Breeding Science 70: 617–622 (2020)
doi: 10.1270/jsbbs.20071

Research Paper

A genetic analysis of the resistance in barley to *Soil-borne wheat mosaic virus*

Kaori Okada[1)], Tsuneo Kato[1)], Tetsuo Oikawa[2)], Takao Komatsuda*[2,3)] and Kiyoshi Namai[1)]

[1)] *Tochigi Prefectural Agricultural Experiment Station*, Utsunomiya, Tochigi 320-0002, Japan
[2)] *Institute of Crop Science, National Agriculture and Food Research Organization (NARO)*, Tsukuba, Ibaraki 305-8518, Japan
[3)] *Graduate School of Horticulture, Chiba University*, Matsudo, Chiba 271-8510, Japan

Soil-borne wheat mosaic virus (SBWMV), a ubiquitous pathogen commonly encountered in temperate regions of the Northern hemisphere, can damage a number of economically important cereal crops, notably wheat and barley. Given that the plasmodiophorid cercozoan *Polymyxa graminis*, which acts as the vector of SBWMV, can survive in the soil for many decades, the only feasible control measure is the deployment of resistant cultivars. Here, a quantitative trait locus (QTL) approach was taken to characterize the genetic basis of the SBWMV resistance exhibited by the barley cultivar Haruna Nijo. The analysis revealed that between 33% and 41% of the variation for the measure chosen to represent resistance was under the control of a gene(s) mapping to a region at the distal end of the short arm of chromosome 2H. In contrast to most of the genes known to encode resistance to soil-borne mosaic viruses, the allele specifying resistance was dominant over those present in a susceptible genotype.

Key Words: *Furovirus*, *Polymyxa graminis*, gene mapping, dominant gene, doubled haploid.

Introduction

The *Soil-borne wheat mosaic virus* (SBWMV) is able to infect barley, wheat, rye and triticale, potentially leading to a significant loss in crop productivity (Cadle-Davidson *et al.* 2006, Shirako and Brakke 1984). The disease was first described in wheat in the USA in 1919, since which time it has also been observed in both Europe and East Asia (Clover *et al.* 2001). The virus belongs to the genus *Furovirus* within the family *Virgaviridae*, and is transmitted by the plasmodiophorid cercozoan *Polymyxa graminis*, which parasitizes the plants' roots (Ohki *et al.* 2017). Having entered the root, the virus translocates to the shoot, inducing stunting and leaf mosaicism. Although the infection of autumn-sown crops typically occurs during the winter months, disease symptoms tend not to occur until the early spring. Resting spores of *P. graminis* harboring the virus can survive in the soil for many decades (Brakke and Langenberg 1988), which means that crop rotation is not an option for controlling the disease, while chemical treatment of the soil is unacceptable on both economic and ecological grounds. As a result, the only practical control measure is to breed for genetic resistance.

A number of related viruses, namely *Barley yellow mosaic virus* (BaYMV), *Barley mild mosaic virus* (BaMMV), *Wheat yellow mosaic virus* (WYMV) and *Wheat spindle streak mosaic virus* (WSSMV), are also transmissable by *P. graminis*. A sustained effort to identify genetic sources of resistance in barley to BaYMV and/or BaMMV has documented to date 22 genes, including *rym1* through *rym19*, although some of these represent alleles at a single locus rather than independent genes (Jiang *et al.* 2020); most of the resistances encoded by these genes are recessive. The product of the *rym4/rym5* alleles is a translation initiation factor (Stein *et al.* 2005), while the resistance encoded by *rym1/rym11* results from deletions in a gene encoding a protein disulfide isomerase-like protein (Yang *et al.* 2014). Following analysis based on the quantitative trait locus (QTL) approach, genes for resistance in bread wheat to WYMV have been mapped to regions on chromosome arms 2DL and 3BS (Suzuki *et al.* 2015, Zhu *et al.* 2012), 6DS (Yamashita *et al.* 2020) and the other chromosomes (Jiang *et al.* 2020), while a locus for resistance to WSSMV has been identified on chromosome arm 2DL (Khan *et al.* 2000). With respect to SBWMV, the presence of *Sbm1*, a gene mapping to the distal end of the bread wheat chromosome arm 5DL, has been correlated with a measure of resistance (Hao *et al.* 2012, Narasimhamoorthy *et al.* 2006), with a smaller contribution from the chromosome arm 2BS locus *Sbm2* (Bayles *et al.* 2007). Both of these genes also condition a measure of the resistance of bread wheat to *Soil-borne cereal mosaic virus* (SBCMV) (Bass *et al.* 2006, Bayles *et al.* 2007, Perovic *et al.* 2009). *Sbm2* may well be

Communicated by Nils Stein
Received June 19, 2020. Accepted September 13, 2020.
First Published Online in J-STAGE on November 28, 2020.
*Corresponding author (e-mail: takao@affrc.go.jp)

identical to the durum wheat locus *QSbm.ubo-2BS* (Maccaferri *et al.* 2011, Russo *et al.* 2012). A second, less effective QTL determining SBCMV resistance was successfully mapped by Maccaferri *et al.* (2011) to a region of chromosome 2A. Variation with respect to the response to infection by SBWMV is known in barley germplasm: resistance is highly variable among Japanese six-rowed varieties, while Japanese two-rowed varieties (including Haruna Nijo) are largely resistant (Aoki *et al.* 2015, Iida *et al.* 1997). Here, a QTL approach was taken to determine the genetic basis of SBWMV resistance in barley.

Materials and Methods

Plant materials

The experiments were based on an established doubled haploid (DH) 92 entry mapping population (Sato and Takeda 2009) created from a cross between the Japanese barley cultivar "Haruna Nijo" (which is relatively resistant to SBWMV) and the wild barley (*Hordeum vulgare* ssp. *spontaneum*) accession "H602". The response to SBWMV of the mapping population entries and the two parental lines was tested in a field nursery at the National Agriculture and Food Research Organization in Tsukuba-Mirai (Ibaraki, Japan). Four sets of the material (each comprising the full set of 92 DH lines) were grown. Two sets of ten plants per entry were sown on 21 October 2015, with leaves sampled on 6 April 2016 (Reps. 1 and 2). The other two sets were both planted on 21 October 2016; one was sampled on 21 March 2017 (Rep. 3) and the other on 4 April 2017 (Rep. 4). The plants were naturally infected by SBWMV. As a negative control, the parental entries were also raised for two weeks in sterilized soil.

ELISA assay

To perform ELISA assays, an antibody recognizing SBWMV, developed by Netsu *et al.* (2011), was obtained from the Central Region Agricultural Research Center (Tsukuba, Japan). A 80 mg sample of leaf tissue harvested from each entry was homogenized in an MM300 mixer mill (Retsch, Haan, Germany) in 0.8 mL PBST buffer (8 g/L NaCl, 2.9 g/L $Na_2HPO_4 \cdot 12H_2O$, 0.2 g/L KH_2PO_4, 0.2 g/L KCl, 0.5 ml/L Tween 20). Following centrifugation (10,000 rpm, 5 min, 25°C) in a rotor AR015-24 (Tomy, Tokyo, Japan), a 0.1 mL aliquot of the supernatant was subjected to a double antibody sandwich-ELISA assay, following the protocol given by Clark (1981). After a 30 min incubation at room temperature, the absorbance of the reaction (405 nm) was recorded using a Model 686 microplate reader (Bio-Rad, Tokyo, Japan). Seven to eight individual plants per mapping population line for each replication were assayed in this way.

QTL analysis

The subsequent QTL analysis rested on the linkage map derived by Sato and Takeda (2009), which comprised 732 SNP and 384 EST loci. Composite interval mapping was performed using model 6 of the Zmapqtl procedure implemented in Windows QTL Cartographer v2.5 software (Basten *et al.* 1996, Wang *et al.* 2006). A genome-wide LOD score threshold consistent with a significance level of 0.05 was determined from a set of 1,000 permutations. A BLASTN search was conducted using the IPK Barley Blast Server (https://webblast.ipk-gatersleben.de/barley_ibsc/), based on both the "Barley Pseudomolecules Aug2015" (Mascher *et al.* 2017) and the "Barley Pseudomolecules Morex v2.0 2019" (Monat *et al.* 2019) databases.

Results

SBWMV response in parents

The proportion of Haruna Nijo plants classed as carrying virus ranged from 3% to 21%, while that for H602 plants ranged from 18% to 72% (**Table 1**). The reaction of Haruna Nijo × H602 F_1 hybrid plants was measured in two of the four batches: their rate of infection rate lay closer to that of Haruna Nijo than to H602 plants, and average degree of dominance was 0.87–0.90, implying that the SBWMV resistance present in Haruna Nijo was a dominant trait. ELISA absorbance values <0.2 were classified as SBWMV negative and those >0.6 as positive (**Supplemental Fig. 1**). In order to reduce noise, plants scoring in the range 0.2–0.6 were excluded from the analysis of infection rate. The same assay applied to a PBST solution (no plant extract) generated a mean absorbance of 0.13 (SE = 0.006, $n = 10$). Leaf extracts of plants grown in sterile soil (negative control) gave a mean absorbance of 0.12 (SE = 0.003, $n = 55$) and a range of 0.10–0.18, whereas positive control plants (cv. Tochinoibuki) grown in the SBWMV field gave a mean absorbance of 1.43 (SE = 0.093, $n = 55$) and a range of 0.65–2.39.

Table 1. The reaction of the mapping family's parents to SBWMV infection

	Rep.1 (West, April 2016)		Rep. 2 (East, April 2016)		Rep. 3 (West, March 2017)		Rep. 4 (West, April 2017)	
	n	%	*n*	%	*n*	%	*n*	%
Haruna Nijo	18	11	14	21	88	3	88	3
H602	18	50	18	72	34	18	35	23
F_1		n/a		n/a	27	4	23	4
d		n/a		n/a		0.87		0.90

n - number of plants, F_1 - Haruna Nijo × H602 F_1 zygotes, *d* - average degree of dominance, n/a - not applicable.

Variation in the SBWMV response

The SBWMV infection rate of each of the DH lines is shown in **Supplemental Table 1**. The outcome of the ELISA carried out on the Rep. 1 plants suggested that the response to SBWMV (absorbance) was bimodally distributed (**Supplemental Fig. 2**). The same assay applied to plants in the other three replications produced a similar result (**Supplemental Fig. 2**). As shown in **Fig. 1**, the SBWMV response across the set of DH lines was similar for all four replicates, in each case demonstrating a pronounced skew towards resistance. The correlation with respect to the response between the four replicates was highly significant (**Supplemental Table 2**).

The genetic basis of SBWMV resistance

QTL analysis was performed on the four data sets of replications (**Supplemental Table 3**). The analysis identified a major locus associated with a reduced rate of SBWMV infection in a region lying between 0.01 and 5.16 cM away from the distal end of chromosome arm 2HS; the effect was reproduced across each of the four plant batches (**Fig. 2**, **Table 2**). The LOD score associated with this locus ranged from 10.5 to 15.3, and the locus was responsible for 33.4–40.7% of the variation for SBWMV infection. The critical map interval was flanked by the EST markers bags37p19 and the 12224-363 SNP (**Fig. 2**), with the positive allele being contributed by Haruna Nijo. Analysis based on all individual plants in each line (combining Rep. 1 through Rep. 4) mapped the QTL in the same interval with the higher LOD score of 21 (**Table 2**, **Fig. 3**). The map interval was physically located between 2.1 and 18.6 Mb away from the distal end of the chromosomal arm in the frame of "Pseudomolecules Aug2015" of Mascher *et al.* (2017) while between 1.7 and 15.5 Mb away in the frame of "Pseudomolecules Morex v2.0 2019" of Monat *et al.* (2019) (**Table 3**). Further loci, each of lesser effect, were identified around 164 cM of chromosome arm 2HL, 153 cM of chromosome arm 3HL and 132 cM of chromosome arm 5HL; however, all three of these putative QTL were only detected in only one of the four plant batches (**Fig. 2**). The Haruna Nijo allele at the putative locus on chromosome arm 5HL contributed positively to resistance, while it was the H602 allele which contributed positively at each of the other two loci (**Table 2**). The LODs associated with the three QTL were all above 3.0 (**Fig. 2**).

Discussion

The rate of SBWMV infection was highly variable, even within a fixed genotype (particularly in the case of the susceptible parent H602), which implies that the interaction between the plant and the virus is strongly modulated by non-genetic factors. As a result, the assessment of the response to infection had to be based on individual plants as the experimental unit, rather than on individual genotypes. Thus, the infection rate was used as the metric of the response rather than the mean viral load accumulated by a fixed genotype, as was used by Suzuki *et al.* (2015) in a similar genetic analysis of the genetic basis of resistance to WYMV. The interpretation of the host response to BaYMV and BaMMV can be complicated by the possibility of disease escape (Shi *et al.* 2019), while the response of Haruna Nijo and H602 to SBWMV infection is modulated by incomplete penetrance of the resistance genes. Nevertheless, the parameter used to quantify resistance in the genetic analysis proved to be robust enough to allow for the

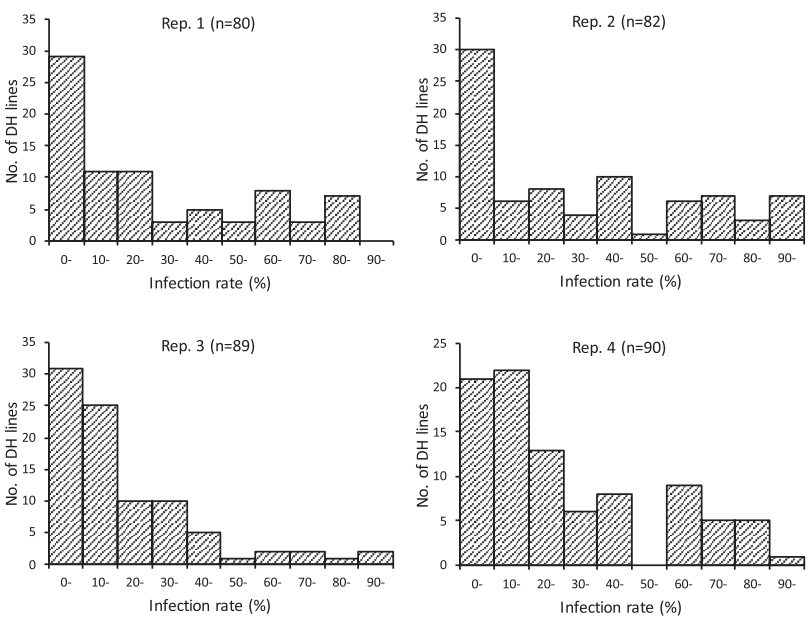

Fig. 1. Frequency distribution of the response to infection by SBWMV in the Haruna Nijo/H602 mapping population. Between 80 and 90 DH lines were analyzed per replicate.

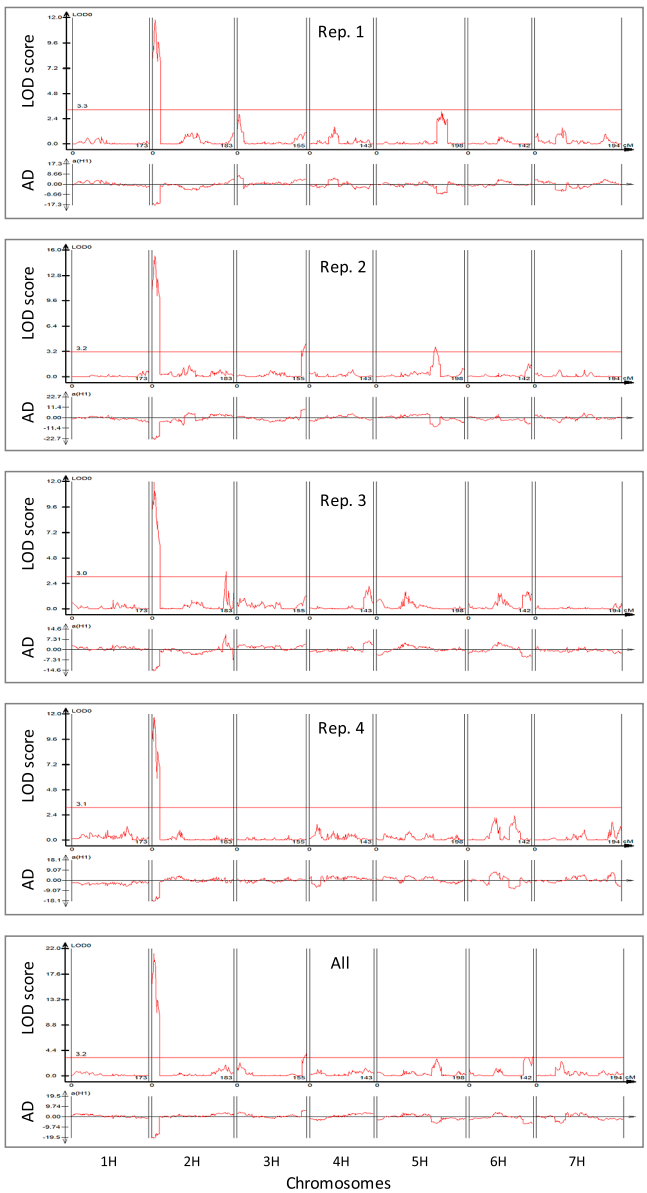

Fig. 2. The detection of QTL underlying SBWMV resistance in barley. Each chromosome represented on the X axis is represented with its short arm on the left. The Y axes record either the LOD score (upper trace) or the additive effect of a QTL allele (lower trace). A negative additive effect indicates that the Haruna Nijo allele permits a less degree of infection.

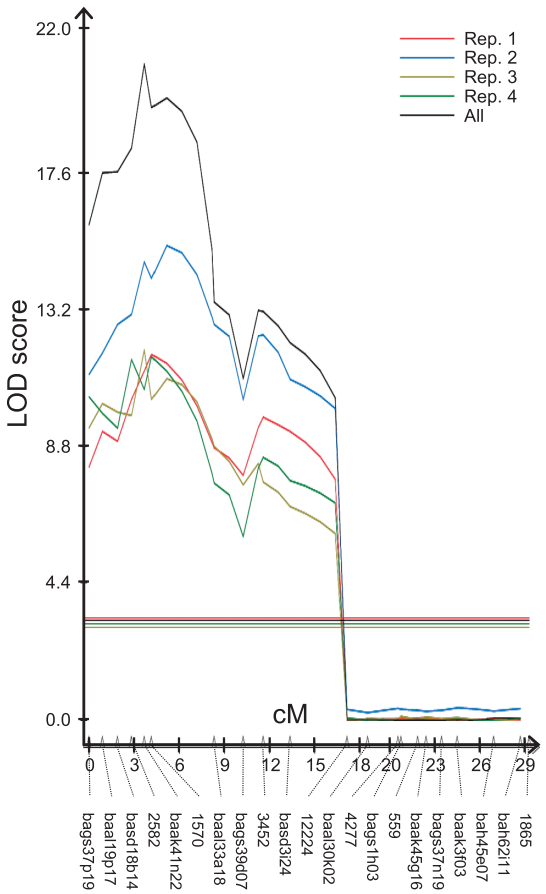

Fig. 3. The site of the QTL conditioning SBWMV resistance maps to a region of the short arm of chromosome 2H.

identification of a QTL which accounted for over one third the overall variation in the rate of SBWMV infection. The reproducibility of this effect across each of the four plant batches gives a measure of confidence that the underlying gene(s) present in the key chromosome arm 2HS region act relatively independently of the environment.

To date, 22 genes conferring resistance to BaYMV and/or BaMMV have been identified in barley (Jiang *et al.* 2020). Most of these act as recessive alleles—for example, the *rym4/rym5/rym6/rym10* alleles each encode an eIF4E variant which promotes resistance (Stein *et al.* 2005), while

Table 2. The loci underlying resistance to SBWMV in Haruna Nijo and H602

Replication	Chr.	Position (cM)	Marker interval (position in cM)	LOD	R^2 (%)	*AD* (%)	Resistant allele
Rep. 1	2H	4.2	bags37p19 (0.0)–12224_363 (17.2)	11.8	33.4	17.3	Haruna Nijo
Rep. 2	2H	5.2	bags37p19 (0.0)–12224_363 (17.2)	15.3	40.7	22.7	Haruna Nijo
do.	3H	153.6	baak40c12 (143.0)–basd24i11 (154.5)	4.3	8.2	10.0	H602
do.	5H	132.1	bah33p03 (128.7)–314_559 (136.3)	3.8	7.2	9.5	Haruna Nijo
Rep. 3	2H	3.7	bags37p19 (0.0)–12224_363 (17.2)	11.9	36.9	14.6	Haruna Nijo
do.	2H	164.0	baak36b07 (163.0)–5483-787 (164.5)	3.5	10.4	11.1	H602
Rep. 4	2H	4.2	bags37p19 (0.0)–12224_363 (17.2)	11.7	38.6	18.0	Haruna Nijo
All	2H	3.7	bags37p19 (0.0)–12224_363 (17.2)	21.1	48.0	19.5	Haruna Nijo
do.	3H	153.6	baak40c12 (143.0)–basd24i11 (154.5)	4.2	5.9	6.7	H602
do.	6H	125.9	2152_1547 (119.8)–basdl12 (127.7)	3.3	4.8	6.1	Haruna Nijo

R^2 - phenotypic variation explaned, *AD* - additive effect for infection rate (%) by one allele.

Table 3. The physical interval on the short arm of chromosome 2H harboring the SBWMV resistance QTL showing the locus' flanking markers

Marker	Clone	Accession	"Barley Pseudomolecules Aug2015"				"Barley Pseudomolecules Morex v2.0 2019"			
			Marker location (bp)	Score	E-value	%ID	Marker location (bp)	Score	E-value	%ID
bags37p19[a]	bags37p19[b]	BJ468276	2096936–2097338	786	0.0	99	1739440–1739842	710	0.0	99
12224-363 SNP[a]	baal26h21[c]	BJ475570	18589160–18589548	654	0.0	97	15464970–15464582	654	0.0	97

[a] Sato and Takeda (2009).
[b] Sato *et al.* (2009).
[c] HarvEST Unigine #32 12224 (Close *et al.* 2009).

rym1/rym11 each encode a variant of PDIL5-1 (Yang *et al.* 2014). The exceptions are $Rym14^{Hb}$ and $Rym16^{Hb}$, dominant genes introduced into cultivated barley from its wild relative *Hordeum bulbosum* (Ruge *et al.* 2003, Ruge-Wehling *et al.* 2006), and *Rym17*, a gene identified in a barley cultivar from Pakistan (Kai *et al.* 2012). The SBWMV resistance mapped in present experiments acted as a dominant trait (mean degree of dominance: 0.87–0.90), which implies that the product of the underlying gene conditions a dominant form of resistance (de Ronde *et al.* 2014). The site of this locus (close to the distal end of the short arm of chromosome 2H) has not so far been identified as harboring genes encoding resistance to BaYMV and/or BaMMV (Jiang *et al.* 2020), and in any case Haruna Nijo plants are resistant to SBWMV (**Table 1**). Thus the locus identified here likely harbors a gene(s) which acts specifically to determine resistance against SBWMV. The SBWMV strain is presumably more closely related to the French strain AJ749657 than to Chinese ones (K. Okada, unpublished data). The observation that some Haruna Nijo plants were characterized as SBWMV susceptible can be interpreted as either reflecting a quantitative form of resistance, the presence of false positives or incomplete penetrance. The identification of robust flanking markers for the resistance gene would enable a straightforward marker-assisted breeding strategy to be designed for its introgression into elite germplasm. Meanwhile, the gene's telomeric location should simplify its positional cloning given that the relationship between physical and genetic distance there is favorable.

The bread wheat gene *Sbm2* conditions resistance to both SBWMV and SBCMV, while the durum wheat *Qsbm.ubo-2BS* QTL conditions resistance to SBCMV; both map to a region of the genome syntenic with the short arm of chromosome 2H (Bayles *et al.* 2007, Maccaferri *et al.* 2011), as does the minor QTL *QSbm.ubo-2AS* (Maccaferri *et al.* 2012). Meanwhile, other minor wheat QTL exerting an effect on SBCMV resistance have been mapped to chromosome arms 2AL, 3AL, 3BL, 5AL and 6BS, sites which are syntenic with the putative SBWMV resistance QTL mapped here to regions of chromosome arms 2HL, 3HL, 5HL and 6HS, respectively. On the basis of matching chromosome locations and the similarity of SBCMV and SBWMV, it is plausible to propose that these wheat and barley genes are orthologous. The development of an effective marker-assisted selection protocol and, particularly, the elucidation of the nature of the resistance gene will require the level of resolution of the QTL's map location to be substantially improved. The latter will be facilitated by the wealth of genomic resources developed in Haruna Nijo (Matsumoto *et al.* 2011, Sato *et al.* 2016).

Author Contribution Statement

K.O., K.N., T.Ko and T.Ka designed the experiments, K.O., K.N. and T.Ka performed the experiments, K.O., T.O. and T.Ko analyzed the data and K.O. and T.Ko wrote the paper.

Acknowledgments

The authors wish to thank T. Sotome for contributing to the planning of this research, K. Sato for providing the mapping population and Y. Fujita, T. Suzuki and H. Horita for help with the ELISA assay. This research was enabled by financial support from NARO.

Literature Cited

Aoki, E., M. Taira, F. Fujita and T. Yanagisawa (2015) Reaction of Japanese barley cultivars to Japanese *Soil-borne wheat mosaic virus*. Proceeding of the 239th meeting, Crop Science Society of Japan, March 25, 2015, p. 231.

Bass, C., R. Hendley, M.J. Adams, K.E. Hammond-Kosack and K. Kanyuka (2006) The *Sbm1* locus conferring resistance to *Soil-borne cereal mosaic virus* maps to a gene-rich region on 5DL in wheat. Genome 49: 1140–1148.

Basten, C.J., B.S. Weir and Z.-B. Zeng (1996) QTL Cartographer: A reference manual and tutorial for QTL mapping. Department of Statistics, North Carolina State University, Raleigh, NC.

Bayles, R., D. O'Sullivan, V. Lea, S. Freeman, G. Budge and K. Walsh (2007) Controlling Soil-borne cereal mosaic virus in the UK by developing resistant wheat cultivars. HGCA Project 2616. HGCA Crop Research News 32: Project Report no. 418.

Brakke, M.K. and W.G. Langenberg (1988) Experiences with *soilborne wheat mosaic virus* in North America and elsewhere. Developments in applied biology II. Viruses with Fungal Vectors. Association of Applied Biologists, Wellesbourne, pp. 183–202.

Cadle-Davidson, L., M.E. Sorrells, S.M. Gray and G.C. Bergstrom (2006) Identification of small grains genotypes resistant to *Soilborne wheat mosaic virus*. Plant Dis. 90: 1039–1044.

Clark, M.F. (1981) Immunosorbent assays in plant pathology. Annu. Rev. Phytopathol. 19: 83–106.

Close, T.J., P.R. Bhat, S. Lonardi, Y. Wu, N. Rostoks, L. Ramsay, A. Druka, N. Stein, J.T. Svensson, S. Wanamaker *et al.* (2009) Development and implementation of high-throughput SNP

genotyping in barley. BMC Genomics 10: 582

Clover, G.R.G., C. Ratti and C.M. Henry (2001) Molecular characterization and detection of European isolates of *Soil-borne wheat mosaic virus*. Plant Pathol. 50: 761–767.

de Ronde, D., P. Butterbach and R. Kormelink (2014) Dominant resistance against plant viruses. Front. Plant Sci. 5: 1–17.

Hao, Y., Y. Wang, Z. Chen, D. Bland, S. Li, G. Brown-Guedira and J. Johnson (2012) A conserved locus conditioning *Soil-borne wheat mosaic virus* resistance on the long arm of chromosome 5D in common wheat. Mol. Breed. 30: 1453–1464.

Iida, Y., K. Okawa, K. Watanabe, T. Chiba, I. Yamazaki, T. Mitamura and T. Konishi (1997) Studies on resistance of barley varieties to soil-borne virus diseases of barley. Bull. Agric. Res. Inst., Ibaraki Agricultural Center 4: 115–174.

Jiang, C., J. Kan, F. Ordon, D. Perovic and P. Yang (2020) *Bymovirus*-induced yellow mosaic diseases in barley and wheat: viruses, genetic resistances and functional aspects. Theor. Appl. Genet. 133: 1623–1640.

Kai, H., K. Takata, M. Tsukazaki, M. Furusho and T. Baba (2012) Molecular mapping of *Rym17*, a dominant and *rym18* a recessive *Barley yellow mosaic virus* (BaYMV) resistance genes derived from *Hordeum vulgare* L. Theor. Appl. Genet. 124: 577–583.

Khan, A.A., G.C. Bergstrom, J.C. Nelson and M.E. Sorrells (2000) Identification of RFLP markers for resistance to wheat spindle streak mosaic bymovirus (WSSMV) disease. Genome 43: 477–482.

Maccaferri, M., C. Ratti, C. Rubies-Autonell, V. Vallega, A. Demontis, S. Stefanelli, R. Tuberosa and M.C. Sanguineti (2011) Resistance to *Soil-borne cereal mosaic virus* in durum wheat is controlled by a major QTL on chromosome arm 2BS and minor loci. Theor. Appl. Genet. 123: 527–544.

Maccaferri, M., R. Francia, C. Ratti, C. Rubies-Autonell, C. Colalongo, G. Ferrazzano, R. Tuberosa and M.C. Sanguineti (2012) Genetic analysis of *Soil-borne cereal mosaic virus* response in durum wheat: evidence for the role of the major quantitative trait locus *QSbm.ubo-2BS* and of minor quantitative trait loci. Mol. Breed. 29: 973–988.

Mascher, M., H. Gundlach, A. Himmelbach, S. Beier, S.O. Twardziok, T. Wicker, V. Radchuk, C. Dockter, P.E. Hedley, J. Russell *et al.* (2017) A chromosome conformation capture ordered sequence of the barley genome. Nature 544: 427–433.

Matsumoto, T., T. Tanaka, H. Sakai, N. Amano, H. Kanamori, K. Kurita, A. Kikuta, K. Kamiya, M. Yamamoto, H. Ikawa *et al.* (2011) Comprehensive sequence analysis of 24,783 barley full-length cDNAs derived from 12 clone libraries. Plant Physiol. 156: 20–28.

Monat, C., S. Padmarasu, T. Lux, T. Wicker, H. Gundlach, A. Himmelbach, J. Ens, C. Li, G.J. Muehlbauer, A.H. Schulman *et al.* (2019) TRITEX: chromosome-scale sequence assembly of Triticeae genomes with open-source tools. Genome Biol. 20: 284.

Narasimhamoorthy, B., B.S. Gill, A.K. Fritz, J.C. Nelson and G.L. Brown-Guedira (2006) Advanced backcross QTL analysis of a hard winter wheat synthetic wheat population. Theor. Appl. Genet. 112: 787–796.

Netsu, O., T. Ohki, H. Kojima, S. Oda, E. Aoki, T. Yoshioka, T. Yanagisawa, K. Ishikawa and T. Sasaya (2011) Development of serological diagnosis by ELISA for specific detection of four soil-borne viruses in wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*). Ann. Rept. Kanto Tosan Plant Prot. Soc. 58: 13–17 (in Japanese).

Ohki, T., T. Sasaya, M. Sayama and T. Maoka (2017) Diversity of rDNA-ITS sequences of *Polymyxa graminis* from wheat and barley in Japan. J. Gen. Plant Pathol. 83: 226–230.

Perovic, D., J. Förster, P. Devaux, D. Hariri, M. Guilleroux, K. Kanyuka, R. Lyons, J. Weyen, D. Feuerhelm, U. Kastirr *et al.* (2009) Mapping and diagnostic marker development for Soil-borne cereal mosaic virus resistance in bread wheat. Mol. Breed. 23: 641–653.

Ruge, B., A. Linz, R. Pickering, G. Proeseler, P. Greif and P. Wehling (2003) Mapping of *Rym14^{Hb}*, a gene introgressed from *Hordeum bulbosum* and conferring resistance to BaMMV and BaYMV in barley. Theor. Appl. Genet. 107: 965–971.

Ruge-Wehling, B., A. Linz, A. Habekuß and P. Wehling (2006) Mapping of *Rym16^{Hb}*, the second soil-borne virus-resistance gene introgressed from *Hordeum bulbosum*. Theor. Appl. Genet. 113: 867–873.

Russo, M.A., D.B.M. Ficco, D. Marone, P. de Vita, V. Vallega, C. Rubies-Autonell, C. Ratti, P. Ferragonio, V. Giovanniello, N. Pecchioni *et al.* (2012) A major QTL for resistance to soil-borne cereal mosaic virus derived from an old Italian durum wheat cultivar. J. Plant Interact. 7: 290–300.

Sato, K., N. Nankaku and K. Takeda (2009) A high-density transcript linkage map of barley derived from a single population. Heredity (Edinb.) 103: 110–117.

Sato, K. and K. Takeda (2009) An application of high-throughput SNP genotyping for barley genome mapping and characterization of recombinant chromosome substitution lines. Theor. Appl. Genet. 119: 613–619.

Sato, K., T. Tanaka, S. Shigenobu, Y. Motoi, J. Wu and T. Itoh (2016) Improvement of barley genome annotations by deciphering the Haruna Nijo genome. DNA Res. 23: 21–28.

Shi, L.J., C.C. Jiang, Q. He, A. Habekuß, F. Ordon, H.Y. Luan, H.Q. Shen, J. Liu, Z.Y. Feng, J. Zhang *et al.* (2019) Bulked segregant RNA-sequencing (BSR-seq) identified a novel rare allele of eIF4E effective against multiple isolates of BaYMV/BaMMV. Theor. Appl. Genet. 132: 1777–1788.

Shirako, Y. and M.K. Brakke (1984) Two purified RNAs of *soil-borne wheat mosaic virus* are needed for infection. J. Gen. Virol. 65: 119–127.

Stein, N., D. Perovic, J. Kumlehn, B. Pellio, S. Stracke, S. Streng, F. Ordon and A. Graner (2005) The eukaryotic translation initiation factor 4E confers multiallelic recessive *Bymovirus* resistance in *Hordeum vulgare* (L.). Plant J. 42: 912–922.

Suzuki, T., M.N. Murai, T. Hayashi, S. Nasuda, Y. Yoshimura and T. Komatsuda (2015) Resistance to *Wheat yellow mosaic virus* in Madsen wheat is controlled by two major complementary QTLs. Theor. Appl. Genet. 128: 1569–1578.

Wang, S., C.J. Basten and Z.B. Zeng (2006) Windows QTL cartographer 2.5. Department of Statistics, North Carolina State University, Raleigh, NC, USA.

Yamashita, Y., C. Souma, R. Ogura and T. Suzuki (2020) A single QTL on chromosome 6DS derived from a winter wheat cultivar 'OW104' confers resistance to *Wheat yellow mosaic virus*. Breed. Sci. 70: 373–378.

Yang, P., T. Lüpken, A. Habekuß, G. Hensel, B. Steuernagel, B. Kilian, R. Ariyadasa, A. Himmelbach, J. Kumlehn, U. Scholz *et al.* (2014) *PROTEIN DISULFIDE ISOMERASE LIKE 5-1* is a susceptibility factor to plant viruses. Proc. Natl. Acad. Sci. USA 111: 2104–2109.

Zhu, X., H. Wang, J. Guo, Z. Wu, A. Cao, T. Bie, M. Nie, F.M. You, Z. Cheng, J. Xiao *et al.* (2012) Mapping and validation of quantitative trait loci associated with wheat yellow mosaic *Bymovirus* resistance in bread wheat. Theor. Appl. Genet. 124: 177–188.