Introduction

Japan is an island nation located between 24° and 46° north latitudes; its climate ranges from subtropical to boreal. Therefore, the most suitable season for potato (*Solanum tuberosum* L.) cultivation differs from region to region. As the optimal temperature for potato cultivation is between 10°C and 23°C (Kurihara et al. 1963), potatoes can be cultivated and harvested at any time all year round in different regions across Japan. Potatoes are grown in summer in Hokkaido and the Tohoku region, in the northern part of Japan, and in winter in Okinawa, the southernmost prefecture. Hokkaido is the largest production area in Japan. However, double cropping in spring and fall is carried out in other regions, including Kyushu, which is the second largest production area. In each cropping season, the cultivation environment varies; in spring cropping, potato is planted when temperatures are relatively low and the day length is relatively short. Thus, potatoes grow under conditions of increasing temperatures and day length. In summer cropping, temperatures and day length increase after planting, reach a peak during the growth period, and then decrease until harvesting. In fall cropping, growth starts when temperatures are high and the day length is relatively long, and both decrease during growing. In winter cropping, growth starts when temperatures are high and the day length is short, and temperatures and day length decrease at the beginning of growth but increase after the middle of the growth period (Levy et al. 1986) (Fig. 1). This multiple cultivation system requires different cultivars adapted to contrasting growth conditions.

Potato cultivars are roughly classified into four types based on their purpose: table use, food processing, and starch production, and other purposes, including colorful potatoes. The per capita annual consumption of potatoes was 13.4 kg in 1970; thereafter, consumption increased gradually, reaching 18.0 kg in 2000. However, there has been a declining trend in recent years, falling to 16.6 kg in 2009 (Ministry of Agriculture, Forestry and Fisheries of Japan). This increase has been accompanied by changes in demand trends. Consumption of table use potatoes continues to gradually decrease. In contrast, consumption of potatoes for food processing such as potato chips, French fries, frozen croquettes, and packed salads, has greatly increased since 1970. The consumption of processed foods, which was negligible in...
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Each breeding station in Japan uses a similar breeding scheme, with minor modification depending on the situation of each station. The potato breeding program begins with the selection of two genotypes that will be used as crossing parents. As the potato predominantly outcrosses and asexually propagates by tubers, its heterozygosity is relatively high compared with that of inbreeding and sexually propagating crops (Xu et al. 2011). Because of their high heterozygosity, F1 progenies obtained from crosses between two genotypes are each genetically unique and show various phenotypes. They are subsequently clonally propagated; thus, a fixation process is unnecessary. Therefore, in potato breeding, the selection of crossing parents and desirable phenotypes from a large population becomes essential. Selection at an early breeding stage, namely, primary individual selection of seedling and secondary individual clonal selection, is carried out based on characteristics with high heritability. At these stages, characteristics with little annual variation such as PCN resistance, flesh color, and tuber shape, are evaluated. In addition, because frequent occurrence of defects such as hollow heart, growth cracks, and brown spot, devastates potato production, lines having such severe defects are eliminated at these stages, although these defects are influenced by environmental conditions. Furthermore, potato chip quality and starch content are evaluated at these stages for potato chip processing and starch production, respectively, and extremely inferior genotypes are eliminated. At later stages, including line selection, preliminary performance yield test, and performance yield test, selection is carried out based on several quantitative characteristics such as yield, maturity, and cooking qualities. During the performance yield test, the clones are tested on a number of fields located in different places (local adaptability test). This is necessary to determine the adaptability of the clones to diverse environments. Because of the low...
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multiplication rate, which is around 10–20 times per cropping, propagation and evaluation of potato plants are carried out in parallel, and thus evaluation of quantitative characteristics in a large plot requires several years. Finally, comparisons of selected lines with existing cultivars are conducted in several farmers' fields. The lines selected following these many experiments are then released as new cultivars (Fig. 2).

**Breeding potatoes for summer cropping**

Potatoes are cultivated in the summer in northern Japan, including Hokkaido and the Tohoku region. Large-scale upland farming with an integrated and mechanized cultivation system has been established in Hokkaido. In summer cropping, potatoes are planted from mid-April to mid-May and harvested from the end of July to mid-October. Because summer cropping has a longer growing period, the yield is higher than that of double cropping and fully matured potatoes with high starch content are produced. Due to the longer growing period, a relatively large number of tubers can enlarge; thus, the tuber numbers of the cultivars used for summer cropping are greater than those of the cultivars used for double cropping (Table 1). To secure the yield during the short growing period in double cropping, cultivars with fewer tubers tend to be selected. Table 1 shows a comparison of characteristics between cultivars of summer and double croppings. Because criteria for tuber size slightly differ among each cropping (tubers above 20g, 30g, and 40g are included in the total tuber yield in summer cropping, spring cropping, and fall cropping respectively), the data of each cropping type cannot be simply compared. However, these data clearly show that there are differences in tuber and stem number, specific gravity, and dormancy period (Table 1). In Hokkaido, cultivars for table use, food processing, and starch production are cultivated. For all purposes, pest and disease resistance and high yield are commonly required objectives. In addition, proper maturity is an important breeding target in potato cultivars in summer cropping. Crop rotation of four crops, potato, winter wheat, sugar beet, and legumes, is common in Hokkaido, in which winter wheat is grown just after potato cultivation. Because winter wheat is sown in mid-September, table use cultivars and most of the food processing cultivars should be harvested before sowing of winter wheat. On the other hand, high yield is the first priority for starch production cultivars; late maturity becomes an advantage for ensuring a long growing
period. A dormant tuber period is also an important target. In contrast to the case with double cropping, in which the preferred dormant period is within 60 to 80 days, the dormant period is relatively longer in summer cropping cultivars (Table 1). This is because tubers harvested in fall should be stored until the following spring. Cultivars with shorter dormant periods tend to produce smaller tubers due to the short day length. Because tubers harvested in fall are sometimes do not sprout due to high temperature or day length, are drastically different between spring and fall cropping systems.

Double cropping of potatoes is carried out under subtropical conditions and in areas such as the Mediterranean region and China (Jansky et al. 2009, Levy et al. 1986, Solmniki 1961, Susnoschi 1981). Potato cultivation using a double cropping system in spring and fall has been adopted in Kyushu (Mori 2001, Nakao and Sayama 2001). Most of the potatoes produced in warm areas are shipped between winter and summer, which is the off-crop-season in Hokkaido, and are then consumed for table use. The potatoes for spring cropping are planted from November to March and harvested between March and June. Mulch is mostly used by growers in spring cropping. Because spring cropping is cultivated during a short time period, mulching is used to promote germination and growth by maintaining an appropriate temperature. The potatoes for fall cropping are planted from September, and harvested from November to January (Mori 2001). Each cultivation period of double cropping is shorter than that of summer cropping in Hokkaido. In addition, as discussed, the growing conditions such as temperature and day length, are drastically different between spring and fall croppings (Fig. 1). Insensitivity or low sensitivity against day length and temperature are required to adapt to such contrasting environments. Some cultivars for summer cropping do not show appropriate growth in fall cropping; they sometimes do not sprout due to high temperature or produce tubers before there is enough vegetative growth due to the short day length. Because tubers harvested in spring cropping are used as seed tubers in fall cropping, it is preferred that the dormant period of the tubers is no longer than 60–80 days (Mori 2001). In fact, to use harvested tubers in spring cropping as seed potatoes in fall cropping, farmers forcibly break the dormancy of the seed potato by high-temperature treatment and forced moisture retention. Cultivars adapted to double cropping have uniform sprouting and early development and are able to rapidly cover the field with green leaves. This is important for efficient photo reception, and early enlargement are also breeding targets.

The potato breeding project began in 1902 in Hokkaido, and introduction breeding was the first approach, which aims to select suitable genotypes from foreign cultivars. As a result of introduction breeding, many cultivars, including ‘Irish Cobbler’ and ‘May Queen’, which are still major cultivars for table use, were selected. Cross breeding began in 1918, and the starch production cultivar ‘Benimaru’, the first cultivar bred by cross breeding in Japan, was released in 1938. Since then, breeding activities have made continued efforts to improve yield, pest and disease resistance, and quality. The current leading cultivar ‘Toyoshiro’ for potato chip processing was released in 1976 (Sakaguchi et al. 1976). Both ‘Konafubuki’, a leading cultivar for starch production, and ‘Hokkaikogane’, a leading cultivar for French fries, were released in 1981 (Asama et al. 1982). After PCN invasion was confirmed in Hokkaido in 1972, conferring PCN resistance became the most important breeding objective. In 1986, the first PCN resistant cultivar in Japan, Toyoakari, was developed, and then many PCN resistant cultivars were developed for each purpose. In addition to these PCN resistant cultivars, several PCN susceptible cultivars with unique characters such as high content of carotenoid or anthocyanin were developed (Mori et al. 2009a, 2009b) (Table 2). However, because PCN resistance is currently considered to be a prerequisite characteristic for new cultivars, lines without PCN resistance are eliminated at the early stages of breeding.

### Breeding potatoes adapted for double cropping

Double cropping of potatoes is carried out under subtropical conditions and in areas such as the Mediterranean region and China (Jansky et al. 2009, Levy et al. 1986, Solmniki 1961, Susnoschi 1981). Potato cultivation using a double cropping system in spring and fall has been adopted in Kyushu (Mori 2001, Nakao and Sayama 2001). Most of the potatoes produced in warm areas are shipped between winter and summer, which is the off-crop-season in Hokkaido, and are then consumed for table use. The potatoes for spring cropping are planted from November to March and harvested between March and June. Mulch is mostly used by growers in spring cropping. Because spring cropping is cultivated during a short time period, mulching is used to promote germination and growth by maintaining an appropriate temperature. The potatoes for fall cropping are planted from September, and harvested from November to January (Mori 2001). Each cultivation period of double cropping is shorter than that of summer cropping in Hokkaido. In addition, as discussed, the growing conditions such as temperature and day length, are drastically different between spring and fall croppings (Fig. 1). Insensitivity or low sensitivity against day length and temperature are required to adapt to such contrasting environments. Some cultivars for summer cropping do not show appropriate growth in fall cropping; they sometimes do not sprout due to high temperature or produce tubers before there is enough vegetative growth due to the short day length. Because tubers harvested in spring cropping are used as seed tubers in fall cropping, it is preferred that the dormant period of the tubers is no longer than 60–80 days (Mori 2001). In fact, to use harvested tubers in spring cropping as seed potatoes in fall cropping, farmers forcibly break the dormancy of the seed potato by high-temperature treatment and forced moisture retention. Cultivars adapted to double cropping have uniform sprouting and early development and are able to rapidly cover the field with green leaves. This is important for efficient photo reception, and early enlargement are also breeding targets.

### Table 1. Comparison of characteristics of table use cultivars between summer and double croppings. The five year means (2009–2013 for summer and fall croppings, 2010–2014 for spring cropping with mulching) were compared. Data of dormancy periods are means of 2009–2010 for Kita-akari, and 2012–2014 and 2012–2013 for Sanjumaru of spring and fall croppings

| Cultivars | Cropping season | No. of tubers per hill | Average weight of tubers | No. of main stems per hill | Specific gravity | Dormancy period |
|-----------|----------------|-----------------------|--------------------------|----------------------------|-----------------|-----------------|
| Summer    |                |                       |                          |                            |                 |                 |
| Irish Cobbler | Summer       | 10.7                  | 82                       | 4.5                        | 1.089           | 114             |
| Kita-akari | Summer        | 12.6                  | 77                       | 4.4                        | 1.044           | 109             |
| Touya     | Summer        | 8.7                   | 114                      | 4.1                        | 1.084           | 115             |
| Haruya    | Summer        | 10.3                  | 102                      | 2.1                        | 1.082           | 112             |
| Double    |                |                       |                          |                            |                 |                 |
| Nishiyutaka | Spring       | 5.2                   | 133                      | 1.5                        | 1.069           | 108             |
|            | Fall          | 4.2                   | 119                      | 2.2                        | 1.059           | 77              |
| Dejima    | Spring        | 4.2                   | 137                      | 1.5                        | 1.072           | 79              |
| Aiyutaka  | Fall          | 4.5                   | 120                      | 3.0                        | 1.064           | 67              |
| Aiyutaka  | Spring        | 5.3                   | 119                      | 1.8                        | 1.066           | 90              |
|            | Fall          | 4.4                   | 117                      | 2.5                        | 1.057           | 69              |
| Sanjumaru | Spring        | 6.0                   | 112                      | 1.7                        | 1.064           | 82              |
|            | Fall          | 4.0                   | 129                      | 2.0                        | 1.057           | 59              |

Tuber number and weight include tubers above 20 g for summer cropping, 30 g for spring cropping, and 40 g for fall cropping.
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Photoreception and to obtain the highest yield (Allen and Scott 1980, Sale 1973). In addition to yield, and pest and disease resistance, which are also required for summer cropping, the breeding targets for double cropping in Japan are early enlargement, short dormancy, and late maturity so that tubers continue enlarging during the growing period. In double cropping, the time required for the early stages of breeding (from primary individual selection of seedling to preliminary performance yield test) is half of that required for summer cropping, because evaluation and selection can be performed twice per year in spring and fall. Using this advantage, good cultivars with high adaptability are selected.

The potato breeding project for double cropping in warm areas began in 1947, and ‘Unzen’ and ‘Tachibana’, which replaced the landrace cultivars, were released in 1955. Later, ‘Dejima’ and ‘Nishiyutaka’ were bred in 1971 and 1978, respectively, and have become the leading cultivars in double cropping (Chishiki et al. 1979, Mori 2001). In 1997, the first PCN resistant cultivar for double cropping in Japan, Fugenmaru, was developed (Mori et al. 1998). Subsequently, several PCN resistant cultivars with additional characteristics have been developed (Table 2).

### Table 2. List of cultivars developed in Japan. Current leading cultivars and cultivars with specific characteristics are tabulated with release year, resistance to PCN, cultivar type, and cropping type

| Cultivar  | Release year | Resistance to PCN, Ro1 | Cultivar type | Cropping type | Note | Reference       |
|-----------|--------------|------------------------|---------------|---------------|------|-----------------|
| Dejima    | 1971         | S                      | Table         | Double        | Leading cultivar for table use in double cropping | Chishiki et al. 1979 |
| Toyoshiro | 1976         | S                      | Chips         | Summer        | Leading cultivar for potato chip processing | Sakaguchi et al. 1976 |
| Nishiyutaka| 1978         | S                      | Table         | Double        | Leading cultivar for table use in double cropping | Chishiki et al. 1979 |
| Hokkaikogane| 1981        | S                      | Table         | Double        | Leading cultivar for French fry processing Tolerance to blackspot bruising | Chishiki et al. 1979 |
| Konafubuki| 1981         | S                      | Fry           | Summer        | Leading cultivar for starch production PVY resistance | Asama et al. 1982 |
| Toyo-akari | 1986         | R                      | Starch        | Summer        | First cultivar with PCN resistance bred in Japan | |
| Kita-akari | 1987         | R                      | Table         | Summer        | First cultivar for double cropping with PCN resistance | Mori et al. 1998 |
| Sayaka    | 1995         | R                      | Salad         | Summer        | Low PGA content Tolerance to blackspot bruising | |
| Touya     | 1995         | R                      | Table         | Summer        | First cultivar for double cropping with PCN resistance | |
| Fugenmaru | 2001         | R                      | Table         | Summer        | Late blight resistance tolerance to blackspot bruising | Senda et al. 1998 |
| Hanashibetsu | 2001       | R                      | Table         | Summer        | Low PGA content | |
| Kitanobe   | 2001         | R                      | Chips         | Summer        | CIS resistance | |
| Inka-no-mezame | 2002    | S                      | Colorful      | Summer        | Dark yellow flesh containing carotenoid | Mori et al. 2009b |
| Kitamuraaki | 2004        | R                      | Colorful      | Summer        | Purple flesh containing anthocyanin | Mori et al. 2009a |
| Harukari   | 2005         | R                      | Table         | Double        | Common scab resistance | Nakao et al. 2003 |
| Aiyutaka   | 2006         | R                      | Table         | Double        | NSK content | Nakao et al. 2004 |
| Kogumaru  | 2006         | R                      | Fry           | Summer        | Low PGA content | |
| Northern Ruby | 2006       | R                      | Colorful      | Summer        | Red flesh containing anthocyanin | Mori et al. 2009a |
| Haruka     | 2007         | R                      | Table         | Summer        | Tolerance to blackspot bruising | Kobayashi et al. 2009 |
| Snow march | 2007         | R                      | Table         | Summer        | Common scab resistance | Iketani et al. 2005 |
| Saikai 31 | 2009         | S                      | Colorful      | Double        | Red flesh containing anthocyanin | Tamiya et al. 2008 |
| Saya-akane | 2009         | R                      | Table         | Summer        | Late blight resistance | |
| Sanjumaru  | 2012         | R                      | Table         | Double        | Common scab resistance | Mukojima et al. 2012 |
| Kitamunashi | 2013        | R                      | Table         | Summer        | Late blight resistance | Tsuda et al. 2013 |
| Poroshiri | 2013         | R                      | Chips         | Summer        | Common scab resistance | |
| Rirachip | 2013         | R                      | Chips         | Summer        | CIS resistance | Fujita et al. 2014 |

S and R for resistance to PCN indicate susceptible and resistance, respectively.

Selection of disease resistant cultivars by marker-assisted selection combined with field evaluation

In 1972, the occurrence of PCN was reported in Hokkaido, Japan, for the first time. The expanse of the total infected areas reached 10,000 ha and is still increasing in Japan. PCNs comprise two species \[G. rostochiensis\] (Woll.) Behrens and \[G. pallida\] (Stone) Behrens and eight pathotypes (Ro1–5 of \[G. rostochiensis\] (Woll.) Behrens and Pa1–3 of \[G. pallida\] (Stone) Behrens). Among the eight PCN
pathotypes, only Ro1 has been found in Japan (Inagaki 1984, Kushida and Momota 2005, Mori et al. 2007). Various resistant cultivars have been introduced from foreign countries, and their characteristics and adaptability in infected areas with PCN have been examined. As the result of tests, ‘Tunika’ was selected and cultivated as a starch production cultivar. ‘Tunika’ has greatly contributed as a parent to the development of PCN resistant cultivars in Japan. Since 1972, the introduction of resistance against PCN has been a top priority (Mori et al. 2007), and now is a prerequisite for new potato cultivars in Japan. The single dominant gene H1, introduced from accession number CPC1673 of S. tuberosum L. ssp. andigena Hawkes, confers nearly perfect and durable resistance to the pathotypes Ro1 and Ro4 (Huijsman 1955). H1 has been widely used to confer resistance to Ro1 around the world, including Japan. The screening for PCN resistance is performed by cultivation in infested fields, or using the plastic cup method, which is a modification of the screening method developed by Phillips et al. (1980). Recently, marker-assisted selection (MAS) using DNA markers linked to the H1 gene has also been carried out in combination with an inoculation test (Asano et al. 2012, Mori et al. 2011, Takeuchi et al. 2008). During the early period of breeding of resistant cultivars, H1 was introduced by crossing susceptible cultivars and resistant cultivars with simplex (H1H1h1h1) genotype. However, nearly 50% of progenies from this combination had to be discarded as susceptible clones, and thus breeding efficiency was low. To improve breeding efficiency, the parental line R392-50, which has H1 in triplex condition (H1H1H1h1), was selected from the R392 population. The R392 population was introduced by Cornell University in the United States, and was derived from a cross between the resistant cultivars ‘Wauseon’ (simplex) and ‘Hudson’ (duplex) (Mori and Nishibe 1987). As nearly 100% of progenies crosses between R392-50 and susceptible cultivars harbor H1, breeding efficiency became high, and various superior cultivars, including ‘Touya’, ‘Early Starch’, ‘Beniakari’, ‘Hanashibetsu’, and ‘Sayaka’, were developed using R392-50 (Mori et al. 2007, Senda et al. 1998). Due to intensive use of R392-50 and its progenies for introduction of PCN resistance, all PCN resistant cultivars developed in Japan have H1 as the PCN resistance gene (Asano et al. 2012).

Twelve viruses are known to infect and damage potatoes in Japan (Maoka et al. 2010). PVY is one of the most important viruses among them, and thus, resistance to PVY is highly desirable. The other important virus is PVX, which causes heavy mosaic symptoms when the plants are coinfected with PVY. Potato leaf roll virus (PLRV) was once the most common virus in seed stocks and caused the greatest yield loss in potato crops, and thus resistance to PLRV was also an important target. At present, however, the establishment of seed certification schemes, combined with intensive rouging of infested plants and insecticide applications, enables growers to control the disease. Extreme resistance genes to PVY have been reported from three different sources: Ry\textsubscript{pad} from S. stoloniferum Schlechtld. et Behé. (Cockerham 1943), Ry\textsubscript{adj} from S. tuberosum L. ssp. andigena Hawkes (Munoz et al. 1975), and Ry\textsubscript{chc} from S. chacoense Bitt. Among these three resistance genes, Japanese breeders have used only Ry\textsubscript{chc} to confer PVY resistance, and ‘Konafubuki’, which is a leading cultivar for starch production, was developed using Ry\textsubscript{chc} (Asama et al. 1982). Ohbayashi et al. (2010) reported that ‘Aiyutaka’, ‘Touya’, ‘Sayaka’, and ‘Kitamurasaki’ have the gene Rx1, which is responsible for extreme resistance to PVX and is derived from S. tuberosum L. ssp. andigena Hawkes CPC1673 (van der Voort et al. 1999).

Potato late blight caused by P. infestans is the most important fungus disease among potatoes worldwide. At present, the major cultivars do not have resistance to P. infestans in Japan. For this reason, late blight can almost be controlled at present by constant application of fungicides for this disease during the cultivation period. However, considering that there is a possibility of the emergence of fungicide-resistant P. infestans strains or of failure to appropriately apply fungicide, cultivation of resistant cultivars combined with fungicide application is an important approach to control late blight. The selection of resistant lines is carried out in a field without fungicidal application against P. infestans. Eleven hypersensitivity-type resistance genes (R genes) against P. infestans have been introgressed into potato cultivars from the Mexican hexaploid wild species S. demissum Lindl. (Black et al. 1953). However, introgression of R genes conferring race-specific resistance into potato cultivars provides only transient resistance, as new races can rapidly overcome the R gene-mediated resistance (Fry et al. 1993). Several cultivars such as ‘Eniwa’ (R1) and ‘Konafubuki’ (R1R3), were developed as resistant cultivars using R genes in Japan; however, these cultivars currently do not show resistance to P. infestans. Therefore, instead of R gene introduction, conferring field resistance against P. infestans is considered to be an effective measure for the development of resistant cultivars. ‘Hanashibetsu’, ‘Sayakane’, and ‘Kitamusashi’ are cultivars with field resistance against P. infestans in Japan (Senda et al. 1998, Tsuda et al. 2013).

Potato common scab is a major disease caused by the Streptomyces species, which reduces the marketability of affected tubers. Three species, S. scabiei, S. turgidiscabies, and S. acidiscabies, have caused common scab in Japan (Miyajima et al. 1998, Takeuchi et al. 1996). To control this disease, growers carry out multiple crop rotations and soil disinfection. In addition, because common scab is suppressed by low pH, farmers do not apply calcium materials to ensure that soil pH is maintained at a low level (Uematsu and Katayama 1990). Because the most effective measure against common scab is the cultivation of resistant cultivars, breeders continue to develop resistant cultivars. The selection of resistant lines for this disease is carried out in a field infected with the Streptomyces species. ‘Yukirasha’, ‘Snow March’, and ‘Poroshiri’ are common scab resistant cultivars,
which have adapted to summer cropping (Iketani et al. 2005, Kobayashi et al. 2002); ‘Haruakari’ and ‘Sanjumaru’ have been bred for double cropping (Mukojima et al. 2012, Nakao et al. 2003). For efficient selection of common scab resistant lines, a space-saving assay (Takahashi et al. 1995a, 1995b) and a stable assay using artificially infested soil have been developed (Kobayashi et al. 2005, Moriga 2010, Sakamoto et al. 2011).

*R. solanacearum* causes bacterial wilt. This disease is one of the most serious problems facing potato production in tropical and subtropical regions, as well as in temperate European countries (Janse et al. 2004). Likewise, in Japan, this disease tends to occur particularly in fall cropping of double cropping and winter cropping in warm regions. *R. solanacearum* is categorized into two phylogenotypes (I, IV), and three biovars (N2, 3, 4) in Japan (Horita et al. 2010). Resistant or tolerant cultivars are mainly cultivated for disease control because agrochemicals are not effective (Fock et al. 2000). *S. phureja* Juz. et Buk. is phylogenetically related to *S. tuberosum* L. and has resistance traits against this bacteria, which are dominant and readily introduced to progenies (Fock et al. 2000). The breeding line Saikai 35 is a tetraploid resistant line to *R. solanacearum* that was derived from *S. phureja* Juz. et Buk. and is used as a parent line in Japan (Mori et al. 2012). The selection of resistance against *R. solanacearum* is carried out in fields infected with the bacteria.

Conferring disease and pest resistance is important in potato breeding. Bioassays for resistance in a greenhouse or field are fundamental, but time- and space-consuming. On the other hand, MAS can be used without special facilities for biological evaluation and is not influenced by growth stages or growing conditions (e.g., temperature, humidity, light intensity, day length) (Mori et al. 2011). Sets of tightly linked STS markers, N146 and N195 for *H1* and RY186 and RY364 for *Ry adg*, have been developed (Takeuchi et al. 2008). Ohbayashi et al. (2010) has developed an STS marker that can distinguish the presence or absence of the PVX resistance gene *Rx1* based on the sequence information of the isolated *Rx1* gene. *R1*, which is one of the eleven *R* genes, was cloned and *R1*-specific primers have been developed (Ballvora et al. 2002). Although *R1* is no longer effective in Japan, the consistent quantitative trait locus for resistance to *P. infestans* was mapped to the same location of *R1* in populations originating from numerous *Solanum* species (Simko 2002). This supports Gebhardt’s hypothesis that qualitative and quantitative resistance phenotypes to *P. infestans* might be the product of different alleles of the same genetic locus, and the hypersensitive cell death triggered by the *R1* allele would be the extreme expression of a quantitative defense response induced by variants of the same gene product (Gebhardt 1994). Kuang et al. (2005) found that *R1* is actually a resistance gene cluster. In Japan, *R2* was introgressed into ‘Hokkai 56’, which is a superior parental line for breeding late blight resistant cultivars. Ohbayashi et al. (2010) has developed STS markers R2-974 and R2-800 for *R2*. The selection of resistant lines by MAS is carried out in conjunction with bioassay evaluation.

At present, a breeding program using MAS is being carried out to select genotypes with multiple resistances to PCN, PVY, PVX, and *P. infestans* in Japan. We developed a multiplex PCR method that simultaneously detects the markers for *H1*, *R1*, *R2*, *Ry adg*, and *Rx1* (Fig. 3). The multiplex PCR method saves labor and decreases the number of tests with DNA markers (Mori et al. 2011). For example, at the Nagasaki Agricultural and Forestry Technical Development Center, genotypes with multiple resistances are selected from 300–400 lines at the line selection stage by multiplex PCR. The lines selected based on MAS are then evaluated for other agronomic characteristics, and disease resistance is confirmed by field evaluation at later stages (Fig. 2).

As mentioned above, the breeding line R392-50 with the triplex (*H1H1H1h1*) genotype for *H1* greatly contributed as a crossing parent in the breeding of Japanese PCN resistant cultivars, because it gives rise to resistant progenies at high frequency (Mori and Nishibe 1987). Furthermore, potato clones with multiple copies of the *Ry adg* allele for resistance to PVY were selected using a marker for *Ry adg*. Most progenies derived from crossing the selected multiplex lines (*RRRR* or *RRRr*) with the nulliplex line (*rrrr*) were positive for the *Ry adg* marker (Andrade et al. 2009, Kaushik et al. 2013). This indicates that breeding of parental lines with multiple copies of disease resistance genes are valuable for resistance breeding. Thus, we are currently carrying out selection of potato clones with multiple copies of *Ry adg* to promote breeding of PVY resistant cultivars. Previously, a progeny test had been required to select the genotype containing multiple copies of resistance genes. However, because a progeny test is labor-intensive and time-consuming, it is impractical for use in the selection of multiplex parents from a large population, especially for multiple resistances. To reduce the time needed for selection of multiplex parents, we recently developed a rapid selection method for multiple lines using quantitative PCR (Asano and Tamiya 2013). This method enables the efficient selection of multiplex genotypes from a large population. However, the DNA marker used for the quantitative PCR analysis, RY364, has a defect in its specificity, that is, RY364 amplified not only in resistant cultivars but also in some susceptible cultivars. Thus, cross combination for selecting multiplex genotypes is limited. Therefore, we have attempted to develop a high-resolution map of *Ry adg* and to improve the DNA markers.
Mori, Asano, Tamiya, Nakao and Mori

The multiplex genotypes and high-precision DNA markers will improve selection efficiency and promote breeding of PVY resistant cultivars.

**Strategies to improve potato qualities**

As mentioned in the introduction, the potato has various uses, and desirable characteristics differ according to its purpose. To achieve commercial success, cultivars for table use and food processing have to fulfill stringent requirements concerning tuber quality traits such as little discoloration after peeling and cooking, tolerance to blackspot bruising, shallow eyes and appropriate shape, greening tolerance, and low potato glycoalkaloid (PGA) content. Peeling potato tubers and exposing them to air cause the flesh color to change from red to brown. This post-peeling discoloration is known as enzymatic darkening or enzymatic discoloration, which is caused by oxidation of polyphenol compounds. Polyphenol compounds such as chlorogenic acid, tyrosine, and caffeic acid are oxidized by polyphenol oxidase (PPO) enzymes in the presence of oxygen to quinones, after which the quinones are transformed to a brown-to-black colored substance, melanin (Friedman 1997). Post-cooking discoloration is a non-enzymatic reaction that occurs when phenol (mainly chlorogenic acid) and iron present in tubers are combined to form iron diphenol during cooking. Potatoes then turn black due to oxidation during the course of cooling after cooking (Friedman 1997). The mechanical impact on potato tubers during harvesting, transport, and storage induces the development of dark patches beneath the intact skin. This phenomenon is referred to as blackspot bruising and leads to rejection of potatoes by consumers and processing industries. When cells are damaged, oxidation of phenols mediated by PPO triggers blackspot formation like as in post-peeling discoloration (Friedman 1997, McGarry et al. 1996, Stevens and Davelaar 1996, Stevens et al. 1998). Although susceptibility of potato tubers to these discolorations and bruises are affected by several conditions such as PPO activity, amount of phenol component, cell architecture, developmental stage, and environmental conditions, there are considerable differences among genotypes (Fig. 4). Thus, cultivars with less discoloration after peeling and cooking are able to be developed by evaluating the degree of discoloration. As a result, almost all recently developed cultivars such as ‘Sayaka’, ‘Haruka’, and ‘Piruka’, do not discolor in the same way as traditional cultivars such as ‘Irish Cobbler’ and ‘May Queen’ (Kobayashi et al. 2009). However, tolerance to blackspot bruising has not well improved in Japanese cultivars. Although ‘Hokkaikogone’, ‘Sayaka’, ‘Hanashibetsu’, and ‘Haruka’ have relatively high tolerance to blackspot bruising, almost all of the other recent cultivars are susceptible to blackspot bruising. This might be due to the difficulty of phenotypic evaluation. As the occurrence of blackspot bruising is influenced by several environmental and developmental conditions, it is difficult to stably evaluate under the same tuber conditions. Tolerance to blackspot bruising is evaluated by artificially making an impact on tubers by a modified soil mixing machine. This requires a large amount of tubers, which become available only at a later stage of the breeding scheme. Improvement of the evaluation method with a small amount of tubers or application of DNA markers (Urbany et al. 2011) and selection of genotypes tolerant to blackspot bruising at the early stages should promote development of tolerant cultivars.

Eye depth, tuber shape, and tuber size are also important components of tuber quality, because each trait is closely related to processing yield, tuber appearance, and processing efficiency. Deep eyes worsen tuber appearance, increase the cost of peeling and trimming in processing, and decrease product yield. Appropriate shapes and sizes are required for table use and food processing, especially for products such as potato chips and French fries, in which the form of tubers remains. Long tubers have to be cut to the appropriate size during potato chip processing; on the other hand, longer tubers are preferred for shoestring cut French fries. The time required for peeling and trimming are also influenced by tuber size. The number of tubers and eyes and skin ratio per unit weight increase in small tubers compared with large tubers. For example, the trimming time for ‘Sayaka’, a food processing cultivar that is used especially for salads and has...
shallow eyes and large tubers, is one-third of that for ‘Irish Cobbler’, an old cultivar with deep eyes and relatively small tubers (Mori 2008).

Light irradiation of potato tubers triggers chlorophyll synthesis and color changes in tuber skin to green (greening). In addition to greening, PAGs such as α-solanine and α-chaconine are also produced by light irradiation. These biochemical processes are independent of each other but are activated by light irradiation. PGA is found in all parts of the potato plant, in which the skins and sprouts contain higher concentrations. When PGA content is raised above 15 mg/100 g fresh weight, it may cause a bitter taste. Consumption of potatoes containing more than 20 mg/100 g fresh weight induces the risk of pain in the abdomen and stomach, gastroenteritis, diarrhea, vomiting, fever, rapid pulse, low blood pressure, and neurological disorders (Friedman and McDonald 1997, Morris and Lee 1984, Slanina 1990). Because of the relationship between tuber quality, safety, and PGA content, it is desirable to select genotypes with low PGA content. Although accumulation of PGA varies continuously among genotypes, it is primarily genetically controlled and is therefore a selectable trait (Friedman and McDonald 1997). Two food-processing cultivars, ‘Sayaka’ and ‘Koganemaru’ for salads and French fries respectively, are released as cultivars with greening tolerance and low PGA content. Moreover, Hokkaido 107 was selected recently as being more tolerant to greening and with a lower PGA content compared with ‘Sayaka’ and ‘Koganemaru’. To evaluate greening tolerance and to measure PGA content are highly laborious, and are therefore carried out at the late stages of breeding. Ozaki et al. (2014) developed a nondestructive estimation method for chlorophyll and anthocyanin content that can determine the extent of greening in potato tubers using an image of the potato skin obtained by a smartphone camera. This smartphone application software is able to display the contents of these two pigments in potato tubers without destruction, thus enabling evaluation of greening tolerance for many samples at an early stage of the breeding scheme. Genes involved in PGA biosynthesis are now being identified. Silencing of these genes drastically reduces PGA content (Itkin et al. 2013, Sawai et al. 2014, Umemoto and Sasaki 2011, 2012, Umemoto 2013). This finding provides a new strategy to reduce or to remove PGA by selecting a mutant for these genes using TILLING (Till et al. 2003), by using natural variations, or by Targeted Genome Editing (Gaj et al. 2013).

In addition to these commonly important characteristics for both table use and food processing potato cultivars, a lower content of reducing sugars is also specifically required for food processing to make foods such as potato chips and French fries. The majority of materials for potato chips are harvested from August to October in Hokkaido and used for the following June in Japan. During this period, potato tubers are stored at low temperature to reduce sprouting, shrinkage, loss of dry matter, and disease loss (Burton and Wilson 1978). However, tubers stored at low temperature accumulate reducing sugars (glucose and fructose), making them unsuitable for processing. This phenomenon is referred to as cold-induced sweetening (CIS). The accumulated reducing sugars react with amino acid groups during processing at high temperature, forming a brown pigmented and bitter tasting product via the non-enzymatic Maillard reaction (Fig. 4). This reaction produces not only a brown pigmented and bitter tasting product, but also neurotoxin acrylamide as a by-product (Mottram et al. 2002, Stadler et al. 2002). The acrylamide contained in potato products is formed almost from glucose, fructose, and asparagine (Amrein et al. 2003, Knol et al. 2010, Rydberg et al. 2003). Acrylamide content and the color of fried products both primarily depend on the content of reducing sugars. We, and others, investigated the relationship between acrylamide content and product color. The results indicated that there is a correlation between product color and acrylamide content (Amrein et al. 2003, Chuda et al. 2003, De Wilde et al. 2005, Ohara-Takada et al. 2005). However, the selection of genotypes by product color as an indicator of acrylamide content is not effective for acrylamide content less than 1,000 μg/kg. Because of recent growing demands for a further reduction of the acrylamide content of fried foods, breeding schemes are currently being reconstructed to effectively select genotypes with low acrylamide content. In these schemes, selection is carried out based on product color and other agronomic traits at an early stage to omit genotypes with extremely high acrylamide content and agronomically undesirable characteristics, and then acrylamide content is measured at a later stage. A cultivar, Kitahime, with CIS resistance was developed in 2001, and cultivated as potato chip processing material for long-term storage. Recently, a cultivar for potato chip processing with CIS resistance, ‘Rirachip’, was released (Fujita et al. 2014). These cultivars were developed based on only product color and reducing sugar content, and acrylamide content was not measured during the breeding process. Thus, direct measurement of acrylamide content in a new scheme should further promote the selection of cultivars with lower acrylamide content.

Future perspectives

The average temperature in potato production areas is predicted to increase between 1.6 and 3.0°C between 2040 and 2069. Climate change will cause a decrease in the global potato yield by 18% to 32% (Hijmans 2003). Hirota et al. (2011) reported that the climate conditions in the summer of 2010 affected crop growth, including potatoes in Hokkaido, and suggested that the range of climate fluctuation will become wider in the future. In 2010, the yield of potatoes was lowered by low temperature at the beginning of May to the beginning of June (early growth stage) and high temperature from mid-June to mid-September. Thereafter, high-intensity rainfall over a short time through July to August caused hollow heart, depressing the quality of potatoes.
In Nagasaki Prefecture in Kyushu, the average temperature in early September (2004–2013) at the time of planting during fall cropping was 27.3°C, which was 2.1°C higher than that of the previous 20 years (1984–2003). After planting seed potatoes, high soil temperature in rows leads to tuber rot in the field, resulting in a delay or a defect in the sprouts. In spring cropping, tuber rot has occurred at high soil temperatures in rows that were covered with mulching. However, because potatoes are sensitive to frost, they are damaged by frost after sprouting in summer and spring croppings, and before harvesting in summer and fall cropping; frost damage causes yield losses. Though the average temperature has been increasing in Japan, the period of frost does not change in each cropping season. Thus, farmers have to cultivate under an unfavorable hot climate in summer cropping, and wait to plant until it become cool, resulting in a reduced growing period in fall cropping. Additionally, a wide fluctuation in temperatures and moisture conditions will greatly influence the growth of potatoes, as was the case in 2010.

Haverkort and Verhagen (2008) suggested that there is a need for breeding of heat-tolerant cultivars. It is important to breed new adapted cultivars under the expected conditions, including high temperature, frost, and wide fluctuation of environmental factors. Already, methods of evaluation for heat and frost tolerance have been developed, and the selection of tolerant genotypes using these methods is underway (Midmore and Prange 1991, Nowak and Colborne 1989, Reynolds et al. 1990, Smillie et al. 1983, Sundbom et al. 1982). In the past, breeders had also tried to select lines with frost tolerance at the seedling stage in Japan, but this method is not carried out at present. As phenotypic variations in heat and frost tolerance are observed among Japanese genetic resources during cultivation, the establishment of effective and easy evaluation methods of a large population is necessary to select cultivars adapted for climate change. In addition to heat and frost tolerance, breeding pest and disease resistant cultivars will become increasingly important, because climate change increases the risk of pests and diseases such as late blight, bacterial soft rot, bacterial wilt, and aphids (Haverkort and Verhagen 2008, Kaukoranta 2008, Roos et al. 2011). Selection of genotypes that show stable growth under fluctuating conditions is also important by comparing multi-year growth data.

For developing cultivars to tackle these problems, potato germplasm with a wide range of genetic diversity and containing useful traits is indispensable. In spite of its importance, genetic diversity in potato breeding is considered to be very narrow. Because of the late blight epidemic in the 1840’s, most of the old cultivars disappeared and there were a few survivors along with a limited number of 19th and 20th century introductions that provided the basis for current modern cultivars (Pavek and Corsini 2001). Furthermore, a few superior clones have been extensively used for breeding as they give rise to excellent progenies. For example, because ‘Early Rose’, derived from ‘Garnet Chili’, and its offspring were widely used to produce modern potato cultivars, ‘Garnet Chili’ can be seen in the pedigree of almost all cultivars in Europe and the United States (Plaisted and Hoopes 1989). Similarly, a large proportion of Japanese cultivars share a common ancestry, ‘Irish Cobbler’. As discussed, the introduction of pest and disease resistance from several relatives into modern cultivars contributed to broadening genetic diversity. However, further improvement in genetic diversity is required for the development of innovative cultivars that will replace current major cultivars, which were developed more than a quarter of a century ago. Currently, a germplasm enhancement program aimed at expanding the Japanese gene pool is underway. In the pre-breeding scheme, Andean landraces and wild species, whose cytoplasm is A, P, M, or W type (Hosaka and Sanetomo 2012), are used as genetic resources. Because D-, Wγ-, and T-type cytoplasms often cause pollen sterility, genotypes with these cytoplasms are eliminated from genetic resources. Long-day adapted genotypes, which can produce tubers under long-day conditions in the Hokkaido region, are selected, and then crossed with 10H17; 10H17 has multiple disease resistance genes such as $R_{y,h}$, $R_{x,1}$, $H_{1}$, and $R_{1}$. It also has P-type cytoplasm which produce high fertile pollen (Hosaka and Sanetomo 2012, Mori et al. 2012). Again, the resulting F$_1$ progenies are evaluated for their tuber production ability under long-day conditions. Subsequently, selected long-day adapted F$_1$ hybrids are crossed as males with the standard cultivar ‘Atlantic’ as the female. Based on the yield in the seedling populations, superior genotypes are selected from the long-day adapted F$_1$ hybrids. These superior F$_1$ hybrids are distributed to breeding stations, and will then be used for developing new commercial cultivars by crossing cultivars or breeding lines at each breeding station (Fig. 5) (Hosaka and Sanetomo, personal communication). It is hoped that innovative new cultivars will be developed through this approach. In addition to the expansion of genetic resources, reconstruction of a breeding scheme and the construction of cooperative frameworks between breeding stations should go forward. Good precedents showing the importance of expansion of genetic resources and cooperation between breeding stations are ‘Haruka’ (Kobayashi et al. 2009) and Saikai 35 (Mori et al. 2012). ‘Haruka’ is a summer cropping cultivar developed by crossing summer cropping cultivar ‘Sayaka’ with the double cropping line T9020-8. Crossing of the cultivar was performed at the Nagasaki Agricultural and Forestry Technical Development Center, but selection was carried out at the Hokkaido Agricultural Research Center. This cultivar has both good quality and adaptability to higher temperature derived from ‘Sayaka’ and T9020-8, respectively. The breeding line Saikai 35 possesses bacterial wilt resistance and PVY resistance, and was derived from S. phureja Juz. Et Buk. and S. chacoense Bitt. The parents of this line were originally derived from summer cropping, but crosses and selection were carried out in double cropping areas. Establishment of evaluation methods for tolerance to climate changes and...
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Fig. 5. Scheme of the germplasm enhancement program using relative species. Letters in parentheses indicate cytoplasm genotype. Black arrows and white arrows indicate flow of male parent development and conditions of selection, respectively. 10H17 is a line with high pollen fertility and multiple disease resistance genes (Ry\text{ide}, Rx1, H1, and R1 genes).

combining them with efficient selection by DNA markers at early stages is essential. Moreover, evaluation of tolerance to climate changes at suitable locations, taking full advantage of Japan’s climate ranges and using cooperative frameworks between breeding stations, for example evaluation of heat tolerance in Kyushu in summer and evaluation of frost tolerance in Hokkaido in late fall, would promote the development of innovative new cultivars.

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