Research Paper

A single QTL on chromosome 6DS derived from a winter wheat cultivar ‘OW104’ confers resistance to *Wheat yellow mosaic virus*

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Wheat yellow mosaic (WYM) is a soilborne disease caused by *Wheat yellow mosaic virus* (WYMV). Symptoms include yellow mosaic coloring of leaves, stunting, and growth inhibition. Severe infection may result in yield loss. WYM is one of the most serious diseases affecting wheat production in East Asia. The most effective control is through breeding resistant cultivars. A winter wheat cultivar, ‘OW104’, shows little to no symptoms in heavily WYMV-infested fields in Hokkaido, Japan. Here we detected *Qym4*, a QTL accounting for 45%–57% of WYMV resistance, in the vicinity of the markers *Xcfd49*, *Xbarc183*, and *Xgpcw4357* on wheat chromosome arm 6DS. F₃ progenies with ‘OW104’ allele at *Qym4* showed significantly higher resistance than those with ‘Hokushin’ homozygote or heterozygote. We developed ‘Hokushin’ near-isogenic lines by backcrossing with ‘Hokushin’ as the recurrent parent and ‘OW104’ as the resistance donor. All the WYMV-resistant BC₅F₁/BC₄F₁ plants carried ‘OW104’ allele only at *Xcfd49*. Our results suggest that the introduction of *Qym4* confers resistance to WYMV in winter wheat.

Key Words: *Triticum aestivum*, disease resistance, SSR marker, marker-assisted selection.

Introduction

Wheat yellow mosaic (WYM) is a soilborne disease caused by *Wheat yellow mosaic virus* (WYMV). WYMV and the closely related *Wheat spindle streak mosaic virus* (WSSMV) are bymoviruses transmitted by the fungus *Polymyxa graminis* (Lu *et al.* 1998, Namba *et al.* 1998). WYMV was first described in Japan and is also present in China (Han *et al.* 1997, Inouye 1969, Sawada 1927), whereas WSSMV is present mainly in Europe and North America. The first incidence of WYMV in Hokkaido, the northernmost island of Japan, was reported in 1991 (Kusume *et al.* 1997). Since then, WYMV has spread rapidly in Hokkaido: infested fields were found in five municipalities in 1994 and 57 municipalities in 2010 (Horita *et al.* 2011).

WYMV isolates in Japan are classified into three pathotypes based on their RNA sequence and infectivity to wheat differential cultivars. Pathotype I, represented by WYMV-T, is mainly isolated from central Japan, whereas pathotype II, represented by WYMV-M, is mainly distributed in northern Japan. Pathotype III has been isolated only from

Fukuoka Prefecture (Ohki *et al.* 2014, Ohto *et al.* 2006).

WYM symptoms include yellow or yellow-striped leaves, dwarfism, and stunted spring growth (Takeuchi *et al.* 2010). WYMV infection leads to ~50% yield loss in the leading variety of wheat, ‘Hokushin’, which was bred in Hokkaido in 1994 (Nishimura *et al.* 2010). Chemical control is costly and inefficient because the vector *P. graminis* is widely present in wheat fields. Alongside cultural practices such as crop rotation, the most effective control is through breeding resistant cultivars. The only WYMV-resistant cultivar registered in Hokkaido is ‘Yumechikara’, a hard winter wheat. There is a strong demand for a WYMV-resistant soft winter wheat cultivar to replace ‘Kitahonami’, the major variety grown on 73% of the wheat field area (Hokkaido 2019).

WYMV-resistant germplasms and molecular markers linked to their resistance have been identified. In the USA cultivar ‘Madsen’, QTLs *Qym1* and *Qym2* on chromosomes 2DL and 3BS, respectively, are required for complete resistance in Hokkaido (Liu *et al.* 2016, Suzuki *et al.* 2015). The resistance of ‘Madsen’ operated exclusively in the root (Liu *et al.* 2016). QTLs from different germplasms have been detected at similar locations as *Qym1* on chromosome 2DL: *YmYF* from a Chinese cultivar ‘Yangfu 9311’, *YmIb* from a European cultivar ‘Ibis’, and *Q. ymym* from a Japanese cultivar ‘Yumechikara’ (Kojima *et al.* 2015, Liu *et al.* 2005, Nishio *et al.* 2010). These QTLs may be allelic and thus

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pyramiding them is not a viable option. In barley, pyramiding *rym* genes achieves resistance to all strains of *Barley yellow mosaic virus* (BaYMV) (Werner *et al.* 2005). It is possible that novel resistant resources may enable us to develop cultivars with pyramided resistance to WYMV.

In a previous study, we screened 11 breeding lines for WYMV resistance (Yamashita *et al.* 2017). Only ‘OW104’, a sprouting-tolerant winter wheat cultivar (Osanai *et al.* 2005) and its progeny, ‘Kitakei 1838’, had no WYM symptoms and no detectable WYMV by enzyme-linked immunosorbent assay (ELISA). Genotypes at *Qym1* and *Qym2*, as represented by SSR markers *Xwmc41* and *Xwmc754* respectively, of ‘OW104’ were different from those in ‘Madsen’, suggesting that a novel gene is responsible for the resistance (Yamashita *et al.* 2017).

The objective of the current study was to identify the genetic region responsible for WYMV resistance in ‘OW104’. The results of segregation analysis using an F₃ population showed that the resistance is controlled by a single major gene. We identified the location of this gene by QTL analysis. By using near-isogenic lines (NILs), we then confirmed that a single QTL, *Qym4*, confers resistance to WYMV.

Materials and Methods

Plant materials

Wheat differential cultivars ‘Nambukomugi’, ‘Fukuhokomugi’, and ‘Hokkai 240’ were used to identify the WYMV pathotype of our field nurseries. For genetic analysis, ‘OW104’, a WYMV-resistant wheat cultivar, and ‘Hokushin’, a susceptible cultivar, were used. A population of 221 F₃ progenies was developed from a cross between ‘OW104’ and ‘Hokushin’. ‘Hokushin’ NILs were developed by backcrossing, with ‘OW104’ as the resistance donor and ‘Hokushin’ as the recurrent parent. BC_nF₁ NILs were evaluated for WYMV resistance in field experiments, and only resistant plants were backcrossed further.

Field experiments for WYMV resistance

Field experiments were performed at nurseries in Date, Hokkaido (42.4N, 140.90E). Wheat lines were sown during late September to early October in 2015–2017. Each cultivar or F₃ line had two replications; 30–40 seeds were planted in each 0.45-m² experimental unit. Leaves were sampled from 10 plants (cultivars and resistance resources) or all the plants (F₃ lines) in early April. The presence of WYMV was assessed by plate-trapped antigen ELISA using polyclonal WYMV-specific antibodies (Ueda *et al.* 1998). WYMV-infected plants were counted and the percentage of infected plants (%IP) was calculated. We assessed cultivars with %IP 0–10% and higher than 80% as resistant and susceptible, respectively.

DNA extraction and PCR

DNA was extracted from young leaves by a modified

cetyl trimethylammonium bromide method (Suzuki *et al.* 2012). PCR was performed using Taq Gold DNA polymerase (Applied Biosystems, USA) and PCR products were analyzed on an ABI Prism 3500 Genetic Analyzer (Applied Biosystems) with GeneMapper software as described previously (Suzuki *et al.* 2015).

Screening for polymorphic molecular markers

The recommended set of 210 SSR markers for hexaploid wheat polymorphism survey (Nitta and Nasuda 2012, <http://wheatssr.lab.nig.ac.jp/markerdb/>) and an additional 166 published SSR markers from Graingenes (<https://wheat.pw.usda.gov/cgi-bin/GG3/browse.cgi?class=marker>) were screened for polymorphism between ‘OW104’ and ‘Hokushin’.

Map construction and QTL analysis

A linkage map was constructed from 167 polymorphic SSR markers by using MAPMAKER/Exp v3.0b (Lander *et al.* 1987). Recombination frequencies were converted into map distances with Kosambi’s mapping function (Kosambi 1943). Composite interval mapping was performed to locate loci associated with the arcsine of %IP by using QTL Cartographer ver. 2.5 (Wang *et al.* 2012, <http://statgen.ncsu.edu/qtlcart/WQTLCart.htm>). The walking speed for composite interval mapping was 1 cM. The LOD threshold value at the 5%-probability level was calculated by a 1000-replicate permutation test (Churchill and Doerge 1994).

Results

WYMV resistance in differential cultivars and major cultivars in Japan

A set of three differential cultivars (‘Nambukomugi’, ‘Fukuhokomugi’, and ‘Hokkai 240’) was used to identify the WYMV pathotype in our nurseries in Date, Hokkaido. These cultivars differ in their susceptibility to Japanese isolates WYMV-M and WYMV-T: ‘Nambukomugi’ is susceptible to WYMV-M and WYMV-T; ‘Fukuhokomugi’ is susceptible to WYMV-T but not to WYMV-M; and ‘Hokkai 240’ is not susceptible to either isolate. The %IP values of ‘Nambukomugi’, ‘Fukuhokomugi’, and ‘Hokkai 240’ in our nurseries were 95%, 0%, and 10%, respectively. Thus, ‘Nambukomugi’ was considered susceptible, and ‘Fukuhokomugi’ and ‘Hokkai 240’ were considered resistant. This indicates that our nurseries were predominantly infested with type II pathotype (which is represented by WYMV-M; Ohto *et al.* 2006).

Of the five major Japanese cultivars tested, ‘Hokushin’, ‘Kitahonami’, ‘Kitanokaori’, and ‘Takunekomugi’ were susceptible to WYMV (%IP, 85%–100%), but ‘Yumechikara’ was resistant (%IP, 0). ‘Madsen’ and ‘OW104’ showed little to no WYM symptoms and their %IP values were 0%–5% (Table 1).

Table 1. WYMV resistance of differential and major Japanese cultivars

Category	Cultivar	%IP	Reaction to WYMV
Differential cultivars	'Nambukomugi'	95	Susceptible
	'Fukuhokomugi'	0	Resistant
	'Hokkai 240'	10	Resistant
Major cultivars	'Hokushin'	95	Susceptible
	'Kitahonami'	85	Susceptible
	'Kitanokaori'	95	Susceptible
	'Takunekomugi'	100	Susceptible
	'Yumehikara'	0	Resistant
Resistant resources	'Madsen'	5	Resistant
	'OW104'	0	Resistant

Fig. 1. Frequency distribution of WYMV %IP in the 'OW104'/'Hokushin' F₃ population. a: 2016, b: 2017.

Frequency distribution of WYMV resistance in F₃ progenies

Two hundred and twenty-one F₃ progenies from a cross between 'OW104' and 'Hokushin' were tested for WYMV-resistance in field experiments for two years. The %IP values of the resistant parental cultivar 'OW104' and susceptible parental cultivar 'Hokushin' were 0% and 94% in 2016 and 2% and 97% in 2017, respectively. In 2016, 176 progenies (80% of the population) had %IP less than 30% and 34 (15%) had %IP higher than 70% (Fig. 1a). Similarly, in 2017, 178 progenies (80% of the population) had %IP less than 30% and 34 (15%) had %IP higher than 70% (Fig. 1b). Therefore, in both years approximately 95% of the population had %IP either less than 30% or higher than 70%.

Fig. 2. Mapping of WYMV resistance QTLs detected in 'OW104'/'Hokushin' F₃ population. Upper panel: genetic linkage map and LOD score plots of chromosome 6D. Genetic distance and physical position from IWGSC RefSeq v1.0 (<https://urgi.versailles.inra.fr/>) of SSR markers are shown in the middle column. Lower panel: description of QTLs detected in 2016 and 2017. **Fig. 3.** Genotypes at *Qym4* (*Xbarc183*–*Xbarc173*) and WYMV resistance of F₃ progenies. Numbers on top of bars indicate average %IP for each genotype.

QTL analysis of the 'OW104'/'Hokushin' population

We constructed a linkage map of a total length of 3139.8 cM with average number of markers per chromosome equal to 8.0. Each chromosome was mapped with at least six markers except for chromosomes 1D and 2A (five markers) and 4D (four markers). A single QTL for the arcsine of %IP, hereafter *Qym4*, was detected at the distal end of chromosome 6DS (from marker *Xbarc183* to *Xbarc173*) in both 2016 and 2017 (Fig. 2, upper panel); *Qym4* accounted for 45% and 57% of phenotypic variance in 2016 and 2017, respectively (Fig. 2, lower panel). F₃ progenies with 'OW104' alleles at *Qym4* had significantly lower %IP

Fig. 4. Graphical genotype of 'Hokushin' NILs. Black boxes indicate presence of 'OW104' allele. Genetic distance was calculated from QTL analysis of the 'Hokushin'/'OW104' F_3 population. F_1 plants were genotyped with only co-dominant SSR markers used in the QTL analysis.

(2016, 0%; 2017, 2%) than 'Hokushin' genotypes (2016, 90%; 2017, 80%) or heterozygotes (2016, 23%; 2017, 20%) by the Tukey-Kramer multiple comparison test (Fig. 3).

Qym4 genotype and WYMV resistance in 'Hokushin' NILs

Two BC_3F_1 'Hokushin' NIL plants and 10 BC_4F_1 NIL plants were developed by backcrossing and WYMV

resistance selection in field experiments. No WYMV was detected in the 12 plants by ELISA. The plants were genotyped with the same set of SSR markers used in the QTL analysis except for dominant markers, which could not differentiate ‘Hokushin’ and heterozygous alleles. Out of the 146 SSR marker loci, the NIL plants were heterozygous for ‘OW104’ and ‘Hokushin’ alleles at 6–20 loci (average 11.6 loci). All of the BC₃F₁/BC₄F₁ NILs carried the ‘OW104’ allele only at *Xcfd49* on chromosome 6DS (Fig. 4).

Discussion

WYMV susceptibility of differential cultivars indicated that the dominant pathotype in our nurseries is type II, which is the dominant pathotype in Hokkaido (Ohki *et al.* 2014, Ohto *et al.* 2006). WYMV was not detected in ‘OW104’ grown in our nurseries; its resistance was comparable to that of other resistant resources such as ‘Madsen’ and ‘Yumehikara’. ‘OW104’ originated from a cross between a spring wheat line ‘OS21-5’ and a WYMV-susceptible winter wheat line ‘61199’ (Osanai *et al.* 2005). We have not tested WYMV resistance of ‘OS21-5’ or its spring wheat progenitors because they do not survive in our field nurseries in winter; further study is necessary to elucidate the origin of the resistance.

The frequency distribution of WYMV %IP in the ‘OW104’/‘Hokushin’ F₃ population implies that a single major gene confers WYMV resistance (Fig. 1). This is supported by the QTL analysis in which only a single major QTL, *Qym4* at the distal end of chromosome 6DS, was stably detected in two years trials. Progenies with the ‘OW104’ allele at *Qym4* (*Xbarc183–Xbarc173*) showed significantly higher resistance than those with the ‘Hokushin’ allele (Fig. 3). ‘OW104’ genotype was conserved only at *Xcfd49* on 6DS among the WYMV-resistant ‘Hokushin’ NILs (Fig. 4). Although it is possible that we failed to detect minor QTLs, especially on regions where marker density was low (Fig. 4), these results indicate that *Qym4* confers WYMV resistance.

Qym4 heterozygotes showed significantly lower %IP than that in ‘Hokushin’ genotypes, suggesting that ‘OW104’ allele at the *Qym4* locus is incompletely dominant for resistance (Fig. 3). Several WYMV-resistance genes in wheat have been reported to be completely dominant, except for *Qym1* whose dominance is incomplete (Suzuki *et al.* 2015, Zhu *et al.* 2012). In contrast, 15 BaYMV-resistance genes are recessive and three are dominant in barley (Kai *et al.* 2012, Ordon *et al.* 2009). The 8.1-Mb *Qym4* region (*Xbarc183–Xbarc173*) includes a sequence homoeologous to the diagnostic molecular marker for *Rym14^{Hb}*, a BaYMV resistance gene, at the distal end of barley chromosome 6H (http://plants.ensembl.org/Hordeum_vulgare/Location/Compare_Alignments/Image?r=chr6H:7901646-7902539;align=9627;db=core, Howe *et al.* 2020, Ruge *et al.* 2003). It is possible that *Rym14^{Hb}* is homoeologous to *Qym4* considering that both genes are

dominantly inherited and located at the similar location of the homoeologous chromosome.

Resistance to WYMV has been extensively studied and QTLs have been detected on 2DL, 3BS, 5AL, 4D and 7BS (Kojima *et al.* 2015, Liu *et al.* 2005, Nishio *et al.* 2010, Suzuki *et al.* 2015, Zhu *et al.* 2012), but not on 6DS. Therefore, *Qym4* is likely to be a novel QTL for WYMV resistance. This presents a possibility to pyramid *Qym4* with other WYMV-resistance QTLs. Resistance QTLs on chromosome arm 2DL have been reported to be closely linked to small grain size and high polyphenol oxidase activity, both of which are considered undesirable traits in wheat breeding (Kasuya *et al.* 2017, Kiribuchi-Otobe *et al.* 2019). Although we have yet to elucidate whether *Qym4* is closely linked to such undesirable agronomic or processing quality traits, our results indicate that *Qym4* can be transferred to breeding materials by marker-assisted selection. The WYMV-resistant NILs developed in this study would be useful to identify linkage between *Qym4* and other agronomic traits and to introduce *Qym4* to breeding materials as well as to identify the candidate gene responsible for WYMV resistance.

Author Contribution Statement

YY and TS designed experiments and developed plant materials. YY, CS, RO, and TS evaluated phenotypes. YY genotyped the materials, performed genetic analysis, and wrote the manuscript.

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Literature Cited

- Churchill, G.A. and R.W. Doerge (1994) Empirical threshold values for quantitative trait mapping. *Genetics* 138: 963–971.
- Han, C., D. Li, Y. Xing, K. Zhu, Z. Tian, Z. Cai, J. Yu and Y. Liu (1997) *Wheat yellow mosaic virus* widely occurring in wheat (*Triticum aestivum*) in China. *Plant Dis.* 84: 627–630.
- Hokkaido (2019) Mugirui-Binran (Statistics for wheat production in Hokkaido). <http://www.pref.hokkaido.lg.jp/ns/nsk/mamemugi/mamemuginran.htm>.
- Horita, H., T. Takeuchi, J. Sasaki, T. Suzuki and T. Kiguchi (2011) Distribution of wheat yellow mosaic disease in Hokkaido. *Ann. Rept. Plant Prot. North Japan* 62: 47–49.
- Howe, K.L., B. Contreras-Moreira, N. De Silva, G. Maslen, W. Akanni, J. Allen, J. Alvarez-Jarreta, M. Barba, D.M. Bolser, L. Cambell *et al.* (2020) Ensembl Genomes 2020—enabling non-vertebrate genomic research. *Nucleic Acids Res.* 48: 689–695.
- Inouye, T. (1969) Filamentous particles as the causal agent of yellow mosaic disease of wheat. *Nogaku Kenkyu* 53: 61–68.
- 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.
- Kasuya, M., S. Ohnishi, T. Sonoda, Y. Yoshimura, T. Suzuki and H. Jinno (2017) Agronomic traits and flour quality in near-isogenic winter wheat lines containing Wheat yellow mosaic virus and eyespot resistance QTL. Breed. Res. (extra issue 131st Meet. Jap. Soc. Breed.) 19: 34.
- Kiribuchi-Otobe, C., M. Fujita, T. Takayama, H. Kojima, M. Chono and Y. Fujita (2019) Breeding of a hard white wheat “Tamaizumi R” with resistance to wheat yellow mosaic virus. Breed. Res. 21: 35–40.
- Kojima, H., Z. Nishio, F. Kobayashi, M. Saito, T. Sasaya, C. Kiribuchi-Otobe, M. Seki, S. Oda and T. Nakamura (2015) Identification and validation of a quantitative trait locus associated with wheat yellow mosaic virus pathotype I resistance in a Japanese wheat variety. Plant Breed. 134: 373–378.
- Kosambi, D. (1943) The estimation of map distances from recombination values. Ann. Eugen. 12: 172–175.
- Kusume, T., T. Tamada, H. Hattori, T. Tsuchiya, K. Kubo, H. Abe, S. Namba, T. Tsuchizaki, K. Kishi and S. Kashiwazaki (1997) Identification of a new wheat yellow mosaic virus strain with specific pathogenicity towards major wheat cultivars grown in Hokkaido. Japanese Journal of Phytopathology 63: 107–109.
- Lander, E.S., P. Green, J. Abrahamson, A. Barlow, M.J. Daly, S.E. Lincoln and L. Newburg (1987) MAPMAKER: An interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1: 174–181.
- Liu, C., T. Suzuki, K. Mishina, A. Habekuss, A. Ziegler, C. Li, S. Sakuma, G. Chen, M. Pourkheirandish and T. Komatsuda (2016) Wheat yellow mosaic virus resistance in wheat cultivar Madsen acts in roots but not in leaves. J. Gen. Plant Pathol. 82: 261–267.
- Liu, W., H. Nie, S. Wang, X. Li, Z. He, C. Han, J. Wang, X. Chen, L. Li and J. Yu (2005) Mapping a resistance gene in wheat cultivar Yangfu 9311 to yellow mosaic virus, using microsatellite markers. Theor. Appl. Genet. 111: 651–657.
- Lu, X., S. Kashiwazaki, M. Tamura and S. Namba (1998) The 3′ terminal sequence of RNA1 of wheat spindle streak mosaic virus canadian isolate (WSSMV-C). Eur. J. Plant Pathol. 104: 765–768.
- Namba, S., S. Kashiwazaki, X. Lu, M. Tamura and T. Tsuchizaki (1998) Complete nucleotide sequence of wheat yellow mosaic bymovirus genomic RNAs. Arch. Virol. 143: 631–643.
- Nishimura, T., T. Suzuki, H. Jinno, S. Asayama, S. Munekata, H. Horita, Y. Yoshimura, S. Kobayashi and M. Sato (2010) Evaluation of yield in breeding wheat lines with high resistance to wheat yellow mosaic virus by repeated backcrossing. Jpn. J. Crop Sci. (extra issue 230th Meet. Crop Sci. Soc. Japan) 78–80.
- Nishio, Z., H. Kojima, A. Hayata, N. Iriki, T. Tabiki, M. Ito, H. Yamauchi and T.D. Murray (2010) Mapping a gene conferring resistance to Wheat yellow mosaic virus in European winter wheat cultivar “Ibis” (*Triticum aestivum* L.). Euphytica 176: 223–229.
- Nitta, M. and S. Nasuda (2012) Report of the project “Polymorphism survey among hexaploid wheat and its relatives by DNA markers” conducted in the second-term National BioResource Project-Wheat, Japan. eWIS 114: online publication (<http://www.shigen.nig.ac.jp/ewis>).
- Ohki, T., O. Netsu, H. Kojima, J. Sakai, M. Onuki, T. Maoka, Y. Shirako and T. Sasaya (2014) Biological and genetic diversity of Wheat yellow mosaic virus (genus *Bymovirus*). Virology 104: 313–319.
- Ohto, Y., K. Hatta and K. Ishiguro (2006) Differential wheat cultivars to discriminate pathogenicity of Japanese wheat yellow mosaic virus (WYMV) isolates. Jpn. J. Phytopathol. 72: 93–100.
- Ordon, F., A. Habekuss, U. Kastirr, F. Rabenstein and T. Kühne (2009) Virus resistance in cereals: sources of resistance, genetics and breeding. J. Phytopathol. 157: 535–545.
- Osanai, S., Y. Amano and D. Mares (2005) Development of highly sprouting tolerant wheat germplasm with reduced germination at low temperature. Euphytica 143: 301–307.
- 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.
- Sawada, E. (1927) Wheat yellow mosaic prevention. J. Plant Prot. 14: 444–449.
- Suzuki, T., M. Sato and T. Takeuchi (2012) Evaluation of the effects of five QTL regions on *Fusarium* head blight resistance and agronomic traits in spring wheat (*Triticum aestivum* L.). Breed. Sci. 62: 11–17.
- 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.
- Takeuchi, T., S. Munekata, T. Suzuki, K. Senda, H. Horita, K. Araki, S. Asayama and M. Sato (2010) Breeding wheat lines resistant to wheat yellow mosaic virus and localization of the resistance gene (*YmMD*) derived from wheat cultivar “Madsen”. Breed. Res. 12: 1–8.
- Ueda, I., Y. Takahashi, M. Isogai, R. Yamana, A. Horisaki, T. Hataya and T. Takeuchi (1998) Detection of wheat yellow mosaic virus by antiserum against the bacterially expressed coat proteins. Jpn. J. Phytopathol. 64: 583.
- Wang, S., C. J. Basten and Z.-B. Zeng (2012) Windows QTL cartographer 2.5. Department of Statistics, North Carolina State University, Raleigh, NC. <http://stagen.ncsu.edu/qtlcart/WQTLCart.htm>.
- Werner, K., W. Friedt and F. Ordon (2005) Strategies for pyramiding resistance genes against the Barley Yellow Mosaic Virus complex (BaMMV, BaYMV, BaYMV-2). Mol. Breed. 16: 45–55.
- Yamashita, Y., T. Suzuki and R. Ogura (2017) Genetic analysis of “OW104”, a novel source of resistance to wheat yellow mosaic virus. Rep. Hokkaido Branch, Japanese Soc. Breed. Hokkaido Branch, Crop Sci. Soc. Japan 58: 80–81.
- 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.