Introduction

Rice (Oryza sativa L.) is the most important crop and essential daily food worldwide (Khush 2003). Wild rice is a rare germplasm resource and very important for biodiversity conservation (Zhang and Xie 2014). The AA-genome species of the genus Oryza have valuable genes for the improvement of cultivated rice, in particular genes conferring resistance to brown planthopper (BPH), small brown planthopper, white-backed planthopper, green leafhopper (GLH), green rice leafhopper (GRH), yellow stem borer, leaf and neck blast, bacterial leaf blight, and sheath blight (Brar and Khush 1997, Fujita et al. 2013, Jena 2010, Khush 1997).

Host-plant resistance has been used to reduce direct damage to plants from insect attack and indirect damage from viral transmission (Brar et al. 2009). Using resistant varieties helps to manage the problems caused by insect pests such as GRH, GLH, and BPH. One of the most serious insect pests of rice, GRH (Nephotettix cincticeps Uhler), is distributed mostly in the temperate regions of East Asia (Ghauri 1971) and is widely distributed in Japan (Hokyo 1971). GRH sucks sap from both the xylem and the phloem of susceptible rice varieties, leading to yield losses in northeastern Japan (Nirei and Nakazato 1975). In addition to causing direct plant damage, GRH transmits viral diseases, such as rice dwarf (Brar et al. 2009) and waika viruses, both of which are common in western Japan (Nakasuji and Nomura 1968). The level of resistance to GRH differs among rice varieties and growth stages (Kishino and Ando 1979). In resistant varieties such as IR24, Lepe-dumai, and Rantaj-emas 2, GRH resistance is strong at the young seedling and booting stages but is weaker at the tiller emergence and other growth stages. Knowledge of such differences may be useful for understanding the genetic mechanisms of GRH resistance (Fujita et al. 2010b).

Several studies to identify genes or quantitative trait loci (QTLs) that confer resistance to GLH and GRH have been reported. Genetic mapping identified a single dominant gene for resistance to GLH on chromosome 4 derived from a cross between the varieties ARC11554 and TN1 (Sebastian et al. 1996). Brar and Khush (2002) reported...
GLH-resistant six accessions of the wild species *Oryza barthii*. A total of six genes and two QTLs conferring GRH resistance have been identified and mapped on seven rice chromosomes using *O. sativa* landraces and other *Oryza* species. The resistance genes include *Grh1* on chromosome 5 derived from IR24, *Pe-bi-hun*, *Singwang*, and ASDD7 (Kadowaki et al. 2003, Mai et al. 2015, Park et al. 2013, Tamura et al. 1999); *Grh2* on chromosome 11 and *Grh4* on chromosome 3 from Lepe-dumai and DV85 (Fukuta et al. 1998, Kadowaki et al. 2003); and *Grh3* on chromosome 6 from Rantaj-emas 2 and Cheongnam (Hur et al. 2015, Saka et al. 2006). One major gene conferring GRH resistance from the Surinam cultivar SML17 and another one from a wild accession of *Oryza nivara* were mapped on the short arm of chromosome 4 and named *Grh6* (Tamura et al. 2004) and *Grh6-nivara* (Fujita et al. 2004), respectively. A wild accession of *Oryza rufipogon* Griff., W1962, is highly resistant to GRH. One gene, *Grh5* on chromosome 8, and a minor QTL, *qGRH4*, have been mapped using a backcross population between the *O. sativa* *ssp.* japonica cultivar “Taichung 65” and W1962 (Fujita et al. 2006, 2010a). Genetic resources of rice landraces were characterized (Mai et al. 2017), but the genetic analyses of GRH resistance are limited. A significant major QTL on the long arm of chromosome 9 (*qGRH9*) is derived from the African rice species *Oryza glaberrima* (Fujita et al. 2010b); however, the genetic basis of GRH resistance of *O. glaberrima* is not completely understood. No genes or QTLs for GRH resistance from another African rice species, *Oryza longistaminata* A. Chev. & Roehrich, have previously been reported.

African wild rice species are valuable sources of genetic and allelic diversity (Brar and Khush 2002, Jena 2010, Khush et al. 1990, Wambugu et al. 2013). Among the six wild species carrying the AA genome, *O. longistaminata* originates from tropical regions of Africa; it is a perennial species characterized by long anthers, strong rhizomes, and tolerance to blight and drought (Jena 2010, Liu et al. 2004, Neelam et al. 2018, Song et al. 1995). Mapping of QTLs for agronomically important traits such as vigorous biomass under low-input conditions and yield-enhancing traits (Gichuhi et al. 2016), QTLs for high ability to use nitrogen efficiently (Yang et al. 2010), rhizomatous expression trait (*Rhz2* and *Rhz3*) and resistance of bacterial blight (*Xa21*) (He et al. 2014, Hu et al. 2003, Khush et al. 1990, Sacks et al. 2003), a novel QTL (*qSPP2.2*) for the number of spikelets per panicle (Kaur et al. 2018), and QTLs for seed vigor-related traits (Jin et al. 2018) has been performed using several mapping populations derived from a cross between accessions of *O. longistaminata* and *O. sativa*. Rawal et al. (2018) reported that *O. longistaminata* has abundant nucleotide-binding site (NBS)-encoding genes, which are important for plant defense. However, unlike with the other AA species, it is difficult to obtain F$_1$ interspecific progeny using *O. longistaminata* because of embryo abortion (Causse et al. 1994, Chen et al. 2009, Sacks et al. 2003).

Development of chromosome segment substitution lines (Ramos et al. 2016) and recombinant inbred lines carrying *O. longistaminata* segments have been developed for QTL analysis of agronomic traits (Gichuhi et al. 2012). Introgression lines (ILs), each carrying a particular chromosome segment from the donor parent in the genetic background of the recurrent parent, have been used to identify genes for quantitative traits by fine QTL mapping (Chetelat et al. 1995, Chetelat and Meglic 2000, Eshed and Zamir 1994, 1995, 1996, Kubo et al. 2002, Yano 2001). The use of ILs for mapping of small-effect QTLs and map-based cloning has been reported (Ebitani et al. 2005, Fukuoka et al. 2010). Several sets of ILs carrying chromosome segments from wild rice in the genetic background of cultivated rice have been developed to detect QTLs for valuable traits (Ahn et al. 2002, Doi et al. 1997, Hirabayashi et al. 2010, Kurakazu et al. 2001, Sobrizal et al. 1999, Tian et al. 2006, Yoshimura et al. 2010).

To understand the genetic basis of GRH resistance derived from *O. longistaminata*, we developed ILs derived from *O. longistaminata* in the genetic background of *O. sativa* *ssp.* japonica cv. ‘Nipponbare’ and detected four QTLs for resistance to GRH.

### Materials and Methods

#### Development of ILs

$F_1$ plants were derived from a cross between *O. sativa* *ssp.* japonica cv. ‘Nipponbare’ as the female parent and African wild rice *O. longistaminata* accession W1413, originally collected from Sierra Leone, as the male parent (Fig. 1). $F_1$ plants were successively backcrossed using Nipponbare pollen to the BC$_2$F$_1$ generation, and whole-genome genotyping was conducted with simple sequence repeat (SSR) markers distributed across all 12 chromosomes.

![Fig. 1. Development of ILs derived from W1413 (O. longistaminata) in the Nipponbare (O. sativa) genetic background. MAS represents marker-assisted selection. NILs mean near-isogenic lines. PYLs mean pyramided lines.](image-url)
BC$_2$F$_1$ plants were selected on the basis of their graphical genotypes; BC$_2$F$_2$ plants were backcrossed with Nipponbare to generate BC$_3$F$_1$ plants. BC$_3$F$_1$ plants with heterozygous for W1413 alleles in the target region of each chromosome were selected to generate progeny. A series of ILs was produced by self-pollination of BC$_3$F$_2$ plants to fix homozygous W1413 alleles in the target introgressed segments in the Nipponbare genetic background. These ILs were used to evaluate GRH resistance; subsequently, BC$_3$F$_3$ and BC$_3$F$_4$ populations were used in QTL analysis.

**Genetic mapping of GRH resistance**

BC$_3$F$_3$ populations derived from individual plants of three ILs (BC$_3$F$_2$) and three sister lines of these ILs were used for QTL analysis. The parental BC$_3$F$_2$ plants carried homozygous segments on chromosomes 1, 2, 3, 4, 5, 7, and 11 and W1413-homozygous segments on chromosomes 1, 2, 5 and 11. Seven BC$_3$F$_4$ populations derived from individual plants of four BC$_3$F$_3$ mapping populations were used for QTL validation. The parents of these four BC$_3$F$_3$ plants carried homozygous segments on chromosomes 2, 4, 5, and 11 and W1413-homozygous segments on chromosomes 2, 5, and 11 in the Nipponbare genetic background.

**Evaluation of GRH resistance**

The GRH strain was collected in Fukuoka Prefecture, Japan, in 1991 and was maintained by continuous rearing on seedlings of Nipponbare, which is susceptible. GRH was kept at 25 ± 1°C and 16 h light: 8 h dark. An antibiosis test for GRH resistance was conducted according to Kishino and Ando (1978) with modifications. Seedlings (10 individuals per IL, six BC$_3$F$_1$ populations, and seven BC$_3$F$_2$ populations) were grown for 7 days and infested with 10 first-instar nymphs in test tubes. Because it was difficult to obtain seeds of W1413 from self-pollination, this accession was maintained as ratoon plants, and young leaves were used for evaluation of resistance. Nymph mortality (NM, %) was calculated at 3 days after infestation (DAI), 5 DAI, and 7 DAI. Seedlings (20 per line) of four pre-NILs (near-isogenic lines), each carrying one QTL, and four pre-PYLs (pyramided lines), each carrying two or four QTLS, were also analyzed to measure the GRH resistance level. Plants were categorized as susceptible (NM <30%), moderately resistant (NM 30%–70%), or highly resistant (NM >70%).

**Whole-genome genotyping and construction of a linkage map**

Total genomic DNA was extracted from freeze-dried leaves as in Dellaporta et al. (1983). The genotypes of SSR loci were determined by PCR amplification in a PCR System 9700 (PerkinElmer, Waltham, MA, USA). Primer sequences of SSR markers are listed in Supplemental Table 1. PCR mixtures (15 μl) contained 50 mM KCl, 10 mM Tris HCl (pH 9.0), 1.5 mM MgCl$_2$, 200 μM each dNTP, 0.2 μM primer, 0.5 unit of Taq polymerase (Takara, Shiga, Japan), and 25 ng of genomic DNA. The thermal cycler was programmed as follows: 5 min at 95°C; then 40 cycles of 95°C for 30 s, 55°C for 30 s, and 72°C for 30 s. PCR products were separated by electrophoresis in 4% agarose gels at 250 V for 1 h in 0.5× TBE buffer. Gels were stained with ethidium bromide and photographed under ultraviolet light.

A genetic linkage map was constructed with 108 polymorphic SSR markers covering all chromosomes using 115 BC$_3$F$_1$ plants. MAPMAKER/EXP 3.0 (Lander et al. 1987) was used to determine the linkage loci and map distances.

**QTL mapping and statistical analyses**

The phenotype and genotype data of BC$_3$F$_3$ and BC$_3$F$_4$ plants were used for standard interval mapping with R/qtl software (Broman and Sen 2009). The critical experiment-wise threshold values of the logarithm of odds (LOD) scores for QTL analysis were calculated by conducting 1000 permutation tests at the significance level of 5%. To assess the average NM of pre-NILs and pre-PYLs, differences between means were statistically analyzed by using Scheffe’s method following analysis of variance at significance level P < 0.05.

### Results

**GRH resistance of the parental lines and F$_1$ plants**

Small leaves of ratoon plants of the W1413 accession of *O. longistaminata*, which were similar to those of seedlings at about 10 days after sowing (DAS), were resistant to GRH. The leaves of W1413 were also resistant at 30 DAS (pre-tillering stage) and 60 DAS (tillering stage), whereas those of Nipponbare were susceptible to GRH at all three stages. At 10 and 30 DAS, average NM of W1413 was 100% ± 0.0% (mean ± SE; N = 5) and that of Nipponbare was 0.0% ± 0.0%. At 60 DAS, it was 93.5% ± 3.0% in W1413, 1.7% ± 3.7% in Nipponbare, and 69.8% ± 4.0% in F$_1$ plants, which were thus moderately resistant to GRH.

**Construction of a series of ILs covering the whole genome of *O. longistaminata***

F$_1$ individuals derived from a cross between Nipponbare (female parent) and W1413 (male parent) were backcrossed with Nipponbare, and 39 BC$_1$F$_1$ plants were developed (Fig. 1). They were backcrossed with Nipponbare, and 115 BC$_2$F$_1$ plants were developed. Graphical genotypes of the BC$_2$F$_1$ plants showed the presence of target heterozygous introgressed segments in all 12 chromosomes. A total of 18 BC$_2$F$_2$ lines (36 plants per line) were grown, and 6 plants per line were backcrossed with Nipponbare. Consequently, 328 BC$_3$F$_1$ plants were developed and genotyped with 108 SSR markers (Supplemental Table 1); of these, 27 BC$_3$F$_1$ lines (36 plants per line) that carried target heterozygous segments on each chromosome were self-pollinated to produce BC$_3$F$_2$ populations. Candidate BC$_3$F$_2$ plants (26 ILs from each BC$_3$F$_2$ plant and 2 ILs derived from the two sister plants of BC$_3$F$_2$ 5-13 and 5-28) were chosen; they were homozygous for W1413 alleles in the target introgressed regions, had heterozygous segments in some chromosomes
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**GRH resistance of the series of ILs**

We evaluated the resistance of the 28 BC$_3$F$_3$ ILs (Fig. 3). Four BC$_3$F$_3$ ILs had moderate to high resistance at 7 DAI: BC$_3$F$_3$ 3 (0%–50% NM), BC$_3$F$_3$ 9 (0%–90% NM), BC$_3$F$_3$ 21 (0%–85.7% NM), and BC$_3$F$_3$ 26 (0%–85.7% NM). IL 3 (BC$_3$F$_3$ 3) carried the segments of W1413 on chromosomes 1 and 5. IL 9 (BC$_3$F$_3$ 9) was homozygous for the target W1413 segment on chromosome 2 with heterozygous segments on chromosomes 4, 5, and 11. IL 26 (BC$_3$F$_3$ 26)
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Carried the target segment on chromosome 11 with small heterozygous segments on chromosomes 4 and 7 (Fig. 2). The number of seeds of BC$_3$F$_2$ 21 was limited because of high sterility. The other 24 ILs had NM from 0% to 30%.

**Candidate QTLs detected in BC$_3$F$_3$ populations**

A total of six BC$_3$F$_3$ populations derived from the candidate BC$_3$F$_2$ plants, namely BC$_3$F$_3$ 3 from BC$_3$F$_2$ 3-6 (Fig. 4a), BC$_3$F$_3$ 103 from BC$_3$F$_2$ 3-4 (Fig. 4b), BC$_3$F$_3$ 9 from BC$_3$F$_2$ 7-11 (Fig. 4c), BC$_3$F$_3$ 107 from BC$_3$F$_2$ 7-35 (Fig. 4d), BC$_3$F$_3$ 26 from BC$_3$F$_2$ 25-4 (Fig. 4e), and BC$_3$F$_3$ 123 from BC$_3$F$_2$ 25-34 (Fig. 4f), were subjected to QTL analysis. The graphical genotypes of the six candidate BC$_3$F$_2$ individuals are shown in Fig. 4.

The BC$_3$F$_2$ 3-6 plant carried W1413-homozygous segments on chromosomes 1 and 5 (Fig. 4a). Among a total of 90 BC$_3$F$_3$ 3 individuals, continuous distribution from low to high NM at 7 DAI was observed (Fig. 4a). However, all plants of BC$_3$F$_3$ population 3 had fixed homozygous W1413 alleles on chromosomes 1 and 5; thus, the cause of segregation of NM in this population was unknown and it was excluded from QTL analysis.

BC$_3$F$_2$ 3-4, a sister plant of BC$_3$F$_2$ 3-6, carried heterozygous segments on chromosomes 1, 3, and 5 (Fig. 4b). Among a total of 76 BC$_3$F$_3$ 103 individuals, a continuous distribution from low to high NM at 7 DAI was observed (Fig. 4b). A significant QTL ($qGRH5$) was detected between RM509 and RM430 on chromosome 5 in the BC$_3$F$_3$ 103 population and explained 12.8% of phenotypic variation (PV) with an additive NM value of 21.6 (Table 1). No significant QTLs on chromosomes 1 and 3 were detected at the 5% significance level.

The BC$_3$F$_2$ 7-11 plant carried heterozygous segments on chromosomes 4, 5, and 11, and a W1413-homozygous

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**Fig. 4.** Graphical genotypes of six individual BC$_3$F$_2$ plants derived from a cross between Nipponbare and W1413, and frequency distributions of nymph mortality (%) at 7 DAI in the six BC$_3$F$_3$ populations derived from these plants. The names of the BC$_3$F$_2$ plant and corresponding BC$_3$F$_3$ population are indicated in the middle of each panel (a–f). Chromosome number is indicated above each chromosome. Black and white rectangles indicate homozygous for W1413 and Nipponbare segments, respectively. SSR markers are listed to the right of each chromosome. Black and white arrowheads indicate average nymph mortality in Nipponbare and W1413, respectively.
segment on chromosome 2 (Fig. 4c). Among a total of 79 BC3F2 9 individuals, a continuous distribution from low to high NM at 7 DAI was observed (Fig. 4c). A significant QTL (qGRH11) was detected between RM5960 and RM6680 on chromosome 11 and explained 11.0% of PV with an additive NM value of 14.6 (Table 1). No significant QTLs on chromosomes 4 and 5 were detected at the 5% significance level in this population.

BC3F2 7-35, a sister plant of BC3F2 7-11, carried heterozygous segments on chromosomes 2, 4, and a W1413-homozygous segment on chromosomes 5 and 11 (Fig. 4d). Among a total of 55 BC3F2 107 individuals, a pseudo-normal distribution from low to high NM at 7 DAI was observed (Fig. 4d). A significant QTL (qGRH4) was detected between RM5414 and RM8213 and explained 22.0% of PV with an additive NM value of 23.9. No significant QTLs on chromosomes 2 and 5 were detected at the 5% significance level.

The BC3F2 25-4 plant carried heterozygous segments on chromosomes 4 and 7, and a W1413-homozygous segment on chromosome 11 (Fig. 4e). Among a total of 84 BC3F2 26 individuals, a continuous distribution from low to high NM was observed (Fig. 4e). One significant QTL (qGRH4 described above) was detected and explained 7.1% of PV with an additive NM value of 23.0 (Table 1). No significant QTLs on chromosome 7 were detected at the 5% significance level.

BC3F2 25-34, a sister plant of BC3F2 25-4, carried heterozygous segments on chromosomes 4, 7, and 11 (Fig. 4f). Among a total of 99 BC3F2 123 individuals, a continuous distribution from low to high NM at 7 DAI was observed (Fig. 4f). A significant QTL (qGRHL1 described above) was detected in the BC3F2 123 population and explained 11.2% of PV with an additive NM value of 12.6 (Table 1). No significant QTLs on chromosomes 4 and 7 were detected at the 5% significance level. Thus, three significant QTLs, qGRH4, qGRHL5, and qGRHL1, were identified in the five BC3F2 populations (Table 1).

**Validation of QTLs for GRH resistance**

Seven BC3F3 individuals were selected from four BC3F3 mapping populations on the basis of the genotypes of candidate QTL regions. The graphical genotypes of the selected individuals are shown in Fig. 5.

The BC3F3 123-47 plant was selected to validate qGRH4 (Fig. 5a). Among a total of 93 BC3F4 4 individuals, bimodal segregation with low and high NM at 7 DAI was observed (Fig. 5a). Only one QTL (qGRH4) was detected in the BC3F4 4 population and explained 14.8% of PV with an additive NM value of 13.7 (Table 2).

The BC3F3 103-41 plant was selected to validate qGRH5 (Fig. 5b). Among a total of 95 BC3F4 9 individuals, a continuous distribution from low to high NM at 7 DAI was observed (Fig. 5b). Only one QTL (qGRH5) was detected in the BC3F4 9 population and explained 12.3% of PV with an additive NM value of 12.6 (Table 2).

The BC3F3 9-76 plant was also selected to validate qGRH5; this plant had a W1413-homozygous segment on chromosome 2 (Fig. 5c). Among a total of 90 BC3F4 15 individuals, a continuous distribution from low to high NM was observed (Fig. 5c). Only one QTL (qGRH5) was detected in the BC3F4 15 population and explained 19.2% of PV with an additive NM value of 13.9 (Table 2).

The BC3F3 123-48 plant was selected to validate qGRH11 (Fig. 5d). Among a total of 93 BC3F4 1 individuals, a continuous distribution from low to high NM at 7 DAI was observed (Fig. 5d). Only one major QTL (qGRH11) was detected in the BC3F4 1 population and explained 21.5% of PV with an additive NM value of 15.2 (Table 2).

In addition, the BC3F3 9-60 plant, which carried heterozygous segments at qGRH4, qGRH5, and qGRH11, and a W1413-homozygous segment on chromosome 2 (graphical genotype identical to that of BC3F2 7-11; Fig. 4e), was selected to validate candidate QTLs. Among a total of 67 BC3F4 2 individuals, a continuous distribution from low to high NM at 7 DAI was observed (data not shown). Only one major QTL (qGRH11) was detected in the BC3F4 2 population and explained 21.1% of PV with an additive NM value of 18.1 (data not shown). No significant QTLs on chromosomes 4 and 5 were detected at the 5% significance level in this population. Thus, only qGRH11 was detected both in the BC3F4 2 and BC3F4 9 populations (Table 1).

The BC3F3 107-8 plant, which carried a heterozygous segment on chromosome 2 and W1413-homozygous segments at qGRH5 and qGRH11 (Fig. 5e), was selected to assess whether a QTL is present on chromosome 2. Among a

**Table 1. Candidate QTLs for nymph mortality detected in advanced backcross (BC3F3) populations derived from a cross between O. sativa cv. Nipponbare and O. longistaminata acc. W1413**

| Population | QTL   | Chromosome | Marker interval       | Peak LOD | PVE (%) | Additive effect | Dominance effect | LOD threshold |
|------------|-------|------------|-----------------------|----------|---------|----------------|------------------|---------------|
| BC3F3 103  | qGRH5 | 5          | RM509--RM430          | 2.1      | 12.8    | 21.6           | 4.7              | 2.1           |
| BC3F3 9    | qGRH11| 11         | RM5960--RM6680        | 2.0      | 11.0    | 14.6           | 15.9             | 1.8           |
| BC3F3 107  | qGRH4 | 4          | RM5414--RM8213        | 3.0      | 22.0    | 23.9           | 8.0              | 2.3           |
| BC3F3 26   | qGRH4 | 4          | RM5414--RM8213        | 1.3      | 7.1     | 23.0           | 2.1              | 1.3           |
| BC3F3 123  | qGRH11| 11         | RM5960--RM6680        | 2.6      | 11.2    | 16.8           | 5.8              | 2.1           |

* Positive values indicate that the W1413 allele increased nymph mortality.

* LOD threshold at the experiment-wise 5% significance level.

PVE represents phenotypic variation explained.
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**Fig. 5.** Graphical genotypes of individual BC$_3$F$_3$ plants derived from a cross between Nipponbare and W1413, and frequency distributions of nymph mortality (%) at 7 DAI in the seven BC$_3$F$_4$ populations derived from these plants. The names of the BC$_3$F$_3$ plant and corresponding BC$_3$F$_4$ population are indicated in the middle of each panel (a–f). Chromosome number is indicated above each chromosome. Black and white rectangles indicate homozygous for W1413 and Nipponbare segments, respectively. Detected QTL regions are shown in ovals. SSR markers are listed to the right of each chromosome. Markers linked to QTLs are underlined. Black and white arrowheads indicate average nymph mortality in Nipponbare and W1413, respectively. In frequency distribution, white, black and gray colors show the Nipponbare homozygous, W1413 homozygous and heterozygous at RM5414 (5a), RM509 (5b, 5c), RM5960 (5d), RM3688 (5e, 5f), respectively.

**Table 2.** Validation of QTLs for nymph mortality detected in advanced backcross (BC$_3$F$_4$) populations derived from a cross between *O. sativa* cv. Nipponbare and *O. longistaminata* acc. W1413

| QTLs    | Chromosome | Marker interval  | Peak LOD | PVE (%) | Additive effect | Dominance effect | Population | LOD threshold |
|---------|------------|------------------|----------|---------|----------------|-----------------|------------|--------------|
| qGRH4   | 4          | RM5414–RM8213    | 3.2      | 14.8    | 13.7           | 10.8            | BC$_3$F$_4$ 4 | 1.5          |
| qGRH5   | 5          | RM509–RM430      | 2.7      | 12.3    | 12.6           | 8.5             | BC$_3$F$_4$ 9 | 1.6          |
| qGRH11  | 11         | RM5960–RM6680    | 5.2      | 21.5    | 15.2           | 10.8            | BC$_3$F$_4$ 1 | 1.5          |
| qGRH2   | 2          | RM3688–RM3515    | 2.7      | 12.6    | 17.7           | 1.9             | BC$_3$F$_4$ 7 | 1.8          |
| qGRH4   | 4          | RM5414–RM8213    | 3.7      | 16.7    | 13.4           | 6.7             | BC$_3$F$_4$ 12 | 1.8         |
| qGRH2   | 2          | RM3688–RM3515    | 3.3      | 15.0    | 13.2           | 0.2             | BC$_3$F$_4$ 12 | 1.8         |

*Positive values indicate that the W1413 allele increased nymph mortality.

* LOD threshold at the experiment-wise significance at 5% level was used in the population.

PVE represents phenotypic variation explained.
total of 93 BC$_3$F$_4$ 7 individuals, a continuous distribution from low to high NM at 7 DAI was observed (Fig. 5e). A novel QTL (qGRH2) was detected between RM3688 and RM3515 on the long arm of chromosome 2 in the BC$_3$F$_4$ 7 population. qGRH2 explained 12.6% of PV with an additive NM value of 17.7 (Table 2).

The BC$_3$F$_1$ 107-24 plant, which carried heterozygous segments on chromosome 2 and at qGRH4, and W1413-homozygous segments at qGRH5 and qGRH11 (Fig. 5f), was selected for validating qGRH2 and qGRH4. Among a total of 92 BC$_3$F$_4$ 12 individuals, a continuous distribution from low to high NM was observed (Fig. 5f). Two QTLs (qGRH2 and qGRH4) were detected in the BC$_3$F$_4$ 12 population. The location of qGRH2 between RM3688 and RM3515 was confirmed; qGRH2 explained 15.0% of PV with an additive NM value of 13.2. The QTL qGRH4 explained 16.7% of PV with an additive NM value of 13.4 (Table 2).

Nymph mortality of pre-NILs and pre-PYLs

Four pre-NILs with W1413-homozygous alleles on the long arm of chromosome 2, the short arm of chromosome 4, the short arm of chromosome 11 and four pre-PYLs (qGRH2/qGRH11-PYL, qGRH4/qGRH11-PYL, qGRH5/qGRH11-PYL, and qGRH2/qGRH5/qGRH11-PYL) were selected from BC$_3$F$_3$ mapping populations and evaluated (N = 20) for GRH resistance (Fig. 6). The young leaves of W1413 ratoon plants were used as the resistant control. At 3 DAI, NM did not differ among the pre-NILs and pre-PYLs, but was significantly lower than that in W1413 (Fig. 6a). At 5 DAI, the NM increased but did not differ significantly among the pre-NILs and pre-PYLs except for qGRH5/qGRH11-PYL, which had the lowest NM, and the pre-PYL carrying four QTLs, which had the highest. The NM of all pre-NILs and pre-PYLs was significantly lower than that of W1413 (Fig. 6b). At 7 DAI, the NM levels of pre-NILs carrying qGRH2, qGRH4, and qGRH5 did not differ significantly from each other, but were significantly lower than those of qGRH11-NIL, the pre-PYLs, and W1413. The NM of the pre-NIL carrying qGRH11 did not differ significantly from those of the pre-PYLs but was lower than those of the four-QTL pre-PYL and W1413. Among all the lines, the pre-PYL carrying four QTLs showed the highest resistance level (97.3% ± 1.3), which was equivalent to that of W1413 (100.0% ± 0.0) (Fig. 6c).

Discussion

Identification of ILs for QTL detection

After fixing W1413 introgression segments on target chromosomes in the Nipponbare genetic background, a series of 28 ILs was evaluated for GRH resistance. Among them, four candidates had moderate to high NM. Candidate IL populations and populations derived from sister plants carrying heterozygous segments were used in QTL analysis. Segregating populations carrying chromosomal segments from W1413 in the Nipponbare genetic background allowed us to map QTLs for GRH resistance from the wild rice species O. longistaminata (Tables 1, 2).

Resistance levels of O. longistaminata and its derivatives

The donor parent, accession W1413, was highly resistant to GRH (up to NM 100.0% ± 0.0% at some stages) when tested by using leaves from ratoon plants. None of the segregating populations contained plants resistant at 3 DAI (Supplemental Figs. 1, 3); however, the NM at 5 and 7 DAI were distributed continuously from susceptibility to resistance (Figs. 4, 5, Supplemental Figs. 2, 4), indicating that multiple additive QTLs control GRH resistance derived from W1413.

Four significant QTLs for GRH resistance

Four significant QTLs (qGRH2, qGRH4, qGRH5, and qGRH11) were validated by using 12 advanced backcross populations (Tables 1, 2). The QTLs qGRH4, qGRH5, and qGRH11 were located on chromosomes 4, 5, and 11, respectively, in similar locations to the previously reported genes Grh6, Grh1, and Grh2, respectively. qGRH4, in the distal region of chromosome 4, was detected between the RM5414 and RM8213 markers (Fig. 5a, 5f); the Grh6-nivara gene, on the short arm of chromosome 4, is tightly linked with RM8213 and is located between the RM5414 and C60248 SSR markers (Fujita et al. 2004). qGRH5 had an LOD peak between the RM3381 and RM509 markers (Table 2, Fig. 5b, 5c), and the Grh1 gene from Pe-bi-hun and IR24 rice landraces is tightly linked with RM3381 (Kadowaki et al. 2003, Tamura et al. 1999, Yasui and Yoshimura 1999). qGRH11, on the long arm of chromosome 11, was similar to a candidate region of the previously mapped Grh2 gene from Lepe-dumai and DV85 rice landraces (Fukuta et al. 1998, Kadowaki et al. 2003, Yazawa et al. 1998). The LOD peak of qGRH11 was detected between the RM5960 and RM6680 markers (Fig. 5d), and qGRH11 is tightly linked with RM5960; the Grh2 gene is tightly linked with the RM5961 marker (Fujita et al. 2010a). A QTL on chromosome 2, qGRH2, was detected between RM3688 and RM3515 (Table 2) in the BC$_3$F$_4$ 7 and BC$_3$F$_4$ 12 populations, which were W1413-homozygous at qGRH5 and qGRH11 in the Nipponbare genetic background. qGRH2 has not been previously reported.

Genetic effects of the detected QTLs (qGRH4, qGRH5, and qGRH11) from W1413 were identified in BC$_3$F$_4$ populations 4, 9, and 1, respectively, all with the Nipponbare genetic background (Table 2). The NM distribution of BC$_3$F$_4$ 4 showed about 50% of the plants was susceptible to GRH (≤30% NM) (Fig. 5a). One QTL, qGRH4, was detected in this population (Table 2). In BC$_3$F$_4$ 9, about 50% of the plants were also susceptible to GRH (≤30% NM) (Fig. 5b). qGRH5 was identified in this population (Table 2). In BC$_3$F$_4$ 1, about 35% of the plants had susceptible to GRH (≤30% NM) (Fig. 5d). A major QTL, qGRH11, was detected in this population (Fig. 5d, Table 2). No plant materials...
for detection of qGRH2 (heterozygous only on chromosome 2) in the Nipponbare genetic background were available in BC3F7 mapping populations, but it was detected as a significant QTL in the background of qGRH5 and qGRH11 in BC3F7 (Fig. 5e, Table 2).

QTL analysis of BC3F3 populations detected qGRH4 in BC3F7 107 and 26, which were W1413-homozygous at qGRH11 (Fig. 4d, 4e, Table 1). However, qGRH4 was never detected as a significant QTL when qGRH11 was heterozygous (in BC3F9 9 and 123; Fig. 4c, 4f, Table 1). These findings suggest that the major effect of qGRH11 masked those of the minor QTLs.

In BC3F4 2, qGRH11 was identified as a major QTL (high PV explained [PVE] and high additive value) in the presence of heterozygous qGRH4 and qGRH5 regions and W1413-homozygous qGRH2 (data not shown). About 40% of BC3F4 2 plants and 25% of BC3F4 1 plants (containing only qGRH11) were highly resistant (≥60% NM) (Fig. 5d). These data suggest that a combination of qGRH11 with other minor QTLs increases resistance; the number of individuals (N = 67) in BC3F4 2 was insufficient to detect the individual effect of the minor QTLs (data not shown). The BC3F4 15 population, in which we detected qGRH5 and which was W1413-homozygous at qGRH2, had an increased proportion of plants with high resistance (≥60% NM) (Fig. 5c); in this population, qGRH5 had a high PVE and increased additive value (Table 2). BC3F4 9, in which we detected qGRH5 in the absence of other significant QTLs, had an increased proportion of susceptible plants (≤30% NM) (Fig. 5b). These results indicate a combined effect of two additive QTLs, qGRH4 and qGRH5, in BC3F4 15.

Among the detected QTLs, qGRH11 from W1413 is a major QTL with the highest PVE (21.5%) in the BC3F4 1 population (Table 2). The other minor QTLs are qGRH4 (PVE = 14.8%–16.7%) in BC3F4 4 and 12, qGRH5 (PVE = 12.3%–19.2%) in BC3F4 9 and 15, and qGRH2 (PVE = 12.6%–15.0%) in BC3F4 7 and 12 (Table 2).

**Pyramiding of four resistance alleles**

BC3F4 12 had an increased proportion of plants with moderate to high resistance (≥50% NM), and 25% of plants were susceptible to GRH (Fig. 5f). Two QTLs, qGRH2 and qGRH4, were detected in the presence of W1413-homozygous qGRH5 and qGRH11 in BC3F4 12 (Table 2). Therefore, the combined effect of the four QTLs from W1413 conferred high resistance to GRH.

Pre-NILs and pre-PYLs were evaluated to ascertain the effect of each QTL and of various combinations (Fig. 6). At 3 DAI, the NM of all lines was significantly lower than that of W1413, with no differences among the lines. At 5 DAI, the NM of all pre-NILs and pre-PYLs gradually increased, and the resistance of the pre-PYL carrying four QTLs was significantly greater than that of other lines. At 7 DAI, the NM of all lines increased further, and that of the pre-PYL carrying four QTLs did not differ significantly from that of W1413. Thus, the resistance level of W1413 at 7 DAI can be largely explained by the combined effects of the four resistance alleles (qGRH2, qGRH4, qGRH5, and qGRH11). Otherwise, evaluation of W1413 young ratoon leaves expressed the resistance of additional QTLs besides from these four alleles and additional QTLs might not be detected in this study.

In conclusion, we developed a series of ILs from a cross between Nipponbare and W1413, and mapped four GRH resistance QTLs using advanced backcross populations. The resistance of the pre-NILs, and pre-PYLs increased gradually with time: all lines were susceptible at 3 DAI, but became moderately resistant at 5 DAI and highly resistant at 7 DAI. Our results suggest that multiple QTLs control GRH resistance in W1413. The chromosomal locations of qGRH4, qGRH5, and qGRH11 were identical to those of previously reported GRH resistance genes Grh6, Grh1, and Grh2, respectively. In addition, we identified qGRH2, a new QTL for GRH resistance. The genetic effect of qGRH11 was the largest and the other QTLs had minor effects. We conclude that at least these four QTLs contribute to the resistance to GRH derived from *O. longistaminata*.
Author Contribution Statement

HWT and HY designed the experiments. HWT, YY, MVT, and HY developed plant materials. HWT conducted the genetic analysis. HWT and HY wrote the paper.

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