Introduction

Breeders for any crop species try to increase the productivity and to improve the quality of products to meet human demands in plant breeding programs. Rice, *Oryza sativa* L., is one of the most important cereal grains in the world today. During the last century, genetic improvements in local elite varieties and the modernization of cultivation systems have enabled stable rice production around the world, including in Japan. Crop breeding programs aim to control genetic diversity including the collection, induction, and combination among crop species for desirable phenotypes to meet human demands (Fu 2015, Louwaars 2018). The bottleneck effect on phenotypic selection in elite rice varieties during rice breeding programs in Japan have dramatically narrowed down their genetic diversity through the modernization of rice breeding programs in Japan to reach ideal types (Ebana et al. 2008, Fujino et al. 2015, 2017, Shinada et al. 2014, Yamamoto et al. 2010, Yonemaru et al. 2012). However, it is unclear which genes have generated the changes in desirable phenotypes in elite rice varieties.

Various rice varieties have been differentiated by natural selection and utilized to meet human demands in accordance with local cultures. The determination of genetic differentiation of rice varieties across latitudinal gradients may be the consequence of their adaptation to local ecological and environmental factors. Japan, which spans from 136°04W 20°25N to 148°45W 45°33N, encompasses a wide range of environmental conditions. Hokkaido, 139°45W 45°33N to 148°45W 45°33N, is the northernmost region of Japan and one of the northern limits of rice cultivation around the world (Fig. 1a, 1b). Rice breeding programs in Hokkaido have spanned 100 years, and seed yield and eating quality have been greatly improved due to intensive selection based on phenotypic dissection, involving both genomics and phenomics (Fujino et al. 2015, 2017, Shinada et al. 2014).

Over the 100 years of rice breeding programs in Hokkaido, desirable traits for productivity and quality have been improved (Fujino et al. 2017). In addition, genome-wide marker analysis has clearly demonstrated that shifts in genetic population structures have occurred five times (Shinada et al. 2014). The shift of genetic diversity in the local gene pool may be managed with the use of exotic germplasm for human demands in rice breeding programs in Hokkaido (Fujino et al. 2015, 2017, Shinada et al. 2014). Next-generation sequencing (NGS) technology is now available for both plant biology research and plant breeding (Kim et al. 2016, Wang et al. 2018, Zhang et al. 2016, Zhou et al.)

Review

Marker-assisted selection in rice breeding programs in Hokkaido

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Rice breeding programs in Hokkaido over the past 100 years have dramatically increased productivity and improved the eating quality of rice. Commercial varieties with high yield and good eating quality, such as Kirara 397, Hoshinoyume, and Nanatsuboshi, have been continuously registered since 1990. Furthermore, varieties with better eating quality using *Wx*1-1, which reduces amylose content to improve the taste of sticky rice, such as Oborozuki and Yumepirika, were registered in 2006 and 2008, respectively. However, to the best of our knowledge the genomic changes associated with these improvements have not been determined. Better understanding of the relationships between DNA sequences and agricultural traits could facilitate rice breeding programs in Hokkaido. Marker-assisted selection (MAS), which can select the plants with chromosomal regions tagged with DNA markers for desirable traits, is an advanced technology to manage genetic improvements. Here, we summarize the current states of MAS in rice breeding programs in Hokkaido before huge data sets of genome sequences using next-generation sequencing technology come into practical use in rice breeding programs.

Key Words: marker-assisted selection, rice, plant breeding programs, genetic improvement of traits.
donors within the shortest generation time possible. The theoretical role of MAS in plant breeding programs is described in elsewhere (Cobb et al. 2018, Das et al. 2017). Here, we summarized the current statue of MAS in rice breeding programs in Hokkaido before huge data sets of genome sequences generated by NGS come to the fore in practical rice breeding programs. In addition, we discuss the role of MAS in practical rice breeding programs in Hokkaido.

**History of rice cultivation in Hokkaido**

Recent genetic and archaeology findings demonstrated that Asian cultivated rice *O. sativa japonica* was domesticated in the Yangtze River valley in southern China 10,000 years ago (Choi et al. 2017, Fuller 2011, Huang et al. 2012, Yang et al. 2012). Rice cultivation subsequently expanded around the world along with human migrations. Rice cultivation was introduced to Japan around 1000 BC, and it then spread over Japan in the Middle Yayoi period around 350 BC (Fuller 2011, Takamiya 2001). Rice cultivation in Hokkaido has been tried since the 1600s. In addition to naturally long day length conditions, the climate in Hokkaido includes cold precipitation and chilling temperature in the spring and autumn, which are all unfavorable for rice growth. Furthermore, low temperature at the reproductive phase severely causes to impair rice yield.

Based on historical records, rice cultivation in Hokkaido was tried several times in southern Hokkaido in the 1600s but these attempts largely failed (Fig. 2A, 2D). In the 1800s, rice cultivation was attempted again in southern Hokkaido along with the expansion of the Japanese society. In the 1850s, rice cultivation was successfully carried out in Ono city, southern Hokkaido. A couple of rice cultivation systems and rice varieties with adaptability together contributed to the expansion of rice cultivation areas over Hokkaido. A farmer named Kyuzo Nakayama chose a rice variety named Akage for rice cultivation in 1873, which has an extremely early heading date due to its *ghd7osprr37* genotype (Fig. 2B, 2D) (Fujino et al. 2019a). In addition, he facilitated seedling growth using warmed water during the low temperature period in spring. During the 1770s (Tenmei), rice varieties with extremely early heading date were cultivated in the Tohoku region to escape low temperature at the reproductive phase, which remarkably reduces yield. These might be the ancestors of Akage. Since then, rice cultivation had expanded even to northern Hokkaido. In 1927, rice cultivation was established in Enbetsu, the northern-limit of rice cultivation around the world (Fig. 2C, 2D).

**Rice breeding programs in Hokkaido in the 20th century**

After the rediscovery of Mendel’s laws, the local government in Hokkaido commenced rice breeding programs in 1915. In 2017, Hokkaido was a significant rice productivity area in Japan (Supplemental Table 1). Three rice varieties,
Yield limits the adaptability in crops, and in rice this is determined by three major components; days to heading (DTH), panicle number (PN), and seeds per panicle. The expression of yield-related traits including these three major components can be affected by epistatic interactions and environmental conditions (Ando et al. 2010, Li et al. 2003, Liang et al. 2014, Wang et al. 2015, Wang and Li 2008, Xing et al. 2002, Zhou et al. 2018). We can categorize them into “breeding-syndrome traits”.

Together with the cultivation system, a genotype suited to improved productivity could be established by optimizing adaptability. In the initial phase of plant breeding programs, the main efforts focus on the maximization and stabilization of seed yield in local environmental conditions. Plant architecture including breeding-syndrome traits shifted dramatically over the short time span, from large to compact (Fujino et al. 2017). The rice variety Kitaake, which is the most significant variety in the genetic population structure of group V, showed compact plants during the rice growth compared with a rice landrace Akage, which belongs to group I (Table 1). Kitaake showed earlier heading date, shorter culm length (CL), and greater panicle number than Akage (Fig. 3A–3D, Table 1). Plants with shorter CL exhibit resistance to lodging, which causes a decrease in
Various traits are involved in breeding-syndrome traits. A simple question arises as to how many genes contribute to improve breeding-syndrome traits during rice breeding programs in Hokkaido. A single gene for DTH, *Hd1*, may function in these traits. Functional *Hd1* exhibits earlier DTH with short CL, greater PN, and short PL (Fujino et al. 2019a). Functional *Hd1* (allelic to *Lm*), versus a loss-of-function *hd1*, may contribute to the southern–northern distribution among Japanese rice varieties (Yokoo and Kikuchi 1977, Yokoo et al. 1980). Of note, functional *Hd1* was transferred into the gene pool of rice breeding programs in Hokkaido (Fujino et al. 2019a). This could shape the fitness as adaptability to agriculture, leading to significant rice production in Japan. The de novo mutations in loss-of-function *ghd7* and *osprr37*, which showed extremely early heading date, might be generated in rice varieties with loss-of-function *hd1* in the northern distribution of rice.

### Premium traits

In rice breeding programs in Hokkaido, the eating quality of rice, as part of the world heritage WASHOKU, was intensively improved in the late 1900s. Various traits may be involved as part of good eating quality such as amylose content, whiteness (white/dark with blight), stickiness (degree of stickiness), and hardness (soft/hard). The eating quality of cooked rice largely depends on degree of amylose content. Many genes that reduce the amylose content in rice grain have been identified and have contributed to improving the texture for better eating quality to favorable for the seed yield (Fig. 3C). Early heading in DTH is essential for adaptability to conditions in Hokkaido (Fujino et al. 2019a), and it controls yield-related traits. In particular, a negative correlation between DTH and PN is favored for rice cultivation in Hokkaido (Fujino et al. 2019a). These yield-related traits are also associated with various morphological components, including panicle architecture. Earlier DTH caused by *Heading date 1 (Hd1)* (Yano et al. 2000) is associated with greater PN and short panicle length (PL) (Fujino et al. 2019a). These yield-related traits exhibited a balance between them with a strong impact on not only yield but also seed quality. Altered panicle architecture might contribute to grain filling nature (Fig. 3D, Table 1), leading to high quality of the grains. Phenotypic changes are commonly observed between Akage and Kirara 397, which belongs to group V (Fig. 3A–3D).

### Table 1. Changes in phenotype involved in yield related traits

| Category       | Trait             | Phenotypic value |
|----------------|-------------------|------------------|
|                | Akage             | Kitaake          | Yumepirica     |
| Yield          | Total Yield       | 57.3             | 50.3            | 72.6            |
| (kg/ha, YLDt)  | 100               | 88.1             | 126.7           |
| Plant          | Days to heading   | 98               | 89              | 91              |
| architecture   | (day, DTH)        | 100              | 90.8            | 92.9            |
| Culm length    | 93.7              | 59.4             | 64.5            |
| (cm, CL)       | 100               | 63.4             | 68.8            |
| Panicle number | 419               | 511              | 848             |
| (number, PN)   | 100               | 122.0            | 202.4           |
| Panicle        | Panicle length    | 20.9             | 15.4            | 15.9            |
| architecture   | (cm, PL)          | 100              | 73.7            | 76.1            |
| Seeds per panicle | 92.4         | 58.3             | 59.3            |
|                  | (number, SP)      | 100              | 63.1            | 64.2            |

Phenotypic values are cited from Fujino et al. (2017), which were measured in 2013 at Kamikawa exp. Station, Pippu, Hokkaido, Japan. Upper and lower rows indicate phenotypic values and ratio with “Akage” being 100, respectively.

Fig. 3. Phenotypic difference between genotypes. A–E: Rice plants (Kirara397 on the left and Akage on the right in each panel) grown in the experimental paddy field in natural environmental conditions (Sapporo, Hokkaido, 2018). Plants on 2018-07-04 (A), 2018-08-07 (B), and 2018-09-14 (C), panicles (D), grains (E). Bar indicates 1 cm. Sowing and transplanting were performed on 16 April and 22 May 2018, respectively. Cultivation management followed the standard procedures used at Hokkaido Agricultural Research Center. F: rice variety Hoshinoyume (three leaves on the left) and Kitakurin (right) in a field test for blast resistance in Kamikawa (Pippu, Hokkaido) (Photo by Hitoshi Kiuchi).
Japanese market (Ando et al. 2010, Sato et al. 2002, Takemoto-Kuno et al. 2015). The market in Japan evaluates rice products based on these traits. Amylose content of Akage (22.4%) was dramatically decreased in Kitaake (20.2%) and Yumepirika (16.1%) instead of grain shape (Table 2). In addition, grain appearance, which shows the perfect grain shape, was dramatically improved in Yumepirika (79.6%) and Kitaake (70.1%) rather than Akage (12.2%) (Table 2). We categorized the traits for seed quality into “premium traits”. The phenotype of premium traits could be expressed from novel genes/QTLs in genetic background improved by breeding-syndrome traits (Fig. 3E).

Once the adaptability for local environments, breeding-syndrome traits, has been optimized, plant breeding programs will focus on the quality of the products, premium traits. For human demands as part of local culture, quality of products may be shaped by novel genes among local varieties.

**MAS in rice breeding programs in Hokkaido**

Phenotypic selection during the rice breeding programs in Hokkaido has improved various agronomic traits (Fujino et al. 2017). To facilitate rice breeding programs in Hokkaido, MAS has been actively carried out since the first attempt of MAS for a stripe resistance gene Svb-i (Hayano-Saito et al. 2000) in 1996. In the initial phase, MAS was carried out for research purposes rather than for the development of new varieties due to the limited number of available DNA markers. Increased number of available DNA markers for various traits has given a great impact on the application of MAS in rice breeding programs (Table 3, Supplemental Table 3).

Because genes for amylase content and disease (blast fungus) resistance have large effects on these traits, improvements in these traits are useful for MAS using DNA markers targeted to the desired alleles. Control of amylase content is a major strategy for rice breeding programs for the improvement of eating quality. Wx1-1 for low amylose content was identified on the short arm of chromosome 6 (Ando et al. 2010), and rice variety Yumepirika harboring Wx1-1 exhibited sticky eating quality. This eating quality has been evaluated as a premium characteristic in the Japanese market.

Previously, we identified the blast resistant gene Pi-cd on chromosome 11 as a major genetic factor in the local rice population in Hokkaido (Fig. 3F), although it may be derived from a rice variety Cody from USA (Shinada et al. 2015b). The Pi-cd locus is distributed specifically in tropical japonica (upland) rice varieties over the world and might be introgressed from wild relative O. meridionalis (Fujino et al. 2019c). Pi-cd is only one blast resistance gene, which has been used in rice breeding programs in Hokkaido. The rice variety Kitakurin was registered in 2014 and exhibits good eating quality and vigorous resistance to rice blast (http://www.pref.hokkaido.lg.jp/ns/uskome/index3.htm). Pi-cd plays a major role in blast resistance in Kitakurin (Fujino et al. 2019c, Shinada et al. 2015b).

Rapid changes in the virulence characteristics of populations raises a continuous threat to the effectiveness of existing blast-resistant varieties, because breakdown of resistance in newly developed resistant varieties is often observed due to evolution of new virulent pathogen strains. However, MAS for the utilization of the known resistance genes/QTLs could be reliable in achieving disease resistance in a variety. This approach accelerated the monogenic nature of blast resistance in a local gene pool. Accurate understanding of the genetic structure and genes controlling virulence is required in management strategies for the durability of blast resistance in rice.

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**Table 2. Changes in phenotype involved in grain quality traits**

| Category      | Trait                  | Akage | Kitaake | Yumepirika |
|---------------|------------------------|-------|---------|------------|
| Grain shape   | Grain length (mm, GL)  | 4.95  | 4.82    | 5.12       |
|               | Grain width (mm, GW)   | 2.83  | 3.00    | 2.81       |
|               | 1000-grain weight (g, TGW) | 22.3 | 24.2    | 23.0       |
| Grain quality | Witness of brown rice (Number, WB) | 21.8 | 19.1    | 20         |
|               | Amylose content (%) (AC) | 100  | 90.2    | 71.9       |
|               | Protein content (%) (PC) | 100  | 91.5    | 91.9       |
|               | Grain appearance (%) (GA) | 12.2 | 70.1    | 79.6       |

Phenotypic values are cited from Fujino et al. (2017), which were measured in 2013 at Kamikawa exp. Station, Pippu, Hokkaido, Japan. Upper and lower rows indicate phenotypic values and ratio with “Akage” being 100, respectively.

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**Table 3. MAS in rice breeding programs in Hokkaido**

| Year | Trait                  | Gene/QTL | Reference       |
|------|------------------------|----------|-----------------|
| 2005 | Blast resistance       | Pb1      | Hayashi et al. 2010 |
| 2005 | Rice stripe virus resistance | Stvb-i | Hayano-Saito et al. 2000 |
| 2005 | Low temperature tolerance | Cbi-Ccb2 | Saito et al. 2001 |
| 2005 | Low temperature tolerance | qCTB-8 | Kuroki et al. 2007 |
| 2010 | Blast resistance       | pi21     | Fukuoka et al. 2009 |
| 2010 | Blast resistance       | Pi35     | Nguyen et al. 2006 |
| 2010 | Blast resistance       | Pi39     | Terashima et al. 2008 |
| 2010 | Amylose content        | qAC9.3   | Ando et al. 2010 |
| 2010 | Amylose content        | Wx1-1    | Ando et al. 2010 |
| 2010 | Amylose content        | Wx-mq    | Saito et al. 2002 |
| 2010 | Amylose content        | Wx-a     | Yamanaka et al. 2004 |
| 2017 | Amylose content        | qAC2     | Takemoto-Kuno et al. 2015 |
| 2017 | Amylose content        | Wx-mq    | Saito et al. 2002 |
| 2017 | Amylose content        | Wx1-1    | Ando et al. 2010 |
| 2017 | Amylose content        | Wx9-C9.3 | Ando et al. 2010 |
| 2017 | Blast resistance       | pi21     | Fukuoka et al. 2009 |
| 2017 | Blast resistance       | Pi-km    | Costanzo and Jia 2010 |
| 2017 | Blast resistance       | Pb1      | Hayashi et al. 2010 |
| 2017 | Blast resistance       | Pi39     | Fukuoka et al. 2014 |
| 2017 | Blast resistance       | Pi39     | Liu et al. 2007 |
| 2017 | Blast resistance       | Pi-cd    | Shinada et al. 2015b |
| 2017 | Seedling establishment | qSUS1    | Iwata et al. 2010 |
| 2017 | Low-temperature germinability | qLGP2-1 | Fujino et al. 2008 |
| 2017 | Root characteristic    | Do1      | Uga et al. 2013 |
| 2017 | Yield                  | Gx1      | Ashikari et al. 2005 |
| 2017 | Amylopectin property   | sb1      | Okamoto et al. 2013 |
We are able to select plants homozygous for the gene/QTL targeted in a single generation using MAS. This is the main advantage of MAS compared with conventional strategies. When selection is carried out based on phenotypic values, it is difficult to distinguish plants that are homozygous or heterozygous for the target gene/QTL. To determine the genotype of traits, progeny testing needs to be carried, which is laborious, expensive, and time-consuming. Conversely, with MAS we can select the desired genotype directly, facilitating rice breeding programs.

This efficiency of MAS is dependent on the heritability of the traits targeted. In the next section, we will focus on the efficiency of selection not on the selection process itself for plants with desirable genotypes but also in the improvement of traits. We have to manage genetic diversity to meet human demands. Therefore, it is necessary to clarify which genes in any germplasm exhibit a novel phenotype in agronomic traits of interest. Consequently, MAS should focus on agronomic traits to meet human demands in the future.

| Gene/QTL | Locus | Desirable allele | Reference |
|----------|-------|-----------------|-----------|
| Gene    | Wx    | Amylose content in rice grain | Wx1-1 | Decrease | Hokkai No. 287 | Ando et al. 2010 |
| Gene    | AC2   | Amylose content in rice grain | AC2 | Decrease | Kuiku No. 162 | Takemoto-Kuno et al. 2015 |
| Gene    | AC9.3 | Amylose content in rice grain | AC9.3 | Decrease | Hokkai PL-9 | Ando et al. 2010 |
| Gene    | H65   | Heading date | h65 | Promote | Bozu No. 6 | Wei et al. 2010, Fujino et al. 2013 |
| Gene    | OsPrr37 | Heading date | Ospr37 | Promote | na | Koo et al. 2013, Fujino et al. 2019b |
| Gene    | Hdi7  | Heading date | Hdi7 | Promote | na | Yano et al. 2000, Fujino et al. 2019b |
| Gene    | qLTG3-1 | Cold tolerance at the seed germination | qLTG3-1 | Promote | na | Fujino et al. 2008, Fujino and Iwata 2011 |
| QTL     | qCTF7 | Cold tolerance at the fertilization stage | qCTF7 | Tolerance | Eikei 88223 | Shidama et al. 2013 |
| QTL     | qWCR  | Grain quality (Whiteness of cooked rice) | qWCR | Whiteness | na | Shidama et al. 2015a |

**Genes/QTLs for the desirable traits**

At least 98 genomic studies on various agronomic traits have been carried out using rice varieties in Hokkaido during the past 10 years (Supplemental Table 3). Among these, desirable genes/QTLs for trait improvement have been identified (Table 4). These DNA markers have already been utilized for MAS and facilitated improvements in the traits.

Understanding of the origins of desirable alleles can facilitate rice breeding programs. We have divided these origins into three categories (Table 4). The first is de novo mutations under intensive human demand during rice cultivation in Japan. Second is natural variation, which occurred before rice came to Japan and involves genetically diverse germplasm from all over the world. The third is induced mutations generated by chemical mutagens and ionizing radiation. Taken together, all kinds of genetic variations are significant for improvements in traits for human demands.

In addition, desirable alleles for important traits frequently existed in the local germplasm. Desired alleles at qLTG3-1 locus for low temperature germinability has been selected along with the cultivation system (Fujino et al. 2004, 2008, Fujino and Iwata 2011). There were three alleles at the qLTG3-1 locus. First, a functional allele, is found in Italica Livorno, the IL allele. Second, the NP allele is found in Nipponbare, where a single amino acid substitution was present in a conserved domain of qLTG3-1, which led to a reduction in function. Third, a loss-of-function allele caused by a 71 bp deletion is found in rice variety Hayamasari, the HY allele. In landraces and varieties from the initial phase of rice breeding programs in Hokkaido, most varieties carried the IL allele, then the predominant allele shifted to the NP allele, and finally it shifted to the HY allele (Fujino and Iwata 2011). The rapid shifts in alleles for qLTG3-1 indicated that there were strong selection pressures toward weaker germinability at low temperature during rice breeding programs in Hokkaido (Fujino and Iwata 2011). The mutant alleles might become adaptable to the cultivation system in Hokkaido.

**Prospects**

Shaping the cultivation systems and phenotypes in a variety by intensive artificial selections has decreased the genetic diversity in plant breeding programs (Fu 2015, Louwaars 2018). For human demands in the future, the control of genetic diversity may be significant for how to establish desirable genotypes using diverse exotic germplasm over cultivated species and their wild relatives, which is clearly and genetically distinguishable from local elite varieties. Depending on the status of plant breeding programs, the control of genetic diversity in an elite variety may be critical for the activity of plant breeding programs.

Cross (hybridization) breeding strategies are a major driver for the control and increase of genetic diversity in local gene pools, especially for those with an inbreeding habit such as rice. The utilization of exotic germplasm as a parental variety can be used to explore the genetic diversity of local gene pools and may break the balance of elite phenotypes from the combination of desirable traits/genes. The modernization of rice breeding programs with molecular...
technology may dramatically and immediately reduce genetic diversity, forming a bottleneck.

Novel phenotypes are generated from novel genes themselves and genetic interactions (Fujino et al. 2019a, 2019b). For example, extremely earlier heading date is expressed in EARLY DUO, ghd7osprr37, in natural variation but also in EARLY TRYO, Hdlghd7osprr37, derived from rice breeding programs (Fig. 4) (Fujino et al. 2019a). Plant breeding programs can construct novel combinations of genes that never occur in natural variations, exhibiting novel phenotypes. However, we could not fully elucidate which combinations of genes generate novel phenotypes. This is a limitation of plant breeding programs rather than MAS.

**Conclusion**

Molecular techniques for MAS are enough for practical application in rice breeding programs. As well as the methodological advantages and significance of MAS, we should also further examine the consequences of MAS in the improvement of traits. Conventional strategies in rice breeding programs can involve several genetic steps. Firstly, we collect genetically and phenotypically diverse germplasm from all over the world. Second, we evaluate the trait values in these germplasms. Then, we identified genes/QTLs, and introduced them into elite local varieties. Conversely, MAS facilitates not only the selection of rice plants but also all the processes in rice breeding programs. We can design new varieties using available DNA markers only. The resultant new varieties may exhibit a phenotype within an expected range. To break through the limitations of MAS, we should develop new strategies with genomic inputs.

The current rice breeding programs enhanced by MAS looked to combine desirable traits/genes among the local gene pool into a single variety. Although rice breeding programs have had various achievements in meeting current human demands, there still remains an unmet need to control genetic diversity in rice breeding programs for human demands in the future. Now, we are in the genomic-era.

Novel genes/QTLs for desirable traits found in local rice breeding programs, such as semi-dwarf sdll (Asano et al. 2007), could be shared all over the world using molecular techniques with several kinds of resolution: phenotype, Mb level at the chromosomal region, kb level for physical distance, and bp level in the responsible gene itself.

Germplasm under diverse environmental conditions and in different culture conditions is valuable for various human demands (Dwivedi et al. 2016, 2017). Various local populations, such as at the country level, have been analyzed for their genetic diversity as genetic population structures (Table 5). We should use it in field evaluation systems depending on the genetic classification, because phenotypic values are expressed from the results of interactions between the genotype and environment.

**Table 5.** Research on genetical population structure analysis in local rice populations

| Area                  | DNA marker | References          |
|-----------------------|------------|---------------------|
| Hokkaido, Japan       | SSR        | Shinada et al. 2014 |
| Japan                 | SSR        | Fujino et al. 2019a |
|                       | SSR        | Ebana et al. 2008   |
|                       | SNP        | Yonemaru et al. 2012|
| Argentina             | SSR        | Giarrocco et al. 2007|
| Cambodia              | SSR        | Orn et al. 2015     |
| Indonesia             | SSR        | Thomson et al. 2007 |
| Italy                 | SSR        | Cai et al. 2013     |
| Portugal              | SSR        | Jayamani et al. 2007|
| Thailand              | Indel      | Chakhonkaen et al. 2012|
| USA                   | SSR        | Lu et al. 2005      |
| Vietnam               | RFLP       | Fukuoka et al. 2003 |
| Europe                | SSR        | Courtois et al. 2012|
| Northeast Asia        | SSR        | Wang et al. 2014    |
| Temperate region      | SNP        | Reig-Valiente et al.2016 |

DNA marker indicates SSR; Simple Sequence Repeat, Indel; Insertion and deletion, SNP; Single Nucleotide Polymorphism, RFLP; Restriction Fragment Length Polymorphism.

**Author Contribution Statement**

KF, HY, and RK envisaged the concept. HY and RK collected recent information on rice breeding programs. KF wrote the manuscript. KF, HY, and RK approved the final manuscript.
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