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 Xgwp4357 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 BC1F3/BC1F1 plants carried ‘OW104’ allele only at Xcfd49. Our results suggest that the introduction of Qym4 confers resistance to WYMV in winter wheat.

Key Words: Triticeae 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-M, 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 ‘Yumchikara’, 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 ‘Yumchikara’ (Kojima et al. 2015, Liu et al. 2005, Nishio et al. 2010). These QTLs may be allelic and thus...
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 WYMV 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 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, 140.9E). 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).
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%.

Table 1. WYMV resistance of differential and major Japanese cultivars

| Category          | Cultivar     | %IP | Reaction to WYMV |
|-------------------|--------------|-----|------------------|
| Differential      | ‘Nambukomugi’| 95  | Susceptible      |
|                   | ‘Fukuhokomugi’| 0   | Resistant        |
|                   | ‘Hokkai 240’ | 10  | Resistant        |
| Major             | ‘Hokushin’   | 95  | Susceptible      |
|                   | ‘Kitahonami’ | 85  | Susceptible      |
|                   | ‘Kitanokaori’| 95  | Susceptible      |
|                   | ‘Takunekomugi’| 100 | Susceptible        |
|                   | ‘Yumecichikara’| 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%.

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

Two BC$_1$F$_1$ ‘Hokushin’ NIL plants and 10 BC$_2$F$_1$ NIL plants were developed by backcrossing and WYMV resistance in ‘Hokushin’ NILs

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.
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 BC$_3$F$_1$/BC$_3$F$_1$ 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, Ohno 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 ‘Yumechikara’. ‘OW104’ originated from a cross between a spring wheat line ‘OS21-5’ and a WYMV-susceptible winter wheat line ‘61199’ (Osaai 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’ F$_3$ 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$^{1bh}$, a BaYMV resistance gene, at the distal end of barley chromosome 6H (http://plants.ensembl.org/Hordeum_vulgare/Location/Compara_Alignments/Image;r =chr6H:7901646-7902539;align=9627;db=core, Howe et al. 2020, Ruge et al. 2003). It is possible that Rym14$^{1bh}$ 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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