

Molecular mapping of *Rym17*, a dominant and *rym18* a recessive barley yellow mosaic virus (BaYMV) resistance genes derived from *Hordeum vulgare* L.

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Abstract PK23-2, a line of six-rowed barley (*Hordeum vulgare* L.) originating from Pakistan, has resistance to Japanese strains I and III of the barley yellow mosaic virus (BaYMV). To identify the source of resistance in this line, reciprocal crosses were made between the susceptible cultivar Daisen-gold and PK23-2. Genetic analyses in the F₁ generation, F₂ generation, and a doubled haploid population (DH45) derived from the F₁ revealed that PK23-2 harbors one dominant and one recessive resistance genes. A linkage map was constructed using 61 lines of DH45 and 127 DNA markers; this map covered 1268.8 cM in 10 linkage groups. One QTL having a LOD score of 4.07 and explaining 26.8% of the phenotypic variance explained (PVE) for resistance to BaYMV was detected at DNA marker ABG070 on chromosome 3H. Another QTL having a LOD score of 3.53 and PVE of 27.2% was located at marker Bmag0490 on chromosome 4H. The resistance gene on chromosome 3H, here named *Rym17*, showed dominant inheritance, whereas the gene on chromosome 4H, here named *rym18*, showed recessive inheritance in F₁ populations derived from crosses between several resistant lines of DH45 and Daisen-gold. The BaYMV recessive resistance genes *rym1*, *rym3*, and *rym5*, found in Japanese barley germplasm, were not allelic to *rym18*. These results revealed that PK23-2 harbors two previously unidentified

resistance genes, *Rym17* on 3H and *rym18* on 4H; *Rym17* is the first dominant BaYMV resistance gene to be identified in primary gene pool. These new genes, particularly dominant *Rym17*, represent a potentially valuable genetic resource against BaYMV disease.

Introduction

Barley yellow mosaic virus (BaYMV) causes severe disease in barley (*Hordeum vulgare* L.) in Asia and Europe. BaYMV is transmitted to barley roots through infection by the soil-borne fungus *Polymyxa graminis* during the winter, and it causes mosaic symptoms on growing leaves the following spring (Toyama and Kusaba 1970). To overcome this disease in fields contaminated with BaYMV, introduction of resistance into barley cultivars is the most efficient and economical procedure. At present, 14 resistance genes derived from *H. vulgare* and two dominant genes from *Hordeum bulbosum* have been reported. These resistance genes have been localized on chromosomes 1H (*rym7*), 2H (*Rym16^{Hb}*), 3H (*rym4*, 5, 6, and 10), 4H (*rym1*, 8, 9, 11, 12, and 13), 5H (*rym3*), 6H (*rym15* and *Rym14^{Hb}*), and 7H (*rym2*) by genetic and molecular analyses (Ukai and Yamashita 1980; Graner and Bauer 1993; Ordon and Friedt 1993; Graner et al. 1995, 1999; Bauer et al. 1997; Konishi et al. 1997; Iida et al. 1999; Ruge et al. 2003; Werner et al. 2003; Le Gouis et al. 2004; Ruge-Wehling et al. 2006).

In Europe, BaYMV, BaYMV-2, and barley mild mosaic virus (BaMMV) cause disease in susceptible winter barley cultivars. Resistance in European winter barley cultivars is conferred by the resistance genes *rym4* and *rym5*. In Japan, BaYMV has differentiated into distinct strains, designated Japanese strains I to V (Kashiwazaki et al. 1989; Sotome et al. 2010). Modern Japanese resistant cultivars have been

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bred to contain recessive resistance genes *rym5*, effective against Japanese strains I, II, IV and V, and *rym3*, effective against strains I, II and III. Cultivars harboring both *rym3* and *rym5* are resistant to all strains of BaYMV currently identified in Japan. However, in general, viruses such as BaYMV undergo frequent genome rearrangement, enabling them to defeat resistance genes in the host (Sotome et al. 2010). To address this threat, it is necessary to identify and introduce new resistance genes or to pyramid three or more of the existing resistance genes in breeding programs.

In the past, we collected wild barley (*Hordeum vulgare* L.) originating from Pakistan, and one of them was established as a line, PK23-2, by pure-line selection. We investigated the resistance of PK23-2 and revealed that PK23-2 harbored novel BaYMV resistance genes. Furthermore, PK23-2 appeared to contain at least one dominant resistance gene (Furusho et al. 2002). Here, we evaluated the resistance of PK23-2 and several types of progeny populations, including doubled haploid lines, and we investigated the inheritance of resistance by a molecular approach to identify genetic resources for use in barley breeding programs.

Materials and methods

Plant material

PK23-2, a six-rowed accession of *H. vulgare* from Pakistan, was established by pure-line selection (Furusho et al. 1997). Daisen-gold is a two-rowed cultivar of *H. vulgare* that is susceptible to all known Japanese strains (I–V) of BaYMV. To perform segregation analysis, F₁ and F₂ populations were bred from reciprocal crosses between Daisen-gold and PK23-2, and a set of doubled haploid lines (DH45) was produced from the F₁ by the Hordeum bulbosum method (Furusho et al. 1990). To test for dominance of the resistance genes in PK23-2, we chose seven resistant DH45 lines (DH45-1, -10, -63, -67, -68, -69, and -72) based on heading stage for cross with Daisen-gold. F₁ populations were produced by making crosses between each resistant DH45 line and Daisen-gold. Moreover, to classify the recessive resistance gene discovered in PK23-2 (see Results), a genetic complementation test was performed using crosses between DH lines containing only the recessive resistance gene and two-rowed barley materials containing known resistance genes to Japanese strains I, II and III of BaYMV: Chikukei ym1-1 (*rym1*, 4H), Harushizuku (*rym3*, 5H).

Evaluation of resistance to BaYMV

The parental lines PK23-2 and Daisen-gold were sown each year from 2006 to 2010. The F₁ and F₂ populations were

sown in 2006, and the corresponding F₃ population was sown in 2007. The DH45 lines were sown each growing season from 2008 to 2010. F₁ populations from each resistant DH45 line (DH45-1, -10, -63, -67, -68, -69, and -72) and Daisen-gold were sown to clarify the dominance in the resistance genes in 2010. Among four DH lines (DH45-10, -63, -67 and -69) carried only the recessive resistance gene, each DH45-63 and -69 and two barley materials containing known resistance genes were crossed and the obtained F₁ progenies were sown to test for allelism to known recessive resistance genes in 2010. These plant materials were sown in early November of each year and evaluated the following year. For PK23-2, Daisen-gold, each F₁ and 61 lines of DH45, ten seedlings were scored in each year of evaluation. For F₂ population, 106 individuals of the F₂ were scored in 2007 of evaluation. The test field was contaminated with BaYMV Japanese strains I and III. Individual plants were scored as resistant or susceptible to BaYMV based on mosaic symptoms on the leaves; scoring was performed every 9–10 days (three times) during the reproductive stage. Plants showing mosaic symptoms at any of the three scoring times were scored as susceptible. Evaluations of resistance to BaYMV in 61 lines of DH45 were performed for 3 years. The presence of the virus was confirmed using the DAS-ELISA method (Usugi et al. 1984) when the symptoms were not unequivocal.

DNA extraction and QTL analysis for BaYMV resistance genes

The linkage map construction and QTL analysis were performed by using the 61 lines of the DH45 population. For dominance analysis of the resistance genes in PK23-2, we investigated graphical genotypes of seven resistant DH45 lines (DH45-1, -10, -63, -67, -68, -69, and -72). Genomic DNA was extracted from young leaves by using a DNeasy Plant Mini Kit (QIAGEN, Japan) according to the manufacturer's protocol. Simple sequence repeat (SSR) markers (Ramsay et al. 2000) and sequence tagged site (STS) markers (Blake et al. 1996; Mano et al. 1999) were selected and designed to construct the linkage map and detect QTLs for resistance to BaYMV. When polymorphisms could not be detected using STS markers, the PCR products were digested with 11 endonucleases (*AccII*, *AluI*, *AvaII*, *Csp6I*, *HaeIII*, *HinfI*, *Hinf6I*, *MboI*, *MnlI*, *MspI* and *TruI*) to generate cleaved amplified polymorphic sequence (CAPS) markers. PCR amplifications were done in a final volume of 15 µL, each containing 0.5 units of *Taq* polymerase (TaKaRa, Japan); 0.3 µM of each primer, 250 µM of dNTPs, 1 × buffer supplied with the polymerase, and 50 ng genomic DNA. PCR amplification conditions for SSR markers were 5 min at 95°C; followed by 35 cycles of 1 min at 95°C, 1 min at 55°C, and 1 min at 72°C; followed

Table 1 Response to BaYMV of F₁, F₂, and doubled haploid (DH) lines derived from crosses between Daisen-gold and PK23-2

Crossing parent		Generation	Number	Observed number ^a		Expected number ^b		χ^2 value	P value
♀	♂			Resistant	Susceptible	Resistant	Susceptible		
PK23-2	–	P	10	10	0	–	–	–	–
Daisen-gold	–	P	10	0	10	–	–	–	–
PK23-2	Daisen-gold	F ₁	10	10	0	–	–	–	–
Daisen-gold	PK23-2	F ₁	10	10	0	–	–	–	–
Daisen-gold	PK23-2	F ₂	106	90	16	13	3	0.93	0.33
						3	1	5.55	0.02
Daisen-gold	PK23-2	H ^c	61 ^d	47 ^d	14 ^d	3	1	0.14	0.71
						1	1	17.85	0.00
						7	1	6.09	0.01

^a Evaluation performed in test field contaminated with Japanese strains I and III of BaYMV

^b 13:3 is the expected segregation ratio for an F₂ population harboring one dominant gene and one recessive gene, 3:1 indicates the expected ratio for an F₂ population harboring a single dominant gene. 3:1 is the expected ratio for a DH population harboring two resistance genes, 1:1 and 7:1 are the expected ratios for DH populations harboring one and three resistance genes, respectively

^c H indicates generation of DH

^d Numbers in DH indicate numbers of the lines, which contain 10 individuals

by 7 min incubation at 72°C. For STS or CAPS markers, the annealing time and elongation time were 2 min and 3 min, respectively; the rest of the conditions were as described for the SSR markers. PCR was done with a PC-818 thermal cycler (ASTEC, Japan). Amplified fragments with SSR markers were separated in 3.0% agarose gel electrophoresis, and those with STS or CAPS markers were separated in 1.0% agarose gel electrophoresis.

Initially, 480 DNA markers were screened for polymorphism between Daisen-gold and PK23-2. The 127 DNA markers that detected polymorphisms between the parents were selected for use in constructing the linkage map. The segregation ratios of all markers were checked in the DH45 population by the χ^2 test using the MAPL software (Ukai et al. 1995). For construction of genetic map, recombination values were calculated based on the model of doubled haploid and converted into genetic map distances (cM) by Kosambi function. QTL analysis of resistance to BaYMV was done using MAPL with a log-likelihood (LOD) of 2.0 for the doubled haploid model.

Results

Segregation analyses for BaYMV resistance in the F₁, F₂, and DH45 populations

The field was effective for evaluation of the plant materials: Daisen-gold was severely infected by BaYMV, whereas no symptoms were detected on the leaves of PK23-2 and the F₁ populations grown in the same field (Table 1). The reaction of the F₁ populations against BaYMV revealed that

PK23-2 had at least one dominant resistance gene. Of the 106 F₂ individuals evaluated for resistance in the infected field, 90 were uninfected and the remaining 16 showed mosaic symptoms. This observed segregation was not different from the expected segregation ratio (13 resistant: 3 susceptible) for an F₂ generation segregating for two unlinked resistance genes, one dominant and one recessive. Moreover, in the DH45 population, 47 lines were resistant and 14 lines were susceptible in the infected field. This observed segregation was not significantly different from a ratio of 3 resistant: 1 susceptible, as expected if PK23-2 harbored two unlinked resistance genes.

Map construction and QTL analysis

To construct a linkage map and perform QTL analysis for resistance to BaYMV, 61 lines of DH45 were screened with the 127 DNA markers found to be polymorphic between the parents. A total of 121 markers in ten linkage groups were assigned to the seven chromosomes of barley (Fig. 1). The linkage map covered 1268.8 cM. Two QTLs for resistance to BaYMV were detected: one on chromosome 3H and one on 4H. On chromosome 3H, the QTL at CAPS marker ABG070 with *Mbo*I had an LOD score of 4.07 and explained 26.8% of the phenotypic variance explained (PVE). On chromosome 4H, the QTL at SSR marker Bmag0490 had a LOD score of 3.53 and PVE of 27.2%.

Test for dominance of newly identified resistance genes

To test for dominance of the two resistance genes detected by QTL analysis, F₁ populations derived from crosses

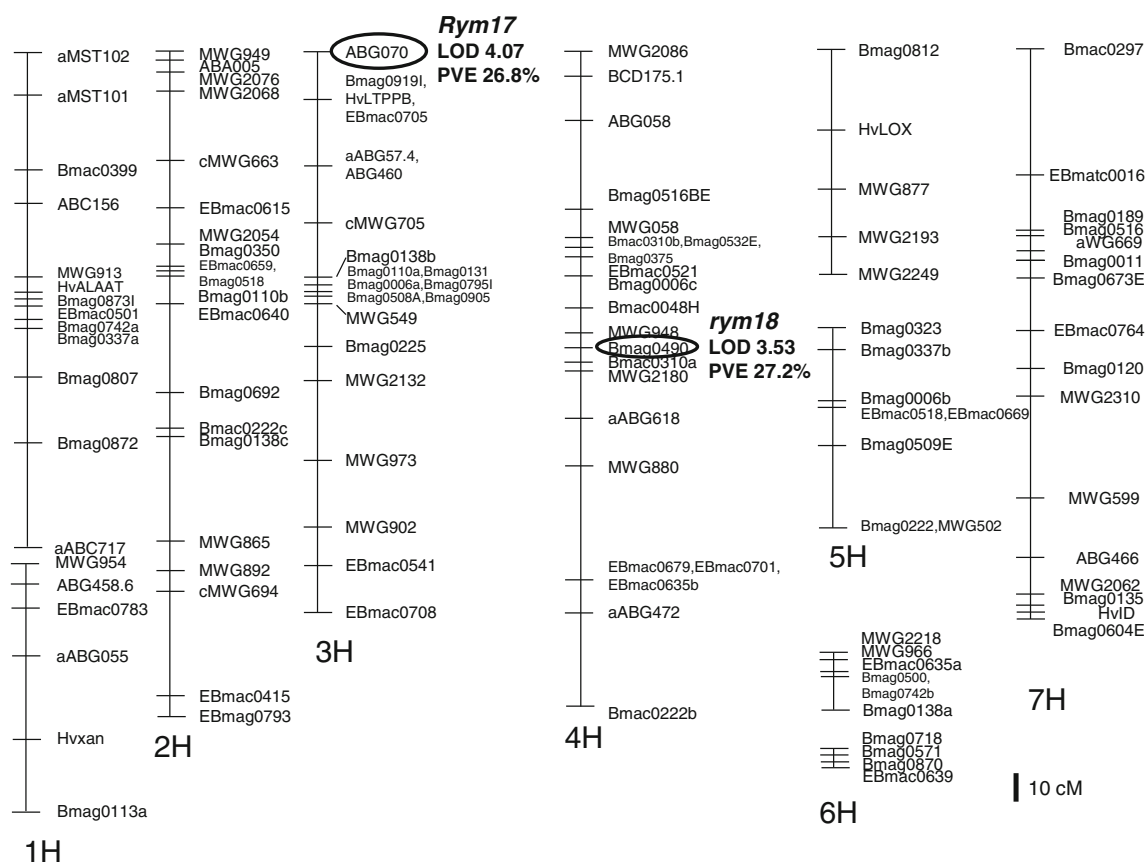


Fig. 1 QTL analysis of resistance genes to BaYMV from DH45 population. Mapping of resistance genes *Rym17* and *rym18* in a population of doubled haploid (DH45) lines derived from a cross between Daisen-gold and PK23-2. Ovals indicate QTLs for resistance to BaYMV

between each resistant DH45 line (DH45-1, -10, -63, -67, -68, -69, and -72) and the susceptible Daisen-gold parent were examined for response to Japanese BaYMV strains I and III (Fig. 2). DNA marker analysis was used to identify the source of the DNA segments containing CAPS markers ABG070 with *Mbo*I and SSR marker EBmac0705 near the QTL on chromosome 3H, and CAPS marker MWG948 with *Tru*I, SSR marker Bmag0490, and SSR marker Bmac0310 near the QTL on chromosome 4H. DH45-1, -68, and -72 contained segments from PK23-2 in both of these QTL regions associated with BaYMV resistance. In contrast, DH45-10, -63, -67, and -69 had segments from PK23-2 only in the QTL region on chromosome 4H; the region around the QTL on chromosome 3H was derived from Daisen-gold. F₁ populations derived from DH45-1, -68, and -72 showed no mosaic symptoms, whereas F₁ populations derived from DH45-10, -63, -67, and -69 were severely infected by BaYMV. These results revealed that the QTL on 3H behaved as a dominant gene and the QTL on 4H behaved as a recessive gene. Lines DH45-1, -68 and -72 had at least the dominant resistance gene, and lines DH45-10, -63, -67, and -69 had only the recessive resistance gene. To test for allelism to known sources of resistance, each DH45-63 and -69 were crossed to two barley lines known

to carry *rym1* or *rym3* (Table 2). All of the F₁ populations were susceptible in the contaminated field. These data showed that the recessive resistance gene in PK23-2 was different from *rym1* and *rym3*.

Discussion

BaYMV disease is caused by infection with soil-borne BaYMV and results in severe yield loss in barley production. The only current procedure to prevent the disease is the introduction of resistance genes into cultivars. Prior to the present study, 14 recessive genes derived from *H. vulgare* and two dominant genes from *H. bulbosum* had been mapped to the seven chromosomes of barley. To overcome the threat of further differentiation of strains in BaYMV, it is necessary to introduce novel resistance genes derived from previously untapped genetic resources into modern cultivars. Until now, no completely dominant BaYMV resistance gene derived from *H. vulgare* had been reported. Dominant resistance genes have several advantages as preferable genetic resources in backcross breeding programs or production of F₁ hybrid because of convenient introduction of resistance into objective cultivar. In this study, we

Fig. 2 Genotypes and phenotypes to BaYMV in resistant DH lines. Graphical genotypes for five DNA markers linked to BaYMV resistance QTLs on 3H and 4H in seven resistant doubled haploid (DH) lines. “F₁” refers to the F₁ generation derived from a cross between each resistant DH line and the susceptible parent Daisen-gold. *White* and *gray rectangles* indicate chromosome regions from Daisen-gold and PK23-2, respectively

Name	Resistance phenotype	Genotypes on each QTL in DH line					Resistance phenotype of F ₁
		3H markers		4H markers			
		ABG070	EBmac0705	MWG948	Bmag0490	Bmac0310	
Daisen-gold	S						S
PK23-2	R						R
DH45-1	R						R
DH45-68	R						R
DH45-72	R						R
DH45-10	R						S
DH45-63	R						S
DH45-67	R						S
DH45-69	R						S

Table 2 Response to BaYMV of F₁ lines derived from crosses between each two-rowed barley with known recessive resistance gene and each DH line harboring a *rym18*

Crossing parent		Generation	Number	Observed number ^a	
♀	♂			Resistant	Susceptible
Chikukei ym1-1 (<i>rym1</i>)	DH45-63	F ₁	10	0	10
Chikukei ym1-1 (<i>rym1</i>)	DH45-69	F ₁	10	0	10
Harushizuku (<i>rym3</i>)	DH45-63	F ₁	10	0	10
Harushizuku (<i>rym3</i>)	DH45-69	F ₁	10	0	10

^a Evaluation performed in test field contaminated with Japanese strains I and III of BaYMV

focused on the unidentified sources of resistance in PK23-2, a line originating from Pakistan. PK23-2 showed no mosaic symptoms on its leaves in any year from 2007 to 2011 in the infected field contaminated with Japanese BaYMV strains I and III, whereas Daisen-gold consistently showed infection symptoms when grown at the same time and under the same conditions. Heterozygous F₁ populations derived from reciprocal crosses between Daisen-gold and PK23-2 were completely resistant to BaYMV. The segregation of response to BaYMV in the F₂ and DH populations was consistent with a model of one dominant resistance gene and one recessive resistance gene being present in PK23-2. Furthermore, QTL analysis and dominance testing revealed that the dominant gene, here named *Rym17*, and the recessive gene, here named *rym18*, are located adjacent to DNA marker ABG070 on chromosome 3H and Bmag0490 on chromosome 4H, respectively. The total PVE at nearest DNA markers located adjacent each QTL was 54.0%. We consider that the lower total PVE is due to distances between resistance genes and nearest DNA markers and also due to fewer numbers of DH lines and polymorphic DNA markers for high resolution QTL analysis. For this resolution, it needs further genetic analysis to reveal the details of two QTLs using large scale segregating population containing solely resistance gene. To date, there

has been no report of the identification of a resistance gene at the distal part on 3H in *H. vulgare*. The reaction of the F₁ populations from Daisen-gold and PK23-2 against Japanese BaYMV strains I and III revealed that *Rym17* in PK23-2 conferred resistance to both strains of BaYMV. Moreover, the response of DH45-10, -63, -67, and -69, which carried only the recessive resistance gene revealed that *rym18* was also resistant to the strains. In the previous studies, *Rym14^{Hb}* and *Rym16^{Hb}* were identified as dominant BaYMV resistance genes derived from *H. bulbosum* (Ruge et al. 2003; Ruge-Wehling et al. 2006), but use of these genes to improve commercial cultivars of *H. vulgare* carries the risk of linkage drag. In addition, it would be difficult to investigate or isolate these genes because of biased recombination in interspecific crosses. We consider that PK23-2 is a more useful genetic resource to overcome the threat of BaYMV disease because it can be used directly to investigate the genetics of resistance or to isolate the dominant resistance gene. In barley, the mechanism of recessive resistance conferred by *rym4* and *rym5* has been identified as eukaryotic translation factor 4E (*Hv-elF4E*) (Stein et al. 2005). In Arabidopsis, *RTM1*, *RTM2*, and *RTM3*, which are dominant resistance genes against tobacco etch virus (TEV), encode RTM proteins. These RTM proteins, multi-protein complex, are considered to confer the resistance

mechanism by inhibition of the long-distance movement of TEV (Chisholm et al. 2000; Whitham et al. 2000; Cosson et al. 2010). Thereby, we consider the resistance mechanisms of *Rym14^{Hb}*, *Rym16^{Hb}*, and *Rym17* differ from that of *Hv-elF4E*. It is interesting to clarify the dominant resistance mechanisms to overcome future threat of BaYMV. No DH line harboring only the PK23-2 allele of *Rym17* was identified by the dominance test among seven resistant DH lines in this study, although we obtained several resistant DH lines containing this region from PK23-2 (Fig. 2). We will investigate the inheritance pattern of those resistant DH lines in an F₂ segregation test, and from this material we hope to eventually isolate *Rym17*. The recessive resistance gene *rym18* on chromosome 4H in PK23-2 was not allelic to *rym1* or *rym3*, which resistance genes to Japanese strains I and III of BaYMV. In the future, we will test whether *rym18* is allelic to resistance genes on chromosome 4H (Ordon et al. 2004). Moreover, identified *Rym17* and *rym18* will be investigated to resistance to other strains of BaYMV using resistant DH lines because of the future threat of further differentiation of strains in BaYMV. In conclusion, PK23-2 harbors one dominant BaYMV resistance gene (*Rym17*) and one recessive resistance gene (*rym18*), and it represents a potential resource for addressing the threat posed by future differentiation of BaYMV.

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