with *Mla* and 711N16.16, which is approximately 190kb from *Mla*, according to Wei *et al.* (2002), who reported that 15 of the 32 predicted genes in the 261 kb region sequenced around *Mla* were associated with defense responses to pathogens.

Co-linearity of gene order between a 19 cM region of barley chromosome 1H containing *Mla* and a 510 kb region at the end of rice

chromosome 5 was established. The rice 510 kb syntenous region contains the bacterial blight resistance gene *xa5*. According to one of the models proposed by Iyer and McCouch (2004), TFIIA (the product of *xa5*) functions as a virulence target via interaction with the Avrxa5 protein. The complex of the two molecules is then detected by a third factor, such as an R (resistance) gene, and this initiates a signaling pathway that leads to bacterial blight resistance. A similar scenario, which is based on the 'guard hypothesis' can be applied to the case of *Mla*. However, since no barley ortholog of *xa5* was detected in the published 261 kb sequence of the short arm of barley chromosome 1H, additional experiments of pathogen isolates will be needed to determine the candidacy of this gene for *RMo1*. An ortholog is sequences of genes that have evolved from a common ancestor and can be traced evolutionarily through different species. By comparing the ortholog sequences of a specific gene among many species, the amino acid sequences, which are conserved, can be determined. These highly conserved sequences are important because they provide information on which amino acids are essential to protein structure and function.

Four blast resistance QTL were identified in the ORO population. Interestingly, the largest-effect QTL, contributed from Baronesse, was detected at the same position as *Mla*. *Mla* is a CC-NBS-LRR R gene; it is co-located with other R (resistance) gene family members and with *RMo1* (Inukai *et al.*, 2006). Blast resistance major genes, QTL and NBS-LRR R gene clusters have been reported in rice also (Wisser *et al.*, 2005). Thus, members of the NBS-LRR R gene cluster could differentiate as major genes and as QTL alleles for blast resistance.

Usefulness

Information on the blast resistance genes in barley is not currently of economic importance because barley is usually not cultivated in rotation

with rice nor in the moist or wet, warm conditions conducive to blast disease development. However, if the area planted with barley expands, or shifts in response to global warming or other factors, the location and linkage relationships of these genes could be of significant importance. Likewise, information on these genes could be of value to rice breeders and geneticists.

CONCLUSION

QTL analyses using the Baronesse/BCD47 DH barley population were performed based on the greatest value of DS for blast isolates, TH16, THL80, THL142 and THL222. One QTL was identified from each isolate; the QTL peak position of all isolates fell in the marker interval from k04435 to Bmac399 on barley chromosome 1H. This QTL had the largest effect. The QTL peaks corresponded to the Sequence Tagged Site (STS) marker M1ax, which confers resistance to barley powdery mildew. Two resistance QTL on chromosome 4H (HVMO3-Bmac030B and EBmac701-k07229) were identified with isolate THL222. HVMO3-Bmac030B and EBmac701-k07229 accounted for 6 and 3% of the phenotypic variance in DS, respectively, and BCD47 contributed the resistance allele at both QTL.

Co-linearity of gene order between a 19.0 cM region of barley chromosome 1H containing *Mla* and a 510 kb region at the end of the short arm of rice chromosome 5 was established. It was determined that the 510 kb syntenous region contains the bacterial blight resistance gene *xa5* and that TFIIA, the product of *xa5*, functions as a virulence target via interaction with the Avrxa5 protein.

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