Introduction

Most cultivars of rice (Oryza sativa L.) are divided into the subspecies indica and japonica. These subspecies have been historically classified based on morphological traits and fertility of hybrid plants (Kato et al. 1928, Matsuo 1952). More recent classification through the use of genome-wide DNA polymorphisms has validated the historical classification and has identified five subspecies-like groups: temperate japonica, tropical japonica, aromatic, indica and aus (Ebana et al. 2010, Famoso et al. 2011, Kovach et al. 2009). The indica rice is grown worldwide and is more prevalent than japonica rice, which is preferentially grown and eaten in temperate regions such as Japan, Korea, northern China, California (USA), and Australia (Garris et al. 2005, Mackill 1995).

Many genetic analyses have used segregating populations derived from crosses between japonica and indica cultivars to detect quantitative trait loci (QTLs) and to identify their underlying genes. So far, more than 8600 QTLs have been reported and more than 200 genes have been isolated by map-based cloning strategies in rice (Matsumoto et al. 2016, Monaco et al. 2014, Yamamoto et al. 2012, Yonemaru et al. 2010). However, although several genetic analyses have identified QTLs involved in the control of natural variation in agronomically important traits in temperate japonica cultivars, the details are still unclear.

In this review, we summarize recent progress in molecular genetic studies of agronomically important traits in closely related cultivars. We collected a huge number of DNA polymorphisms between the cultivars Nipponbare and Koshihikari and unraveled many QTLs and genes involved in the control of agronomically important traits. Understanding the genetic basis for agronomic traits is important for improving agronomic performance in temperate japonica cultivars. Similar strategies are used in genetic analysis and breeding selection of closely related cultivar groups in many other crop species.

Genome sequencing in temperate japonica cultivars

In the past, the low frequency of DNA polymorphism among closely related cultivars such as those of temperate japonica rice has prevented the molecular genetic analysis of variations in agronomic traits. Now, however, the development of genome sequencing technologies has made it possible to detect many DNA polymorphisms even in this...
narrow resource. The International Rice Genome Sequencing Project (IRGSP) released the genome sequence of the temperate *japonica* cultivar Nipponbare in 2005 (IRGSP 2005). This sequence has been used for the design of over 20 000 simple sequence repeat (SSR) markers (IRGSP 2005, McCouch et al. 2002, Monaco et al. 2014). Whole-genome sequencing of other temperate *japonica* cultivars, including Koshihikari, has since been conducted using next-generation sequencing technologies (Matsumoto et al. 2016, 3,000 Rice Genomes Project 2014, Yamamoto et al. 2010). A huge number of single-nucleotide polymorphisms (SNPs) can be collected from comparisons of genome sequences even among temperate *japonica* cultivars. For example, Yamamoto et al. (2010) collected over 67 000 SNPs between Nipponbare and Koshihikari. The use of polymorphic SSR and SNP markers has enhanced the genetic dissection of agronomically important traits in temperate *japonica* cultivars by facilitating QTL analysis (Kobayashi et al. 2013, Kwon et al. 2011, Shibaya et al. 2011) and genome-wide association study (GWAS) (Xu et al. 2016, Yano et al. 2016, Yonemaru et al. 2012). Yano et al. (2016) reported good examples for collection of QTLs by GWAS and identification of genes associated with heading date, plant height, panicle length, and panicle number in germplasm accessions of temperate *japonica* cultivars.

**Koshihikari, an elite Japanese temperate *japonica* cultivar**

Koshihikari was developed in 1956 in Japan. It has been the top cultivar by crop acreage since 1979 (Yokoo et al. 2005). Nipponbare was developed in 1963 and was the leading cultivar until 1978. During the last two decades, Koshihikari has accounted for over 35% of all of plantings across 45 of the 47 prefectures in Japan every year (Takeuchi et al. 2008, Yokoo et al. 2005). Compared with other temperate *japonica* cultivars such as Nipponbare, Koshihikari has an earlier heading date (allowing expansion of cultivation areas), better eating quality, stronger cool-temperature tolerance at the booting stage, and stronger preharvest sprouting resistance, but weaker resistance to leaf blast disease and longer culms (associated with greater susceptibility to lodging).

**Genetic dissection of agronomic traits in Koshihikari**

**Development of backcrossed populations**

Detection of QTLs is a primary step in efforts to understand the genetic basis for agronomic traits in rice, because many agronomic traits are generally controlled by multiple QTLs (Fukuoka et al. 2010a, Hori et al. 2015, Nagata et al. 2015). To identify QTLs involved in the control of agronomic traits in Koshihikari and Nipponbare, we developed two types of segregating populations—backcrossed inbred lines (BILs) and chromosome segment substitution lines (CSSLs)—from reciprocal crosses between the two cultivars (Hori et al. 2010, Matsubara et al. 2008): K-BILs (127 BC2F6 lines) and K-CSSLs (41 BC2F6 lines) in the Koshihikari genetic background, and N-BILs (79 BC2F6 lines) and N-CSSLs (48 BC2F6 lines) in the Nipponbare genetic background.

**Heading date**

Heading date determines where a cultivar can be grown by adjusting the growing season. Early heading date in Koshihikari contributed to the extension of cultivation area into more northern regions in Japan (Hori et al. 2013). We detected QTLs responsible for early heading date in Koshihikari on the long arm of chromosome 3 (Hd16) and on the short arm of chromosome 6 (Hd17) (Matsubara et al. 2008; Table 1, Fig. 1). The Koshihikari allele of Hd16 advanced heading date by more than 10 days and that of Hd17 slightly delayed it.

Map-based cloning revealed that Hd16 encodes a casein kinase-I (Hori et al. 2013). One non-synonymous substitution in the Koshihikari allele of Hd16 advanced heading date. Recombinant protein of the functional Nipponbare Hd16 allele strongly phosphorylated the protein encoded by the other heading date gene, Ghd7, but the recombinant protein of the non-functional Koshihikari Hd16 allele did not. These results show that Hd16 changes heading date by controlling the phosphorylation of the Ghd7 protein (Hori et al. 2013).

Map-based cloning revealed that Hd17 encodes a homolog of the Arabidopsis EARLY FLOWERING 3 protein (Matsubara et al. 2012). Levels of Ghd7, Ehd1, Hd3a, and RFT1 transcripts were changed between Nipponbare and a near-isogenic line (NIL) having the Koshihikari Hd17 allele in the Nipponbare genetic background. Therefore, Hd17 changed rice heading date by controlling the level of Ghd7 transcription and its downstream genes.

Recently, we isolated another heading date QTL, Hd18, which has a small genetic effect of 3 to 6 days, in populations derived from other Japanese temperate *japonica* cultivars (Shibaya et al. 2016). Our results show that the natural variation in heading date among temperate *japonica* cultivars results from combinations of genes with both large and small genetic effects (Hori et al. 2015, 2016a, Matsubara et al. 2014).

**Eating quality and its components**

Rice eating quality largely determines its market price and consumer acceptance, because many consumers pay particular attention to high eating quality (Hori and Yano 2013, Juliano et al. 1964). High eating quality suiting Japanese preferences is one of the major reasons why Koshihikari has been the top cultivar for about 40 years. We evaluated the eating quality of cooked rice grains of the N-BILs and K-BILs (Takeuchi et al. 2008). We detected a QTL with a large genetic effect, qOE3, on the short arm of chromosome 3 in both sets of BILs (Table 1, Fig. 1). The Koshihikari qOE3 allele gave good eating quality with high
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Table 1. QTLs detected in multiple environments in a reciprocal set of backcrossed inbred lines of Nipponbare and Koshihikari (N-BILs and K-BILs)

| QTL symbol | Nearby QTL | Chr. | Nearest SSR and SNP marker | LOD | PVE | AE | Reference |
|------------|------------|------|-----------------------------|-----|-----|----|-----------|
| Heading date (day) | | | | | | | |
| Hd16 | | 3 | 87C10-17 | 63.0 | 67.0 | −5.8 | Matsubara et al. 2008, Hori et al. 2012 |
| Hd17 | | 6 | O007020 | 33.5 | 17.0 | +2.7 | Matsubara et al. 2008, Hori et al. 2012 |
| Eating quality | | | | | | | |
| qOE3 | | 3 | RM4108 | 6.6 | 29.3 | +0.2 | Takeuchi et al. 2008 |
| qGL3 | | 3 | RM4108 | 6.3 | 28.3 | +0.2 | Takeuchi et al. 2008 |
| qTA3 | | 3 | RM4108 | 5.6 | 25.7 | +0.1 | Takeuchi et al. 2008 |
| qST3 | | 3 | RM4108 | 7.3 | 32.0 | +0.2 | Takeuchi et al. 2008 |
| qHA3 | | 3 | RM5849 | 2.5 | 12.4 | −0.1 | Takeuchi et al. 2008 |
| qAC3 | | 3 | RM6300 | 2.3 | 11.2 | −0.3 | Takeuchi et al. 2008 |
| qCL3-2 | | 3 | 87C10–17 | 2.5 | 12.6 | +0.1 | Takeuchi et al. 2008 |
| Culm length (cm) | | | | | | | |
| qCL1 | | 1 | RM8068 | 5.2 | 12.3 | +2.3 | Hori et al. 2009, Hori et al. 2012 |
| qL3-2 | | 3 | 87C10–17 | 9.3 | 24.1 | −3.4 | Hori et al. 2009, Hori et al. 2012 |
| Preharvest sprouting resistance (%) | | | | | | | |
| qL7G3-1 | | 3 | RM4108 | 12.5 | 45.0 | −21.3 | Hori et al. 2010, Hori et al. 2012 |
| Grain shape | | | | | | | |
| qL2 | | 7 | NIAS_Os_a07005384 | 4.9 | 11.1 | +0.05 | Tanabata et al. 2012 |
| qAS7 | | 7 | NIAS_Os_a07005384 | 5.3 | 13.7 | +0.20 | Tanabata et al. 2012 |
| qPL7 | | 7 | NIAS_Os_a07005384 | 6.3 | 14.6 | +0.12 | Tanabata et al. 2012 |
| qLWR8 | | 8 | NIAS_Os_a08005493 | 4.4 | 9.7 | +0.02 | Tanabata et al. 2012 |
| qCS8 | | 8 | NIAS_Os_a08005493 | 4.2 | 9.2 | −0.01 | Tanabata et al. 2012 |
| qL7 | | 11 | NIAS_Os_a10122252 | 4.9 | 11.5 | −0.05 | Tanabata et al. 2012 |
| qL3 | | 11 | NIAS_Os_a10122252 | 11.1 | 30.9 | −0.03 | Tanabata et al. 2012 |
| qCS11 | | 11 | NIAS_Os_a10122252 | 8.4 | 22.1 | +0.00 | Tanabata et al. 2012 |
| qPL11 | | 11 | NIAS_Os_a10122252 | 3.4 | 8.4 | −0.09 | Tanabata et al. 2012 |
| Head brown rice weight (g) | | | | | | | |
| qHBW3 | | 3 | O24J17 | 13.1 | 42.8 | −1.7 | Hori et al. 2012 |
| 1000-grain weight (g) | | | | | | | |
| qTGW3-2 | | 3 | O24J17 | 5.3 | 13.5 | +0.3 | Hori et al. 2012 |
| qTGW11 | | 11 | NIAS_Os_a10122252 | 3.2 | 7.9 | +0.3 | Hori et al. 2012, Tanabata et al. 2012 |
| Grain chalkiness (%) | | | | | | | |
| qMWR6 | | 3 | O24J17 | 6.1 | 14.4 | −0.9 | Hori et al. 2012 |
| qMWR6 | | 3 | P548D347 | 8.6 | 21.5 | −1.1 | Hori et al. 2012 |
| qMWR6 | | 6 | P548D347 | 6.6 | 14.3 | −0.7 | Hori et al. 2012 |
| qMWR8 | | 8 | NIAS_Os_a08005271 | 6.8 | 21.7 | −0.8 | Hori et al. 2012 |
| qMWR11 | | 11 | NIAS_Os_a10122252 | 6.2 | 18.0 | −0.8 | Hori et al. 2012 |
| Leaf blast resistance | | | | | | | |
| qLBR1 | | 1 | NIAS_Os_a01007008 | 3.8 | 12.2 | +0.4 | Fukushima et al. 2010b, Hori et al. 2012 |

Chr., chromosome.
LOD, logarithm of odds.
PVE, percentage of total phenotypic variance explained by the QTL.
AE, additive effect of the Koshihikari allele.

Glossiness, good taste, strong stickiness, and weak hardness of cooked rice grains. The genetic effect of the allele has been confirmed in one N-CSSL that contains a Koshihikari chromosome segment on the short arm of chromosome 3 in the genetic background of Nipponbare (Takeuchi et al. 2008).

qOE3 is a major genetic factor that explains natural variation in eating quality among Japanese temperate *japonica* cultivars. Japanese temperate *japonica* cultivars with the Koshihikari qOE3 allele had higher eating quality and stronger stickiness of cooked grains than other cultivars (Hori et al. 2016c). Several studies also found eating quality QTLs on the short arm of chromosome 3 in segregating populations derived from crosses between Koshihikari and related cultivars (Hori and Yano 2013, Kobayashi and Tomita 2008, Wada et al. 2008, 2013). Therefore, qOE3 will be important for developing temperate *japonica* cultivars with superior eating quality.

Preharvest sprouting resistance

Seed dormancy is important in cereal crops, because weak dormancy allows preharvest sprouting in field conditions. Koshihikari has stronger seed dormancy and preharvest sprouting resistance than other temperate *japonica*
Old Japanese temperate japonica cultivars with the Nipponbare qCL1 allele had significantly shorter culms and lower internodes than other cultivars (Hori et al. 2009). This difference suggests that the Nipponbare qCL1 allele originally distributed in Japanese temperate japonica cultivars. A semi-dwarfing gene, sd1, which encodes a gibberellin biosynthesis enzyme, also significantly contributes to the short culms of temperate japonica cultivars (Asano et al. 2011). Both of these short-culm length alleles have been used to introduce the semi-dwarf phenotype and to improve lodging resistance in Japanese cultivars.

**Resistance to leaf blast disease**

Koshihikari is very susceptible to rice blast disease in most paddy fields in Japan. One QTL for leaf blast resistance was found on the short arm of chromosome 1 in the N-BILs and K-BILs (Fukuoka et al. 2010b, Hori et al. 2012; Table 1, Fig. 1). The Koshihikari allele of this QTL increased preharvest sprouting resistance. The QTL was fine-mapped within a 474-kb region including the low-temperature germinability gene qLTG3-1 isolated by Fujino et al. (2008). However, this QTL region differed from Sdr1, a QTL with a major genetic effect on seed dormancy detected in the BILs of Nipponbare × Kasalath (Takeuchi et al. 2003). Therefore, the allelic difference in qLTG3-1 between Koshihikari and Nipponbare caused differences in both preharvest sprouting resistance and germinability at low temperature.

**Culm length and lodging resistance**

Shortening culm length enhances lodging resistance and, as a result, increases grain yield. Koshihikari has longer culms and weaker lodging resistance than Nipponbare (Hori et al. 2012). A culm length QTL with a large genetic effect, qCL1, was detected on the short arm of chromosome 1 in the N-BILs and K-BILs (Hori et al. 2009; Table 1, Fig. 1). The Nipponbare qCL1 allele decreased culm length and lower-internode lengths. qCL1 was fine-mapped within a ~660-kbp region that differed from the regions containing the known dwarfing genes d18 and d2. These results suggest that qCL1 is a novel culm length gene.
yield. Koshihikari has strong cool-temperature tolerance at booting stage. Takeuchi et al. (2001) detected one QTL, qCT7, with a large genetic effect on the long arm of chromosome 7 in doubled haploid lines derived from a cross between Akihikari and Koshihikari. The Koshihikari qCT7 allele increased seed fertility under cold water treatment. To confirm the genetic effect of this QTL, we evaluated cool-temperature tolerance in one K-CSSL (SL624), which contains a Nipponbare chromosome segment around qCT7 in the Koshihikari genetic background (Fig. 2). The seed fertility of plants growing in cold water was 39% in Koshihikari but only 4% in SL624. These data support the previous result of Takeuchi et al. (2001) that qCT7 is associated with strong cool-temperature tolerance at the booting stage in Koshihikari.

**Grain shape and quality under high temperature**

Grain shape directly influences grain yield and quality. Koshihikari has shorter and broader grains than other temperate japonica cultivars. Tanabata et al. (2012) detected QTLs with large genetic effects on grain shape on the long arm of chromosome 11 in the K-BILs (Table 1, Fig. 1). To verify these genetic effects, we evaluated two K-CSSLs (SL636 and SL637) that contain Nipponbare segments of chromosome 11 in the Koshihikari genetic background (Tanabata et al. 2012). Both K-CSSLs had longer grains than Koshihikari, and significantly greater 1000-grain weight. Therefore, we concluded that the Nipponbare alleles of this QTL increased grain length and thus grain yield.

Heat stress at the grain-filling stage seriously reduces grain quality. Grain chalkiness decreases the market value because of grain breakage during milling and inferior cooking and eating quality (Ishimaru et al. 2016, Lisle et al. 2000). Two QTLs with large genetic effects on grain chalkiness were detected on the long arms of chromosomes 8 and 11 (Hori et al. 2012; Table 1, Fig. 1). The Koshihikari alleles of qDWK8 and qDWK11 decreased the ratios of white-base and white-back grains, respectively. We confirmed the genetic effects of the two QTLs in the K-CSSLs SL627 and SL637, in which Nipponbare segments increased the ratios of white-base and white-back grains (Fig. 2). These two QTLs were localized in the same marker intervals as the grain shape QTLs qLWR8 and qL1 (Table 1, Fig. 1).

**Co-localization of QTLs associated with different traits**

We detected a total of 168 QTLs for 45 agronomic traits in the N-BILs, K-BILs, N-CSSLs, and K-CSSLs. Among them, several might show pleiotropic effects on other traits. As mentioned above, QTLs for grain yield, 1000-grain weight, and ratio of white immature grains were co-localized in the same regions on chromosomes 8 and 11 (Hori et al. 2012, Tanabata et al. 2012). These results suggest that grain shape, grain chalkiness, and grain weight are associated with each other. We revealed also that qLTG3-1 was associated with both preharvest sprouting resistance and germi- nability under low temperature (Hori et al. 2010). Moreover, QTLs for eating quality, culm length, grain chalkiness, and grain yield (panicle brown rice weight and 1000-grain weight) were found around the two heading date genes Hd16 and Hd17 (Table 1, Fig. 1). Hori et al. (2012) also reported that 58 of 122 QTLs for 33 agronomically important traits were located around the same two heading date genes. There are at least two possible explanations for co-localization of these QTLs. One is that some traits are greatly influenced by a certain trait, and the QTL clusters represent the pleiotropic effects of a certain QTL or gene. The other is that the QTL clusters consist of multiple QTLs or genes associated with different agronomic traits. Further analysis, such as fine-mapping using a large population, will be required to reach conclusions about the reasons for co-localization of these QTLs.

**Origins of genes and QTLs in Koshihikari**

We investigated the origin of the Koshihikari alleles of nine QTLs with large genetic effects in 306 indica and japonica cultivars and 50 wild accessions (Fig. 3). The Koshihikari Hd16 allele was found only in Japanese temperate japonica cultivars (Hori et al. 2013). The pedigree information shows that the Koshihikari Hd16 allele is likely to have originated from the japonica genealogical tree of Koshihikari. Red and blue letters indicate Koshihikari alleles of nine QTLs/genes in the genealogical tree of Koshihikari. Red and blue letters indicate Koshihikari alleles in Table 1 with positive (+) and negative (−) additive genetic effects, respectively. All cultivars are classified as temperate japonica rice in Hori et al. (2016c).
from an old Japanese temperate japonica cultivar, Moritawase. The Koshikihikari Hd17 allele was distributed among the wild rice accessions and all cultivar groups (Matsubara et al. 2012). The Koshikihikari qLTG3-1 allele was found only in Japanese temperate japonica cultivars (Fujino and Sekiguchi 2011, Hori et al. 2010), and is likely to have been inherited from Norin 1’s ancestors. The genotypes of SSRs and SNPs around each QTL (Hori et al. 2009, Yamamoto et al. 2010, Yonemaru et al. 2012) suggest that the Koshikihikari qOE3, qLBR1, and qCT7 alleles were inherited from Kame-noo, Rikuu 132, and Joushu, respectively. The Koshikihikari qCL1, qL11, and qDWK8 alleles are likely to have been inherited from Norin 1’s ancestors. These results indicate how the ancestral alleles of the QTLs with large genetic effects were combined to create Koshikihikari.

Conclusions and prospects

The large number of SSRs and SNPs distributed throughout temperate japonica rice genomes can overcome the limitation on genetic analysis caused by the low frequency of DNA polymorphisms. The development of various types of segregating populations offers another powerful tool to identify genetic factors associated with agronomically important traits in temperate japonica cultivars. Through the combination of both resources, we detected many new QTLs, confirmed the genetic effects of each QTL, and isolated genes involved in the control of agronomically important traits. Our results provide good examples of genetic dissection for agronomic traits in closely related cultivars including temperate japonica.

Genome-wide association study (GWAS) based on large numbers of SNPs has been used to collect QTLs and to identify genes directly in germplasm accessions without the construction of segregating populations (Huang et al. 2012, Zhao et al. 2011). GWAS has already been applied to genetic analysis in agronomically important traits in japonica cultivars (Yano et al. 2016). GWAS offers potential as a powerful tool for the detection of a lot of QTLs with even small genetic effects in temperate japonica cultivars, because of their relatively simple population structure attributable to their narrow genetic diversity. GWAS could identify additional QTLs and their responsible genes in groups of closely related cultivars.

Climate change is having notable impacts on rice, increasing the occurrence of grain sterility, disease infection, insect damage, and typhoon-caused lodging, and decreasing grain yield and grain quality by increasing chalkiness (Abberton et al. 2016, Kole et al. 2015). In addition to adapting rice to climate change, we need to enhance germination, seedling vigor, and grain yield in direct-seeding culture so as to decrease labor and cost inputs in rice cultivation (Mahender et al. 2015). To develop novel climate-resistant and low-cost-production cultivars, additional genetic analyses are necessary to unravel the genetic factors associated with other important agronomic traits.

Many current Japanese temperate japonica cultivars were developed from Koshikihikari (Yamamoto et al. 2010, Yonemaru et al. 2012), including the top 10 cultivars in Japan (Yokoo et al. 2005). The development of NILs by introducing specific genes is an effective way to improve agronomic traits in these cultivars, because we can easily estimate the genetic effects of each introduced gene in the similar genetic backgrounds. Several cultivars have been developed in this way by the introduction of genes for heading date and resistance to blast disease in the genetic background of Koshikihikari or its relatives (Hori et al. 2016a, Ishizaki et al. 2005, Takeuchi et al. 2006). In addition, the development and screening of thousands of mutant lines could also be used to identify candidate lines for novel cultivars showing superior agronomic performance (Hori et al. 2016b, Takagi et al. 2015). Takagi et al. (2015) developed a novel rice cultivar Kajin showing high salt tolerance by screening from 6000 mutant lines of a temperate japonica rice cultivar Hitomebore. They also identified a responsible gene OsRR22 for the salinity-tolerance phenotype of the mutant line.

However, many agronomically important traits are complex and are determined by multiple loci in rice. Other breeding concepts would therefore be needed to improve quantitative traits, such as grain yield and grain quality, that are controlled by many QTLs with small genetic effects. For example, genomic selection estimates the genetic effect (breeding value) of every locus in the genome by simultaneously accounting for all markers (Meuwissen et al. 2001). Although genomic selection has been used mainly in the breeding of dairy cattle so far (Schaeffer 2006), it might allow us to improve various agronomic traits and to develop novel cultivars in temperate japonica rice.

Our recent studies show good examples of the validity of genetic analysis through the collection of a huge number of DNA polymorphisms and the preparation of various kinds of plant materials in developing novel cultivars in closely related populations such as temperate japonica cultivars.

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