Identification of quantitative trait loci for panicle structure and grain filling using a cross between indica- and japonica-type high-yielding rice cultivars

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Abstract

To enhance the yield potential of rice by breeding, it is important to reveal the genetic factors affecting yield components in high-yielding cultivars. Quantitative trait loci (QTL) analysis for panicle structure and spikelet weight as an index of grain filling was conducted using recombinant inbred lines (RILs) derived from a cross between an indica-dominant high-yielding cultivar, Takanari, and a japonica-dominant high-yielding cultivar, Momiroman in 2012 and 2013 in eastern Japan. The grain-filling ability of Takanari is reported to be better than that of Momiroman. Since grain filling is generally better near the tip of the panicle and decreases as the number of branches from the rachis increases, we classified whole panicles into upper and lower side panicles and spikelets into primary, secondary, and tertiary spikelets according to the number of branches from the rachis. On chromosomes 1, 4, and 6, QTLs regulating the number of spikelets per panicle and panicle structure were detected and were most likely identical to GN1a, SPIKE, and APO1, respectively, which has been previously reported as QTLs regulating the number of spikelets per panicle. Takanari produced much heavier secondary and tertiary spikelets than Momiroman on the lower side panicle. On chromosome 5, novel QTLs regulating spikelet weight were detected. The Takanari allele enhanced secondary and tertiary spikelet weight on the lower side panicle. These results indicate that it may be possible to enhance sink capacity and translocation of source with a combination of novel QTLs detected on chromosome 5 and GN1, APO1, and SPIKE.

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Introduction

The world’s population is estimated to reach 9.8 billion by 2050 (United Nations, Department of Economic and Social Affairs, Population Division, 2017). Global crop production must be increased substantially to feed such a large number of people. Since arable land is limited worldwide (Alexandratos & Bruinsma, 2012), improving crop yield per unit area is essential to avoid global food shortages.

Rice (Oryza sativa L.) is eaten by nearly half of the world’s inhabitants and is a staple food for most populations (GriSP (Global Rice Science Partnership), 2013). Rice cultivated in Asia is mainly classified into indica and japonica based on their morphological and physiological differences (Khush, 1997). Indica is adapted to the tropics (GriSP (Global Rice Science Partnership), 2013) due to its resistance to high temperatures (Yoshida & Hara, 1977); in contrast, japonica resistant to low temperatures (Yoshida & Hara, 1977) and is, therefore, more well adapted to temperate regions (GriSP (Global Rice Science Partnership), 2013). Although the genetic background of most rice cultivars grown in Japan is japonica, indica has also been used to develop high-yielding cultivars (Horie et al., 2005).

Most high-yielding Japanese cultivars can be divided into indica- and japonica-dominant types. An indica-dominant cultivar, Takanari, was developed in 1990 (Imbe et al., 2004) and a japonica-dominant cultivar, Momiroman, was developed in 2008 (Hirabayashi et al., 2010). In order for rice plants to produce a high yield, the ability to produce a lot of source (i.e. photosynthetic products) and sink (i.e. spikelet number × grain weight) and to efficiently translocate the source into sink is necessary. A previous study reported that Momiroman was able to produce more sink than Takanari, whereas Takanari had higher ability to produce source and translocate source into sink than Momiroman (Yoshinaga, Takai, Arai-Sanoh, Ishimaru & Kondo, 2013). In addition, Momiroman had a larger proportion of chalky grain (Hirabayashi et al., 2010) and a lower percentage of filled grain (Yoshinaga et al., 2013).

Several quantitative trait loci (QTLs) such as GN1a, APO1, and SPIKE, which regulate the number of spikelets per panicle, have been isolated from rice (Ashikari et al., 2005; Fujita et al., 2013; Terao, Nagata, Morino & Hirose, 2010). GN1a and APO1 were identified in populations derived from a cross between indica and japonica cultivars (Ashikari et al., 2005; Terao et al., 2010), and the number of spikelets per panicle was increased by alleles from the indica cultivars with japonica cultivar genetic backgrounds (Ashikari et al., 2005; Nakano et al., 2017; Takai et al., 2014; Takai, Nakano, Yoshinaga & Kondo, 2018; Terao et al., 2010). Meanwhile, SPIKE was identified in a population derived from a cross between indica and tropical japonica cultivars (Fujita et al., 2013), and the number of spikelets per panicle was increased by alleles from the tropical japonica cultivar with an indica cultivar genetic background (Fujita et al., 2013; Takai et al., 2017, 2018). Variations in the number of spikelets per panicle caused by GN1a, APO1, and SPIKE alleles were confirmed in a Takanari and Momiroman F2 population (Takai et al., 2018). This means that a combination of GN1a, APO1, and SPIKE alleles could potentially result in greater sink capacity (Takai et al., 2018).

The QTL GPS, which regulates chlorophyll concentration in leaves (i.e. photosynthetic ability per unit leaf area) and is identical to SPIKE, was identified in a population derived from a cross between Takanari and a japonica cultivar, Koshihikari (Takai et al., 2013). Chlorophyll concentration and leaf photosynthesis in flag leaves were increased by the allele from Takanari in plants with a Koshihikari genetic background (Takai et al., 2017, 2013). However, the genetic factors that regulate the ability to efficiently translocate photosynthetic products into sink in Takanari have not yet been determined. Takanari had a higher increasing rate of panicle weight after heading and a higher percentage of filled spikelets than Momiroman (Yoshinaga et al., 2013), suggesting that Takanari might be able to translocate photosynthetic products more efficiently. Thus, the genetic material differences between Takanari and Momiroman could be used to identify the genetic factors regulating translocation ability.

Grain filling in each spikelet is affected by the position of spikelets on the panicle (Morita, 2000; Nakano, Morita, Kitagawa, Wada & Takahashi, 2012; Nakano & Tsuchiya, 2012; Nakano et al., 2017; Terai et al., 2008). Upper spikelets exhibit better grain filling than lower ones (Terai et al., 2008), and grain filling of spikelets decreases as the order of rachis branches increases (Morita, 2000; Nakano et al., 2012; Nakano & Tsuchiya, 2012; Nakano et al., 2017). Therefore, grain weight at each position might be useful as an index of the translocation ability.

The objective of the present study was to detect QTLs regulating panicle structure and grain filling based on spikelet weight at each position using recombinant inbred lines (RILs) derived from a cross between Takanari and Momiroman. The findings detailed herein should contribute to future breeding to enhance the yield potential of rice.
Materials and methods

Plant materials

Two high-yielding cultivars developed in Japan, Takanari and Momiroman (Hirabayashi et al., 2010; Imbe et al., 2004), were used in this study. Takanari was crossed with Momiroman to obtain F₁ seeds. The F₁ plants were consecutively self-pollinated to develop RILs by the single-seed descent method. In total, 68 F₅ and 85 F₆,7 RILs were used for the genetic analysis in 2012 and 2013, respectively.

RILs and parental cultivars were grown on a Fluvisol, which is typical of alluvial areas, in a paddy field at the Institute of Crop Science, National Agriculture and Food Research Organization (NARO) (36°02′N, 140°04′E), Tsukubamirai, Ibaraki, Japan. On 8 June 2012 and 16 May 2013, 23-day-old seedlings of each line were transplanted at one seedling per hill. Each line was planted in three rows with 15 hills per row at a spacing of 15 cm between hills and 30 cm between rows in 2012 and 2013. In 2012, basal fertiliser was applied at a rate of 6 g N m⁻² as a controlled-release fertiliser (2 g LP40, 2 g LPS100, and 2 g LP140 (UCAM AGRI. Co., Ltd., Tokyo, Japan)) with 12 g P₂O₅ m⁻² and 9 g K₂O m⁻². In 2013, basal fertiliser was applied at a rate of 12 g N m⁻² as a controlled-release fertiliser (4 g LP40 and 8 g LP100) with 16 g P₂O₅ m⁻² and 12 g K₂O m⁻². At the panicle initiation stage in 2013, another 6 g N m⁻² was top-dressed as LP40, LP40, LP100, and LP140 release 80% of their total nitrogen content at a uniform rate for up to 40, 100, and 140 days after application, respectively, at 20–30°C. LPS100 releases 80% of its total nitrogen content at a sigmoid rate for up to 100 days after application at 20–30°C.

There were some differences between 2012 and 2013 marked in weather conditions recorded at the nearest weather station Tateno, Tsukuba. Daily mean air temperatures during mid-June and early July were 2.7°C and 2.8°C, respectively, lower in 2012 than in 2013, whereas those during mid-September was 2.8°C higher in 2012 than in 2013. Meanwhile, daily mean solar radiations during mid-June, late July, and late August were 5.2, 4.2, and 4.9 MJ m⁻² day⁻¹, respectively, higher in 2012 than in 2013, whereas those during late September was 4.1 MJ m⁻² day⁻¹ lower in 2012 than in 2013.

Phenotyping

Days to heading after sowing were recorded as the first panicle of five plants for each RIL, and parental cultivars were exerted. At maturity, two hills were harvested, and panicles were sampled and air-dried. Three heaviest panicles on each hill were selected to examine panicle structure and spikelet weight. Whole panicles were divided into eight primary rachis branches (i.e. upper side panicle) from the tip and the others (i.e. lower side panicle), and then, each part of spikelets was divided into primary, secondary, tertiary, and quaternary spikelets according to the number of branches from the rachis, as described by Matsuba (1991) (Figure 1). The number of primary, secondary, tertiary, and quaternary spikelets on the upper side and lower side panicle were counted and weighed. Since the proportion of quaternary spikelets were much lower than those of primary, secondary, and tertiary spikelets, further analyses were not conducted for the proportion of quaternary spikelets and quaternary spikelet weight.

QTL mapping

For QTL analysis using F₅ and F₆,7 RILs, we used the same 105 genome-wide SSR markers and one InDel marker for GN1a used by Takai et al. (2018) when they conducted QTL analysis in an F₂ population. The total DNA of each plant was extracted from a small piece of young leaf by the simple DNA extraction method described by Takeuchi et al. (2008). Linkage maps were constructed in MAPMAKER/EXP 3.0 software (Lander et al., 1987) for F₅ and F₆,7 populations. The chromosomal positions and effects of putative QTLs were determined by composite interval mapping in QTL Cartographer 2.0 software (Basten, Weir & Zeng, 2002). The threshold of QTL detection was based on 1000 permutation tests at a level of significance of 5%. The additive effect and phenotypic variance (R²) explained by each QTL were estimated from the peak logarithm of odds score.

Results

Days to heading

Days to heading were examined together with the number of spikelets per panicle, proportion of spikelets in different positions, and spikelet weight at each position on the panicle because it often pleiotropically affects agronomic traits. Takanari headed 6 days earlier than Momiroman in both 2012 and 2013 (Figures 2 and 3). The days to heading in RILs ranged from 89 to 109 in 2012 and from 95 to 114 in 2013. One QTL for days to heading was detected on the long arm of chromosome 10 in both 2012 and 2013 (Tables 1 and 2, Figures 6 and 7). This QTL explained 24.0–33.3% of R² (Tables 1 and 2). Momiroman allele of the QTL delayed heading.
Number of spikelets per panicle
The number of spikelets per panicle was higher in Takanari than in Momiroman in both 2012 and 2013 (Figures 2 and 3). The number of spikelets per panicle in RILs transgressively segregated ranging from 98 to 381 in 2012 and 104 to 474 in 2013. Three QTLs for the number of spikelets per panicle were detected on chromosomes 1, 4, and 6 in 2012 (Table 1, Figure 6). Additionally, two QTLs for the number of spikelets per panicle were detected on chromosomes 1 and 6 in 2013 (Figure 7). Each QTL explained 18.4–48.0% of $R^2$ (Tables 1 and 2). The Takanari allele on chromosome 1 decreased the proportion of primary and secondary spikelets but increased the proportion of tertiary spikelets (Tables 1 and 2, Figures 6 and 7). In contrast, the Takanari allele on chromosome 4 increased the proportion of primary and secondary spikelets but decreased the proportion of tertiary spikelets (Table 1, Figure 6). The Momiroman allele on chromosome 6 increased the proportion of secondary spikelets (Table 2, Figure 7).

Proportion of spikelets at each position on whole panicle
On the whole panicle, Takanari had lower proportions of primary and secondary spikelets but a higher proportion of tertiary spikelets than Momiroman in both 2012 and 2013 (Figures 2 and 3). Six QTLs for the proportions of primary, secondary, and tertiary spikelets were detected on chromosomes 1 and 4 in 2012 (Table 1, Figure 6). In addition, two QTLs for the proportions of secondary and tertiary spikelets were detected on chromosomes 1 and 6 in 2013 (Table 2, Figure 7). Each QTL explained 16.3–33.1% of $R^2$ (Tables 1 and 2). The Takanari allele on chromosome 1 decreased the proportion of primary and secondary spikelets but increased the proportion of tertiary spikelets (Tables 1 and 2, Figures 6 and 7). In contrast, the Takanari allele on chromosome 4 increased the proportion of primary and secondary spikelets but decreased the proportion of tertiary spikelets (Table 1, Figure 6). The Momiroman allele on chromosome 6 increased the proportion of secondary spikelets (Table 2, Figure 7).

Spikelet weight at each position on whole panicle
There was a large difference between Takanari and Momiroman regarding tertiary spikelet weight (Figures 2 and 3). Takanari produced 9% and 17% heavier primary and tertiary spikelets, respectively, but 1% lighter secondary spikelets than Momiroman in 2012 (Figure 2). In addition, Takanari produced 1% lighter primary spikelets but 24% and 47% heavier secondary and tertiary spikelets, respectively, than Momiroman in 2013 (Figure 3). One QTL for secondary spikelet weight was detected on chromosome 5 in 2012 (Table 1, Figure 6). Similarly, two QTLs for secondary spikelet weight were detected.
on chromosome 5 in 2013 (Table 2, Figure 7). Each QTL explained 24.1–33.5% of $R^2$ (Tables 1 and 2). The Takanari allele on chromosome 5 increased secondary spikelet weight (Tables 1 and 2, Figures 6 and 7).

Proportion of spikelets at each position on upper side panicle

On the upper side panicle, Takanari had a higher proportion of primary and secondary spikelets but a lower proportion of tertiary spikelets than Momiroman in 2012 (Figure 4). On the other hand, Takanari had a lower proportion of primary and secondary spikelets but a higher proportion of tertiary spikelets than Momiroman in 2013 (Figure 5). Six QTLs for the proportions of primary, secondary, and tertiary spikelets were detected on chromosomes 4, 6, and 10 in 2012 (Table 1, Figure 6). In addition, three QTLs for the proportions of secondary and tertiary spikelets were detected on chromosomes 6 and 11 in 2013 (Table 2, Figure 7). Each QTL explained 15.6–31.8% of $R^2$ (Tables 1 and 2). The Takanari allele on chromosome 4 increased the proportion of primary and secondary spikelet number but decreased the proportion of tertiary spikelets (Table 1, Figure 6). The Takanari allele on chromosome 6 decreased the proportion of secondary spikelets but increased tertiary spikelets (Tables 1 and 2, Figures 6 and 7). In contrast, Takanari allele on chromosome 10 increased the proportion of primary spikelets but decreased tertiary spikelets (Table 1, Figure 6). The Momiroman allele on chromosome 11 increased the proportion of secondary spikelets (Table 2, Figure 7).
Spikelet weight at each position on upper side panicle

There was a large difference between Takanari and Momiroman in terms of tertiary spikelet weight (Figures 4 and 5). Takanari produced 8% heavier primary and tertiary spikelets but 6% lighter secondary spikelets than Momiroman in 2012 (Figure 4). In addition, Takanari produced 9% lighter primary spikelets but 2% and 17% heavier secondary and tertiary spikelets, respectively, than Momiroman in 2013 (Figure 5). Four QTLs for primary, secondary, and tertiary spikelet weight were detected on chromosome 5 in 2013 (Table 2, Figure 7). Each QTL explained 18.3–38.7% of $R^2$. The Takanari allele on chromosome 5 increased primary, secondary, and tertiary spikelet weight.

Proportion of spikelets at each position on lower side panicle

On the lower side panicle, Takanari had a lower proportion of primary and secondary spikelets but a higher proportion of tertiary spikelet number than Momiroman in both 2012 and 2013 (Figures 4 and 5). Two QTLs for the proportion of primary spikelets were detected on the short arm of chromosome 1 and the long arm of chromosome 4 in 2012 (Table 1, Figure 6). In addition, four QTLs for the proportions of primary, secondary, and tertiary spikelets were detected on chromosome 1 in 2013 (Table 2, Figure 7). Each QTL explained 15.8–49.0% of $R^2$. The Takanari allele on the short arm of chromosome 1 decreased the proportion of primary and secondary spikelets but increased the proportion...
of tertiary spikelets (Tables 1 and 2, Figures 6 and 7). The Momiroman allele on the long arm of chromosome 1 increased the proportion of primary spikelet (Table 2, Figure 7).

**Spikelet weight at each position on lower side panicle**

There were large differences between Takanari and Momiroman in terms of primary, secondary, and tertiary spikelet weight (Figures 4 and 5). The difference in spikelet weight between Takanari and Momiroman increased as the number of branches from the rachis increases. Takanari produced 10%, 19%, and 64% heavier primary, secondary, and tertiary spikelets, respectively, than Momiroman in 2012 and 2013 (Figures 4 and 5). Three QTLs for secondary and tertiary spikelet weight were detected on chromosomes 5 and 10 in 2012 (Table 1, Figure 6). Similarly, three QTLs for secondary and tertiary spikelet weight were detected on chromosome 5 in 2013 (Table 2, Figure 7). Each QTL explained 14.7–46.2% of $R^2$. The Takanari allele on chromosome 5 increased secondary and tertiary spikelet weight (Tables 1 and 2, Figures 6 and 7). In addition, the Takanari allele on chromosome 10 increased tertiary spikelet weight (Table 2, Figure 6).

**Discussion**

Takanari, which is a high-yielding Japanese rice cultivar, has reportedly produced a brown rice yield exceeding 11 t ha$^{-1}$ (Nagata, Sasaki, Ohdaira & Yoshinaga, 2009). Such a high yield is derived from the ability to produce a lot of photosynthetic products and spikelets, which is related to the GPS allele and $GN1$ and $APO1$ alleles, respectively (Nakano et al., 2017; Takai et al., 2017, 2013, 2014, 2018), and to efficiently translocate source into sink (Kanemura, Homma, Ohsumi, Shiraiwa & Horie, 2007; Ohsumi et al., 2007; Ohsumi et al., 2007; Ohsumi et al., 2007).

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**Table 1.** Putative quantitative trait loci (QTLs) regulating days to heading, number of spikelets per panicle, proportion of spikelets, and spikelet weight at each position on whole, upper side, and lower side panicles in 68 $F_5$ recombinant inbred lines (RILs) derived from a cross between Takanari and Momiroman in 2012.

| Traits                        | Chr. | Flanking makers | LOD | $A$ | $R^2$ |
|-------------------------------|------|-----------------|-----|-----|-------|
| Days to heading               | 4    | RM6748          | 4.4 | 2.4 | 29.0  |
| Number of spikelets per panicle| 1    | GN1a            | 4.4 | 2.4 | 29.0  |
| Proportion of primary spikelets on whole panicle | 10   | RM6673          | 4.4 | 2.4 | 29.0  |

**Table 2.** Putative quantitative trait loci (QTLs) regulating days to heading, number of spikelets per panicle, proportion of spikelets, and spikelet weight at each position on whole, upper side, and lower side panicle in 89 $F_5$ recombinant inbred lines (RILs) derived from a cross between Takanari and Momiroman in 2013.

| Traits                        | Chr. | Flanking makers | LOD | $A$ | $R^2$ |
|-------------------------------|------|-----------------|-----|-----|-------|
| Days to heading               | 4    | RM6748          | 4.4 | 2.4 | 29.0  |
| Number of spikelets per panicle| 1    | GN1a            | 4.4 | 2.4 | 29.0  |
| Proportion of primary spikelets on whole panicle | 10   | RM6673          | 4.4 | 2.4 | 29.0  |

LOD: logarithm of odds; $A$: additive effect of the Takanari allele compared with the Momiroman allele; $R^2$: percentage of phenotypic variance explained by each QTL.
Takai et al., 2006; Yoshinaga et al., 2013). However, genetic factors associated with translocation ability have not yet been determined. Since grain filling in each spikelet is affected by the position of spikelets on the panicle (Morita, 2000; Nakano et al., 2012; Nakano & Tsuchiya, 2012; Nakano et al., 2017; Terai et al., 2008), modification of panicle structure might improve grain yield per unit area (Nakano et al., 2012). In the

Figure 4. Frequency distribution of proportion of spikelets and spikelet weight at each position on upper and lower side panicles in 68 recombinant inbred lines (RILs) derived from a cross between Takanari and Momiroman in 2012.
present study, QTL analysis for panicle structure and spikelet weight as an index of grain filling was conducted using RILs derived from a cross between Takanari and Momiroman.

QTLs for the number of spikelets and the proportion of spikelets at each position on the panicle were detected on chromosomes 1, 4, 6, 10, and 11 (Tables 1 and 2, Figures 6 and 7). On the short arm of chromosome 1, QTLs

Figure 5. Frequency distribution of proportion of spikelets and spikelet weight at each position on upper and lower side panicles in 85 recombinant inbred lines (RILs) derived from a cross between Takanari and Momiroman in 2013.
regulating the number of spikelets per panicle and the proportion of spikelets at each position on the panicle were detected. The Takanari allele increased the number of spikelets per panicle and the proportion of tertiary spikelets on the whole and lower side panicles but decreased the proportion of primary and secondary spikelets on the whole panicles. Since these QTLs were detected in the vicinity of the InDel marker for GN1a, they could be GN1a, which was previously identified and cloned as a single gene controlling the number of spikelets per panicle (Ashikari et al., 2005; Nakano et al., 2017; Takai et al., 2014, 2018). This means that the Takanari allele in this region might increase the number of spikelets per panicle by increasing the proportion of tertiary spikelets on the lower side panicles in plants with a japonica genetic background.

On the long arm of chromosome 4, QTLs regulating the number of spikelets per panicle and the proportion of tertiary spikelets but decreased the proportion of primary and secondary spikelets on the whole and upper side panicles. These QTLs could be SPIKE, which was previously identified and cloned as a single gene controlling the number of spikelets per panicle (Fujita et al., 2013), because a previous study by Takai et al. (2018) also detected a QTL for the number of spikelets per panicle in the same region using a Takanari and Momriroman F2 population and indicated that this QTL may have been SPIKE. Therefore, the Momriroman allele in this region might increase the number of spikelets per panicle by increasing the proportion of tertiary spikelets on the upper side panicle in plants with an indica genetic background. However, these QTLs were not detected in 2013. Although the reason for this is not clear, the detection sensitivity may be changed by varying the environmental conditions.

On chromosome 6, QTLs regulating the number of spikelets per panicle and the proportion of spikelets at each position on the panicle were detected only in 2012 (Table 1, Figure 6). The Momriroman allele increased the number of spikelets per panicle and the proportion of tertiary spikelets but decreased the proportion of primary and secondary spikelets on the whole and upper side panicles.
the number of spikelets per panicle and the proportion of tertiary spikelets but decreased the proportion of secondary spikelets on the upper side panicle. Since Takai et al. (2018) detected a QTL for the number of spikelets per panicle in the F2 population and considered it to be APO1, these QTLs may be APO1, which was previously identified and isolated as a single gene controlling the number of spikelets per panicle (Terao et al., 2010). These results suggest that the Takanari allele in this region may increase the number of spikelets per panicle by increasing the proportion of tertiary spikelets in plants with a japonica genetic background despite a simultaneous decrease in the proportion of secondary spikelets on the upper side panicle.

QTLs for spikelet weight at each position on the panicle were detected on chromosomes 5 and 10 (Tables 1 and 2, Figures 6 and 7). On chromosome 5, the Takanari allele enhanced primary, secondary, and tertiary spikelet weight on the upper side panicle only in 2012 but enhanced secondary spikelet weight on the whole panicle and secondary and tertiary spikelet weight on the lower side panicle in both 2012 and 2013. To the best of our knowledge, no QTLs for secondary and tertiary spikelet weight on the lower side panicle have been fine-mapped in this region. A previous study showed that secondary and tertiary spikelet weight on the lower side panicle is harder to increase than primary spikelet weight on the lower side panicle and those on the upper side panicle in japonica (Morita, 2000; Nakano et al., 2012; Nakano & Tsuchiya, 2012; Nakano et al., 2017; Terai et al., 2008). Takanari produced heavier secondary and tertiary spikelets on the lower side panicle than Momiroman (Figures 4 and 5). In general, there is a trade-off relationship between spikelet weight and the number of spikelets per panicle. However, no QTLs for the number of spikelets per panicle were detected in this region (Tables 1 and 2, Figures 6 and 7). These results suggest that the high translocation ability in Takanari might be caused by a particular allele of the QTL on chromosome 5. This means that the heavier secondary and tertiary spikelets on the lower side panicle in Takanari might be a characteristic of better grain filling.
On chromosome 10, one QTL regulating tertiary spikelet weight on the upper side panicle was detected in the only 2012 (Table 1, Figure 6). The Takanari allele increased tertiary spikelet weight on the upper side panicle. However, the QTL in this region for days to heading was detected in both 2012 and 2013 (Tables 1 and 2, Figures 6 and 7). The Momiroman allele delayed heading. It is known that grain filling decreases with delaying heading due to low temperature (Satake, 1980). Thus, these QTLs might have a pleiotropic effect.

We detected QTLs on chromosomes 1 and 6 which increased the number of spikelets per panicle and the proportion of tertiary spikelets on the lower and upper side panicles, respectively, with Takanari alleles. We believe that these QTLs are considered most likely identical to GN1a and APO1 (Tables 1 and 2, Figures 6 and 7). Similarly, on the long arm of chromosome 4, we detected QTLs which increased the number of spikelets per panicle and the proportion of tertiary spikelets on the upper side panicle with Momiroman alleles. These QTLs were considered to be most likely identical to SPIKE (Table 1, Figure 6). The results indicate the possibility of producing larger panicles (much more spikelets per panicle) by combining QTLs. Interestingly, Takanari produced much heavier secondary and tertiary spikelets than Momiroman. We detected novel QTLs between RM17836 and RM3476 on chromosome 5 which regulate spikelet weight (Tables 1 and 2, Figures 6 and 7). The Takanari allele enhanced secondary spikelet weight on the whole panicle and secondary and tertiary spikelet weight on the lower side panicle. These QTLs could be responsible for grain filling ability. To breed cultivars with higher a yield potential than Takanari and Momiroman, enhancing sink capacity and translocation ability using a combination of the novel QTLs detected on chromosome 5 and GN1, APO1, and SPIKE is important.

Conclusions

QTL analysis for panicle structure and spikelet weight as an index of grain filling was conducted using RILs derived from a cross between an indica-dominant high-yielding cultivar, Takanari, and a japonica-dominant high-yielding cultivar, Momiroman. On chromosomes 1, 4, and 6, QTLs regulating the number of spikelets per panicle and panicle structure were detected and were most likely identical to GN1a, SPIKE, and APO1, respectively. Takanari produced much heavier secondary and tertiary spikelets than Momiroman on the lower side panicle. On chromosome 5, novel QTLs regulating spikelet weight were detected. The Takanari allele enhanced secondary and tertiary spikelet weight on the lower side panicle. It may be possible to enhance sink capacity and translocation ability of source with a combination of novel QTLs detected on chromosome 5 and GN1, APO1, and SPIKE.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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