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Review

Advances in table grape breeding in Japan

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In Japan, few grape cultivars related to *Vitis vinifera* existed 200 years ago, on account of Japan's high rainfall. Many *V. labruscana* and *vinifera* cultivars were introduced to Japan in the 19th century. *Labruscana* was grown instead of *vinifera*, mainly because of severe disease problems and a high incidence of berry cracking. Grape breeding for table use started in the 20th century, with the goal of combining the berry quality of *vinifera* with the ease of cultivation of *labruscana*. By 1945, three strategies were used: 1) crossing among introduced diploid *vinifera* and *vinifera*-related cultivars of Japanese origin, 2) interspecific crossing in tetraploid cultivars, and 3) interspecific crossing in diploid cultivars, resulting in 'Neo Muscat', 'Kyoho', and 'Muscat Bailey A'. Later, tetraploid interspecific crossing over generations developed many 'Kyoho'-related cultivars, including 'Pione', many of which have large berries, intermediate flesh texture between the two species, a labruscan or neutral flavor, and moderate disease resistance. Interspecific diploid crossing over generations developed 'Shine Muscat' in 2006, with large berries, crispy flesh, a muscat flavor, no cracking, seedless fruit by gibberellin application, and moderate resistance to downy mildew and ripe rot.

Key Words: breeding, disease, grape, interspecific cross, Japan, quality, table.

Introduction

Einset and Pratt (1975) provided a review on grape breeding in "Advances in Fruit Breeding". Furthermore, Reisch and Pratt (1996), and Reisch *et al.* (2012) wrote reviews on grape breeding, adding key advances in grape science. These reviews were written in English, and were widely read around the world. They only briefly mentioned breeding in Japan, so this review focuses on advances in table grape breeding in Japan, emphasizing its history and achievements; this is the first round review written in English on this theme. Disease resistance is a particularly important factor in Japanese breeding, since *Vitis vinifera* L., the most important grape species, has weak disease resistance in Japan. Unfortunately, even today, descriptions of the varietal differences in disease resistance of cultivars developed in Japan have mostly been based on field observations rather than scientific experiments, and field data are likely to fluctuate in response to environmental factors, except for anthracnose (Kono *et al.* 2009, 2012, 2013) and ripe rot (Shiraishi *et al.* 2006, 2007).

World grape production was 77,181 kt in 2013 (FAOSTAT 2015). Grape production in Japan was 190 kt in 2013, around only 0.2% of the total world production. It ranks 40th among countries in the world. Large grape producers in the world were China (11,550 kt), Italy (8,010 kt), USA (7,745 kt), Spain (7,480 kt), France (5,518 kt), Turkey (4,011 kt), and Chile (3,298 kt). This production was mainly for wine, but a considerable part was for table fruit use. However, in Japan, grape production is important; the annual yield in 2013 was 103 billion yen, ranking third after citrus and apple among woody fruit crops. Around 90% of grape production was for table use, and the rest for wine and juice production.

The most common grape species used for both the production of wine and table use around the world is *V. vinifera* L., which originated in western Asia, most likely in the region between the Black and Caspian Seas (Einset and Pratt 1975), where the grapevine still grows wild. It is adapted to a dry and moderately warm climate during its growing season. Countries with a high production of *V. vinifera* have areas with such a climate. In contrast, Japan has a humid climate throughout its growing season, with annual precipitation ranging from 1,000 to 3,000 mm, despite having a wide area with a moderately warm climate. Many fungal diseases attack grapevines during rainfall. Thus, Japan's high amounts of rainfall have interfered with the development of *V. vinifera* production.

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Origin of grape cultivars for table use and introduction to Japan

V. vinifera was spread around the Mediterranean region by humans, eventually reaching wide areas of Europe (Einset and Pratt 1975). Many varieties have been developed for wine and table use since ancient times. It also spread eastwards, possibly along the Silk Road, and reached dry northwestern China, where various varieties were developed. As it spread eastward through China, rainfall increased, so some varieties tolerant of higher rainfall were also developed in northern and eastern China. Varieties developed poorly in Korea and Japan, where annual precipitation is more than 1000 mm. The oldest cultivar known in Japan ('Koshu') was documented in 1186 in Katsunuma, Yamanashi Prefecture (Kikuchi 1948), where the annual precipitation is 1081 mm and the annual mean temperature is 13.8°C.

Goto-Yamamoto (2000) and Goto-Yamamoto *et al.* (1998, 2006, 2009, 2013) showed phylogenetic relationships of grape species and cultivar groups among Asian, European, and American origin. 'Koshu' has recently been estimated to be derived from the backcross (*V. davidii* × *V. vinifera*) × *V. vinifera* by SNP marker analysis (Natl. Res, Inst. Brewing 2013) although the scientific paper on that has not been published yet. *V. davidii* (Rom. Caill.) Foëx is a species native to China. 'Koshu' was recorded to be cultivated with 15 ha in 1716 (Kikuchi 1948), so its production was small in Japan during the 18th century. 'Juraku' was also recorded to have been cultivated, but has since become extinct (Kikuchi 1948). 'Murasaki', a cultivar of Japanese origin, was identical to or very close to 'Koshu' (Goto-Yamamoto *et al.* 2008).

Wild *Vitis* species also are distributed in Japan, including *V. ficifolia* Bunge, *V. austrokoreana* Hatus, *V. flexuosa* Thunb., *V. saccharifera* Makino, *V. yokogurana* Makino, *V. shiragae* Makino, *V. coignetiae* Pullat ex Planch., and *V. quinquangularis* Rehder (Nakagawa *et al.* 1991). The chromosome number is $2n = 38$ in *V. flexuosa*, *V. saccharifera*, and *V. shiragae* (Yamane 1982). These species are adapted to the Japanese climate, and may be a good source for introducing disease resistance and environmental adaptability, but they have been poorly utilized in the breeding of table grapes.

European people migrated and settled in the northern and east coastal regions of North America where there is considerable rainfall, in the 17th century. The early colonists brought *V. vinifera* with them, but its cultivation failed due to a lack of resistance to diseases and soil pests and due to low winter temperatures in the more northern areas (Einset and Pratt 1975). They gradually recognized that wild native species were adapted to local conditions, and provided good sources of resistance against these problems. During the 19th century, many cultivars were developed through crossing *V. vinifera* and *Vitis* species native to North America, including *V. labrusca* L., *V. linsecumii* Buckley, *V. aestivalis* Michx., *V. riparia* Michx., *V. rupestris* Scheele, *V. champinii* Planch., *V. cinerea* (Engelm.) Engelm. ex Milladet, and by selecting good clones from plants of native species and/or hybrid seedlings. These species belong to subgenus *Vitis*, and have 38 somatic chromosomes like *V. vinifera*; thus, intercrossing among these species is easy and fertile, even though they are geographically or ecologically distant. The species that was used most often as a cross parent was *V. labrusca* (the fox grape), which provided large-berried fruit, cold resistance, and a distinctive flavor (Einset and Pratt 1975). Therefore, Bailey, L. H. defined labrusca-like species as *V. labruscana*, with "labruscan grape" as its English name: Vineyard varieties (such as 'Concord') which show strong labrusca likeness are derivatives or hybrids from it; its leaves are mostly thinner, with less rusty-tomentose flowers which are in heavy pointed or shouldered clusters, the grapes are larger and ameliorated in flavor, and cultigen (Bailey and Bailey 1930).

The Tokugawa shogunate that governed feudal Japan, implemented a seclusion policy that excluded foreigners from 1633 to 1858. During this period, Japan was isolated from foreigners with few exceptions. The Meiji Government, which was established in 1868, ended this policy and provided an opportunity to introduce foreign culture and foreign plants from around the world. The first grapevine introduction from the USA occurred in 1868 (Kikuchi 1948). Thirty cultivars were grown in 1873, and around one hundred cultivars including both *V. vinifera* and *labruscana* cultivars were introduced by 1884 (Kikuchi 1948).

These *vinifera* and *labruscana* cultivars and 'Koshu' were tried to be grown in various locations, resulting in the failure of the cultivation of *vinifera* cultivars owing to serious disease damage. In contrast, *labruscana* cultivars grew successfully over a wide area, and 'Koshu' was grown mainly in Yamanashi and Osaka Prefectures, which have a moderately warm climate with relatively low rainfall.

The first statistics on the cultivation of grape varieties in 1934 showed a total of 7,324 ha planted with 'Delaware' 33.1%, 'Koshu' 22.8%, 'Campbell Early' 22.7%, and others 21.4% (Kikuchi, 1948). 'Delaware' and 'Campbell Early' are *labruscana* cultivars, the former is a hybrid deriving from *V. aestivalis*, *V. labrusca*, and *V. vinifera*, the latter from *V. labrusca* and *V. vinifera*. "Others" included a cold-hardy *labruscana* cultivar, 'Niagara'.

Fortunately, 'Koshu' is tolerant to anthracnose (Kono *et al.* 2013) but sensitive to downy mildew. The main cultivation areas in Japan were Yamanashi, Nagano, and the Seto Inland Sea coastal region, at that time. Rainfall from May to September is 660 mm in Katsunuma (Yamanashi Prefecture), Japan, versus around 330 mm in Florence, Italy. Grape phylloxera, an insect that attacks grapevine roots, has been completely overcome by using resistant rootstocks derived from American native species, which were developed in Europe.

Important Japanese grape diseases include anthracnose (*Elsinoe ampelina* (de Bary) Shear), downy mildew

(*Plasmopara viticola* (Berkeley et Curtis) Berlese et de Toni), ripe rot (*Glomerella cingulata* (Stoneman) Spaulding et Schrenk, and *Colletotrichum acutatum* J.H. Simmonds), gray mold (*Botrytis cinerea* Persoon), powdery mildew (*Uncinula necator* (Schweinitz) Burrill), leaf spot (*Psudocercospora vitis* (Leveille) Spegazzini), bitter rot (*Melanconium fuligineum* (Scribner et Viala) Cavara), and Phomopsis cane and leaf spot (*Phomopsis viticola* (Saccardo) Saccrado). Fortunately, Pierce's disease (*Xylella fastidiosa*) has never been found in Japanese vineyards. Black rot (*Guignardia bidwellii* Ellis) has not been a serious problem in Japan. Powdery mildew infects through windborne spores, gray mold attacks under humid conditions, and the remaining diseases infect mostly through rain.

Anthracnose, downy mildew, and ripe rot remain serious diseases even now in Japan, not only for *vinifera* cultivars but also *labruscana* cultivars. Presently, fungicides have been developed, and leaf spot, bitter rot, Phomopsis cane and leaf spot are seldom seen in well-managed commercial vineyards. Fruit bagging techniques can also protect fruit from diseases and are used widely.

Anthracnose is one of the oldest European grape diseases, and is indigenous to Europe and North Africa (Einset and Pratt 1975). *Labruscana* grape cultivars introduced into Japan are generally tolerant, and some *vinifera* grape cultivars are also tolerant (Einset and Pratt 1975, Kono *et al.* 2013).

Downy mildew, black rot, and powdery mildew are of North American origin, and caused serious damage in Europe in the 19th century (Einset and Pratt 1975). Sources of resistance to many diseases may be found in many native American species (Einset and Pratt 1975).

It is easy to imagine that *vinifera* cultivars sustained serious damage just after these cultivars were introduced, although there were no scientific records of disease damage at that time. Cultivation of 'Muscat of Alexandria', a superior *vinifera* table grape cultivar, started in Okayama Prefecture in 1886 but only within glasshouses, and its cultivation area reached 22 ha in 1936 (Kikuchi 1948). However, the fruits were not eaten by ordinary people owing to its high price (Kawakami 1940).

Characteristics of introduced *vinifera* and *labruscana* cultivars for table use and breeding targets

Table 1 summarizes the general characteristics of the *vinifera* and *labruscana* cultivars introduced for table use in Japan, although individual cultivars differ to a greater or lesser degree from the description. The factors that most strongly limited the cultivation of *vinifera* cultivars in Japan were their disease sensitivity and berry cracking habit. In addition, lower cold hardiness prevents their cultivation in northern Japan, although some cold-hardy *vinifera* cultivars for wine use, such as 'Müller Thurgau' and 'Kerner', have been cultivated on a small scale.

The eating quality of the *labruscana* cultivars were acceptable to Japanese consumers, but those who had tasted *vinifera* cultivars, preferred to eat those. In particular, *vinifera* cultivars suitable for table use such as 'Muscat of Alexandria', 'Alphonse Lavallée', and 'Cardinal' are characterized by crispy or nearly crispy flesh and a muscat or neutral flavor (Sato and Yamada 2003).

The national institute for fruit tree science in Japan, presently NARO Institute of Fruit Tree Science, developed a method for sensory evaluation of the flesh texture in grape cultivars/selections in 1984 that is based on two key dimensions: firmness (softness) and ease of mastication (Fruit Tree Research Station 1984). In standard cultivars, the flesh of 'Campbell Early' was firm and not easy to masticate, that of 'Delaware' was moderately firm and not easy to masticate, that of 'Kyoho' was moderately firm and intermediate between easy and not easy to masticate, and that of 'Muscat of Alexandria' was firm and easy to masticate. This evaluation method has been generally used for testing cultivars/selections by national and prefectural institutes since 1984.

Sato *et al.* (1997) made these sensory evaluations more objective by developing an instrumental penetration test. The easiness to masticate the flesh measured the deformation of flesh at the first penetration by plunger to flesh (DFP), and firmness as the maximum force at the first penetration (MF). Berries with crispy flesh are described as "firm and easy to masticate", with DFP $\leq$ 2.5 mm and MF $\geq$ 0.9 N (Sato and Yamada 2003). They found a positive correlation between DFP and MF in *labruscana* cultivars, and as a result, no *labruscana* cultivars had crispy flesh. In contrast, all *vinifera* table-use cultivars had a low DFP, so no *vinifera* table-use cultivars were difficult to masticate, although both cultivar groups showed wide variation in flesh firmness (**Fig. 1**).

Consequently, Japanese grape breeders have attempted to breed new cultivars that combine crispy flesh and a favorable flavor derived from *vinifera* cultivars, with ease of cultivation (mainly disease and berry cracking resistance) from *labruscana* cultivars.

Table 1. General characteristics of *labruscana* and *vinifera* grape cultivars for table use, introduced to Japan

Species	Fruit ripening time	Berry weight	Berry flesh texture	Flavor	Sweetness	Berry cracking occurrence	Necrotic berry disorder	Shelf life	Berry shattering in full maturity	Disease resistance	Cold hardiness
Labruscana grape cultivars	Early	Small	Not easy to masticate	Foxy	High	Low	None	Short	Easy	High	High
Vinifera grape cultivars for table use	Late	Large	Crispy or nearly crispy	Muscat or neutral	Low	High	Partly have	Long	Difficult	Low	Low

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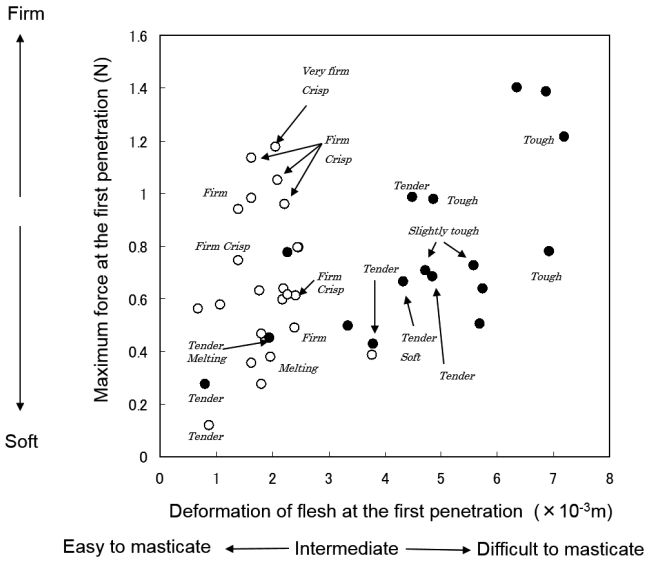

Fig. 1. Varietal difference in berry flesh texture as evaluated by penetration test. ○ and ● indicate *V. vinifera* and *V. labruscana*, respectively (Sato *et al.* 1997).

Fig. 2. 'Neo Muscat' fruit cluster.

Three breeding strategies and achievements in the initial stage of grape breeding in Japan

The main achievements of the initial Japanese grape breeding, which began before World War II, were 'Neo Muscat', 'Muscat Bailey A', and 'Kyoho', which were developed by 1) crossing among diploid (2*x*) introduced *vinifera* cultivars and *vinifera*-related cultivars of Japanese origin, 2) between diploid *vinifera* and *labruscana* cultivars, and 3) between tetraploid (4*x*) *vinifera* and *labruscana* cultivars, respectively. These cultivars have been grown extensively in Japan since around 1950.

'Neo Muscat' (diploid vinifera cultivars)

'Neo Muscat', the offspring of a cross between 'Muscat of Alexandria' and 'Koshu-sanjaku', was developed by M. Hirota, a private breeder, in 1932 (Yamane 1996) (**Fig. 2**). 'Koshu-sanjaku' is related to 'Koshu' although its exact origin is unknown, and has been classified as *V. vinifera*.

'Neo Muscat' has yellow-green, medium-sized berries (5 to 7 g), and the flesh is intermediate for mastication and has a muscat flavor; there is little berry cracking. Generally, it is more tolerant to diseases than many introduced *vinifera* cultivars, although it is less tolerant than *labruscana* cultivars. Its cultivation area peaked at 1649 ha in 1978. It can be grown in the field without plastic covering in regions with relatively low rainfall during the growing season, such as Yamanashi Prefecture. Its muscat flavor is widely accepted. Presently, the cultivation area has decreased to 46 ha in 2012 (Ministry of Agriculture, Forestry and Fisheries (MAFF) 2015), mainly because of the relatively small berries, the laborious berry thinning that is required, the presence of seeds, and relatively low disease resistance.

'Muscat Bailey A' (diploid interspecific cultivar)

Z. Kawakami, a private grape breeder, started cross-breeding between *labruscana* and *vinifera* cultivars in 1921, aiming at the improvement of grape cultivars mainly for wine use and partly for table use. He mentioned that the aim of breeding was to improve the unfavorable flavor (foxy flavor) of *labruscana* cultivars both for wine use and for table use, and in addition, unfavorable soft mass flesh of *labruscana* cultivars for table use (Kawakami 1940). He released 22 new cultivars, including 'Muscat Bailey A' (**Fig. 3**) and 'Rose Ciotat' for dual use, 'Red Millennium' for table use, and 'Black Queen' for wine use (Kawakami 1940).

'Muscat Bailey A', an offspring from a cross of 'Bailey' (*V. labruscana*) and 'Muscat Hamburg' (*V. vinifera*), was cultivated on a maximum of 1944 ha in 1982 mainly for table use and partly for wine use. The berry is deep purple, and has no cracking habit. The flesh is slightly difficult to masticate and firm with a specific foxy flavor. It generally has moderate disease resistance.

'Muscat Bailey A' was cultivated on 471 ha in 2012 (MAFF 2015), mainly for table use. Since the latter half of the 1970s, most of the fruit has been made seedless by two applications of gibberellic acid (GA), to the flowers before blossoming and to the fruit clusters, adding streptomycin spraying to flower clusters. 'Muscat Bailey A' is currently one of the most widely produced grape cultivars for the production of Japanese red wine; 1234 t of fruit were used along with 1016 t of 'Merlot' for red wine production in 2012 (MAFF 2015).

Fig. 3. 'Muscat Bailey A' fruit cluster.

Fig. 4. 'Kyoho' fruit cluster.

'Kyoho' (tetraploid interspecific cultivar)

Y. Ohinoue, a private breeder, crossed 'Ishiharawase' and 'Centennial', resulting in the release of 'Kyoho' in 1945 (Yamane 1996) (**Fig. 4**). 'Ishiharawase' and 'Centennial' are tetraploid bud sports of 'Campbell Early' (*V. labruscana*) and 'Rosaki' (*V. vinifera*), respectively. His goal was presumed to be developing a cultivar with large berries as a result of its tetraploid nature.

'Kyoho' has large and purple berries (12 to 14 g) with flesh intermediate between easy and difficult to masticate and with a distinct but favorable foxy flavor. The berry has skin that slips easily, the berries show very little or no cracking, but an easy shatter habit (berries detach easily) in clusters at full maturity, the berries have a short shelf life. 'Kyoho' generally has moderate disease resistance. The cultivation of 'Kyoho' had been retarded for a long time owing to the difficulty of acceptable fruiting, although the eating quality and large berries are very attractive for Japanese consumers. The most appropriate fruiting occurs with weak shoots, which can be produced by light pruning in winter. Adoption of this approach has greatly increased the area of 'Kyoho' cultivation. Its cultivation area has increased gradually since the mid-1960s, reaching a peak of 6660 ha in 1998. 'Kyoho' has been the most produced Japanese cultivar since 1994.

Currently, the Japanese market demands filled bunches with good appearance. Sufficient filling of the fruit cluster is achieved by trimming the flower clusters to 7 cm from the bottom just before blooming for seeded fruit production. 'Kyoho' requires a short time for berry thinning when suitable fruit cluster filling can be achieved, leading to less expensive production.

In the 1990s, as the cultivation area increased, the price of seeded 'Kyoho' grapes decreased. Therefore, many growers changed from production of seeded berries to seedless berries in response to consumer preferences in an effort to maintain prices. Recently, 'Kyoho' was cultivated on 5176 ha in 2012 (MAFF 2015). A considerable amount of production was as seedless berries, which are achieved by GA applications, and recently, adding streptomycin spraying. GA applications to flower/fruit change berry flesh texture depending on the cultivar and environmental conditions (Sato and Yamada, 2004). In addition, forchlorfenuron (F) is sometimes added to GA in its application. Seedless 'Kyoho' fruit with nearly crispy flesh may sometimes be available in markets.

The start of grape breeding in public institutions, and secondary introduction of *vinifera* grape cultivars from the USSR (1950s–1970s)

Grape breeding in Japan began with private breeders, as described in the previous section. However, due to governmental funding and control, grape breeding had been carried out at the Yamanashi Fruit Tree Prefectural Experimental Station since 1950, later also at the Fukuoka Agricultural Research Center since 1974.

A national institute for fruit crops was established in 1902, but had little involvement with grape research. The institute established its Akitsu Branch in 1968 in Hiroshima Prefecture, in the coastal region of the Seto Inland Sea, and grape breeding began there.

The national institute introduced a total of 74 *vinifera* cultivars from the USSR from 1965 to 1967, and tested them at Akitsu. They reported the characteristics of the cultivars, and selected two cultivars with high eating quality and large berries: 'Rizamat' and 'Katta Kurgan' (Kurihara *et al.* 1976). These have been used as important cross parents,

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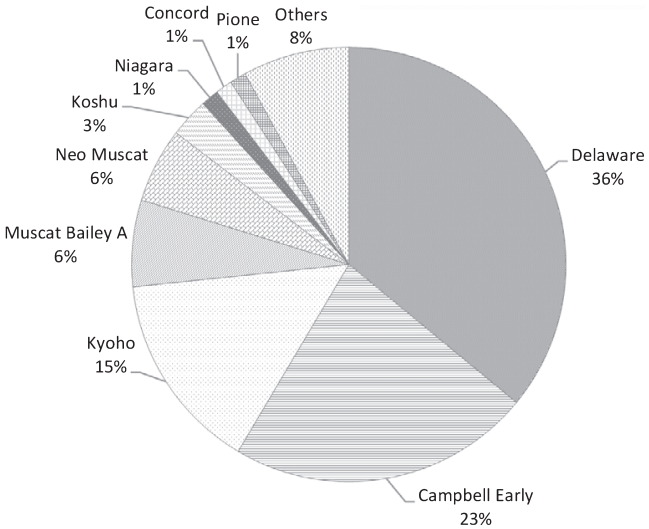

Fig. 5. Varietal share in grape cultivation area in Japan (1978). Based on MAFF statistics (1978).

although their berries are likely to crack. The vines of these cultivars have also been reported to be sensitive to anthracnose (Kono *et al.* 2013).

Viticulture in 1978 and subsequent cultivar trends

The total Japanese vineyard area increased to 29628 ha in 1978, which was planted with 'Delaware' (36%), 'Campbell Early' (23%), 'Kyoho' (15%), 'Muscat Bailey A' (6%), 'Neo Muscat' (6%), 'Koshu' (3%), 'Niagara' (1%), 'Concord' (1%), and 'Pione' (1%) (**Fig. 5**). The production of seedless 'Delaware' by application of GA to the flower and fruit clusters began in the 1960s, and all production since has been of seedless berries. 'Muscat Bailey A' also produced mostly seedless berries. The fruit of the other cultivars contained seeds at that time. Seedless fruit production was difficult for 'Campbell Early' and 'Niagara' (Nagata and Kurihara 1982). 'Campbell Early' fruit had lower sugar content than the other leading cultivars, although it had high disease resistance, high yield, and good cold-hardiness. Production of leading cultivars other than 'Kyoho' and 'Pione' saturated consumer demand in 1978. Consumer demand has shifted to a preference for large, seedless fruit, and the crispy flesh that *vinifera* cultivars provide. As a result, the production of cultivars that failed to provide these characteristics, especially 'Campbell Early', decreased.

Trends for new cultivars in Japan (1978 to 2015)

The Plant Variety Protection and Seed Act was established in Japan in 1978, in response to the International Union for the Protection of New Varieties of Plants. Since then, many newly developed cultivars have been registered by MAFF under this law, with the goal of protecting the rights of breeders. As of May 2015, 164 grape cultivars had been registered, of which 130 are suitable for table use (MAFF 2015). Of the 130 cultivars, 21 are spontaneous bud-sports of existing cultivars, and mostly leading cultivars, which are distinguished by ripening time, berry skin color and so on. Most of the bud-sport cultivars have not been grown widely.

From the MAFF web-page data (MAFF 2015), 109 of the 130 cultivars resulted from crossing; 3 cultivars were from crosses among *labruscana* cultivars, 61 were among *labruscana*, interspecific, and *vinifera* cultivars, and 39 were among *vinifera* cultivars, excluding cultivars whose parental origin could not be determined. In addition, these 3 and 39 cultivars resulted from intraspecific crosses between diploid cultivars, whereas 70% of the 61 cultivars were developed from crosses between tetraploid cultivars, most of which were closely related to 'Kyoho'. Thus, breeding of table grapes has been proceeding with an emphasis on tetraploid interspecific breeding of cultivars/selections closely related to 'Kyoho', and with an emphasis on *vinifera* diploid breeding. In addition, 74 of the 109 cultivars were developed by private breeders; the rest were developed by public institutions. The 3 *labruscana* cultivars include 'North Red' and 'North Black', which are cold-hardy cultivars developed by the national institute and are adaptable to cold regions, where 'Kyoho' and its related tetraploid cultivars cannot grow well (Yamane *et al.* 1991, 1992b).

Seedlessness

As we noted earlier, Japanese consumers increasingly prefer seedless fruit. Seedless fruit production of 'Delaware' requires good technique in judging the timing of GA application to flower clusters, 2 weeks before blossoming, in shoots with uniform growth. Growers therefore needed a new cultivar that facilitates seedless production.

Thus, from the 1960s to 1980s, grape breeding at the Yamanashi Prefecture Fruit Tree Experimental Station and at the national institute emphasized the development of cultivars that produce seedless berries without requiring GA application. Crossing seeded diploid cultivars with seedless diploid cultivars derived from 'Thompson Seedless' and 'Monukka' yielded a total of 2073 offspring from 53 crosses among *labruscana* and *vinifera* cultivars, only 5.4% were seedless (Sato *et al.* 1994). When 'White Corinth' and 'Black Corinth' were used as seedless diploid parents, no offspring were seedless. The low percentage of seedless offspring compared with those in reports of stenospermocarpic seedlessness (Loomis and Weinberger 1979, Weinberger and Harmon 1964) may possibly have resulted from differences in the definition of "seedless", which depended on consumer demand in each country. In addition, the seedless offspring generally had small berries, and many seedless offspring derived from 'Himrod' had a shattering habit of berries at full maturity.

In contrast, seedless fruit production achieved by GA application succeeded for 'Kyoho' and 'Pione', which are tetraploid interspecific cultivars, in the early 1980s. The

technique is easy: GA application to the flower cluster at the full-bloom stage and to the fruit 2 weeks later (Dan 1996). This provides large seedless berries. The table grape breeding program at the national institute changed from stenospermocarpic seedlessness to GA-based seedlessness. On the other hand, many cultivars have allele controlling female flower type heterozygously (Yamane *et al.* 1990), resulting in yielding offspring having not hermaphrodite but female flowers.

Breeding in the Fukuoka Agricultural Research Center, where the goal has been to develop new cultivars suitable for growing under plastic covers, resulted in the release of 'Shurei' in 2010, a *vinifera* diploid seedless cultivar with red, medium-sized seedless berries (6 g), that does not require GA application, although the plants lack high disease resistance.

New interspecific tetraploid cultivars closely related to 'Kyoho'

The release of 'Kyoho' and its successful cultivation encouraged the development of new tetraploid cultivars closely related to 'Kyoho'. These cultivars were initially developed by private breeders, and subsequently by public institutions too.

Tetraploid bud-sport cultivars from diploid cultivars are the source of cross parents in tetraploid breeding. 'Ishiharawase', 'Red Pearl', and 'Centennial' were bud-sports of 'Campbell Early', 'Delaware', and 'Rosaki', respectively. These are periclinal chimeras, with a first 2*x* layer and a second 4*x* layer (Yamane *et al.* 1978). The reproductive cells are derived from the second layer, so crossing among these tetraploid cultivars yields tetraploid offspring.

Yamane and Kurihara (1980) artificially produced tetraploid clones of 'Neo Muscat' and 'Thompson Seedless' by means of colchicine treatment to the axillary buds of the growing shoots. Notsuka *et al.* (2000) obtained tetraploid clones from 29 diploid cultivars by colchicine treatment to axillary buds in shoots growing *in vitro*, and tested the performance of the induced tetraploid clones of 8 cultivars. Berry weight in the tetraploids increased to an average of 1.3 times that of the original diploid cultivars.

Like 'Kyoho', the tetraploid cultivars derived from 'Kyoho' generally have large berries and moderate disease resistance, and can be grown in open fields in much of Japan. However, they have 'Kyoho'-like eating quality, some have softer flesh than 'Kyoho', and some have a relatively high frequency of berry cracking. Most are not remarkably superior to 'Kyoho', and have been cultivated only on a small scale, except for 'Pione' and 'Fujiminori'.

'Pione'

H. Ikawa, a private breeder, released 'Pione' in 1973. 'Pione' was an offspring from a cross between 'Kyoho' and 'Muscat of Alexandria 4*x*' (Yamane *et al.* 1978). The pedigree has not been elucidated by using DNA markers, yet.

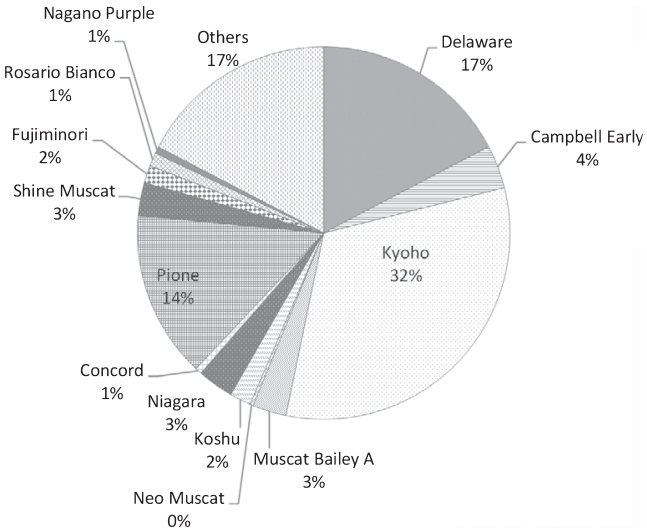

Fig. 6. Varietal share in grape cultivation area in Japan (2012). Based on MAFF statistics (2015).

'Pione' has characteristics resembling 'Kyoho': purple berries, flesh texture similar to that of 'Kyoho', a different but foxy flavor, and general vine characteristics similar to those of 'Kyoho'. However, its berries weigh 2 to 3 g more than those of 'Kyoho', and its poor fertilization habit makes it more difficult to obtain filled fruit clusters. Its general disease resistance seems to be comparable to that of 'Kyoho', but with less tolerance of ripe rot.

'Pione' has been cultivated mostly with seedless production by GA application, easily with full-filled fruit clusters. The large berries of 'Pione' promoted its cultivation. Thus, the area of 'Pione' cultivation has increased continuously since 1980, reaching 2327 ha in 2012, third after 'Kyoho' and 'Delaware' (**Fig. 6**).

'Fujiminori'

K. Aoki, a private breeder, released 'Fujiminori' in 1983. 'Fujiminori' was an offspring from Ikawa Selection 682 × 'Pione'. It has stable black and very large berries (15 g or more), with softer flesh than those of 'Kyoho' and a distinct foxy flavor in seeded fruit. Seedless production by GA application is available. The berries are likely to crack. Its color and berry size are accepted in the Japanese market, and the cultivation area had reached 246 ha in 2012 (MAFF 2015).

Other tetraploid cultivars

Tetraploid cultivars closely related to 'Kyoho' that were cultivated on more than 1.0 ha in 2012 (MAFF 2015) were as follows. The cultivars with black or dark purple berries were 'Takao', 'Aurora Black', 'Black Olympia', 'Takatsuma', 'Izunishiki', 'Black Beet', and 'Honey Black'; those with red berries were 'Aki Queen', 'Beni-izu', 'Gorby', 'Sunny Rouge', 'Ruby Roman', 'Olympia', 'Ryuho', 'Shinano Smile', 'Benifuji', and 'Benizuiho'; and those with white

berries were 'Suiho', 'Honey Venus', and 'Tamayutaka'. The cultivation area for each of those cultivars was less than 50 ha in 2012, except for 'Takao', 'Aki Queen', and 'Aurora Black' (MAFF 2015). 'Aurora Black' (77 ha in 2012) is a 'Pione'-like cultivar with stable dark-purple berries that are darker than those of 'Pione' (Ogoro *et al.* 2003). Its parentage is unknown. Mr. Hideo Ikawa released several cultivars and selections in the 1970s, which were used as cross parents in other breeding.

The Tokyo Agricultural Experiment Station released 'Takao' in 1971, which was obtained from open-pollinated seedlings of 'Kyoho' (Ashikawa 1973). 'Takao' is a hypotetraploid (aneuploid) with $2n = 75$ chromosomes (Yamane *et al.* 1978). It bears fruit clusters in which most berries are seedless and weigh 4 to 5 g, but the berries can be increased to between 8 and 10 g by means of a single GA application to the flower clusters. Its cultivation peaked at 148 ha in 1988, and it was cultivated on 84 ha in 2012.

Cultivars with large red berries are popular in the Japanese market, but stable coloration has not been obtained in most of the red tetraploid cultivars owing to the effects of variations in temperature, crop, and light interception by the leaves. 'Aki Queen', which was released by the national institute (Yamane *et al.* 1992a), has a favorable foxy flavor, but its unstable skin coloration has slowed down its cultivation, which reached 80 ha in 2012.

'Ruby Roman', released by the Ishikawa Agriculture Research Center in 2005, has very large red berries, and its fruit commands a high price, but it has potentially serious berry cracking and its flesh is soft and not easy to masticate in seeded fruit (Shima *et al.* 2006).

'Sunny Rouge', released by the national institute in 1997, is distinguished by early ripening (Yamada *et al.* 2003a). 'Suiho', released by the Fukuoka Agricultural Research Center in 1994, is distinguished by its very large seedless berries, which result from GA applications (Matsumoto *et al.* 1995). 'Honey Venus', released by the national institute in 1998, has a high sugar content (2° Brix higher than 'Kyoho'), and firm flesh (Sato *et al.* 2004, Yamada *et al.* 2003b).

'Queen Nina' and 'Sunverde'

The above tetraploid cultivars released, lack berries with crispy flesh that *vinifera* diploid cultivars for table use have, for seeded fruit. Many of those cultivars were evaluated for seeded fruit in the 1980s. The response of GA and F applications to flesh texture in these cultivars has not been elucidated well.

Crossings among cultivars with berry flesh texture intermediate between easy and difficult to masticate like 'Kyoho' and 'Pione' did not yield offspring with a crispy flesh texture easily for seeded fruit. Many tetraploid cultivars were released by private breeders, whose objectives were generally to improve 'Kyoho' partly: larger-sized berry, easy and stable deep-purple coloration in berry skin, or red-colored berry skin.

Grape breeding conducted by the national institute has consistently emphasized crispy flesh. It has been carried out by choosing cultivars/selections with firmer flesh that is easier to masticate as cross parents. This program released 'Queen Nina' in 2009 and 'Sunverde' in 2010, both producing seedless berries with crispy or nearly crispy flesh after two GA applications to the flower/fruit cluster (Sato *et al.*, 2004, Sato *et al.* 2013, 2014). 'Queen Nina' plants have very large red berries (15 to 20 g). 'Sunverde' also produces large berries (12 to 14 g), with white slip-skin. The typical fruit yield is less than that of 'Kyoho' in 'Queen Nina', but comparable in 'Sunverde'. 'Sunverde' berries are likely to suffer damage on the skin during flowering time although the mechanism of the phenomenon has not been elucidated well.

New triploid cultivars

Triploid cultivars obtained from crosses between diploids and tetraploids should be seedless. Seven new cultivars from crosses between diploid and tetraploid have been registered in MAFF since 1978.

H. Nakamura, a private breeder, crossed 'Red Pearl' with 'Muscat of Alexandria', resulting in 'King Dela', although the ploidy level has not been elucidated experimentally. 'King Dela' produces berries with a weight of around 3 g after two GA applications to the flower/fruit clusters, with flesh that is not easy to masticate. Its early ripening and berry size (larger than 'Delaware') has led to acceptance by consumers, and its cultivation peaked at 69 ha in 1997. By 2012, its cultivation area had decreased to 39 ha (MAFF 2015).

The strategy of crossing 'Kyoho' with diploid cultivars was adopted in some institutional breeding. Generally, berries in triploid cultivars have poor parthenocarpy, and require one or more GA application to the flowers or fruit clusters to obtain a sufficiently filled fruit cluster at maturity. 'Honey Seedless' (Yamane *et al.* 1993), 'Summer Black' (Ozawa *et al.* 2000a), and 'Kai Mirei' (Ozawa *et al.* 2000b) were developed by this approach, and have medium-sized berries after GA application. They were not attractive to consumers after the 1980s when 'Kyoho' dominated the market, and they are rarely grown commercially at present.

'Nagano Purple', a triploid offspring from 'Kyoho' × 'Rizamat' (Minemura *et al.* 2009, Osawa *et al.* 2011), was released in 2001. Its large berry size after two GA applications (13 to 14 g), crispy flesh, a favorable foxy flavor, ease of consumption without peeling, and seedlessness are popular with consumers, although the berries have a tendency to crack in the field. Its cultivation area has been increasing, and reached 95 ha in 2012.

New *vinifera* cultivars developed crosses among *vinifera* cultivars

The strategy of crossing among *vinifera* cultivars is advantageous in developing cultivars with large berries with

crispy flesh texture and a muscat or neutral flavor, but cannot develop cultivars resistant to many diseases. In addition, it is disadvantageous in developing resistant to cracking, and physiological necrotic berry disorder (Nakano 1988). Costly cultivation under plastic has been helping the production of *vinifera* cultivars in a market with high prices for large berries with crispy flesh texture.

'Kaiji'

'Kaiji' was registered as a new cultivar in 1977. It was developed by S. Uehara, a private breeder, by crossing 'Flame Tokay' with 'Neo Muscat'. It has attractive, large (10 g) red berries with crispy flesh, a neutral flavor, and no cracking. The fruit have long keeping qualities without berry shattering, and its late ripening time compared with 'Kyoho' allows this cultivar to command a high price in the market. On the other hand, it is sensitive to many diseases. In addition, its berries are likely to develop the physiological necrotic berry disorder. An early-ripening bud-sport of 'Kaiji' was subsequently developed. 'Kaiji' and its early-ripening bud-sport have been grown as seeded fruit, mostly in open fields in Yamanashi Prefecture. Their cultivation area peaked at 524 ha in 1994, and decreased to 293 ha by 2012 (MAFF 2015), mainly owing to their relatively low disease resistance.

'Rosario Bianco'

'Rosario Bianco' was developed by N. Uehara, a private breeder, and was registered in 1987. It resulted from a cross between 'Rosaki' and 'Muscat of Alexandria'. It bears large white berries (10 to 13 g) with crispy, juicy flesh that has a neutral flavor. However, it is generally sensitive to diseases. Its cultivation area reached 187 ha by 2012 (MAFF 2015).

'Seto Giants'

'Seto Giants' was developed by S. Hanazawa and T. Ohmori, private breeders, and was registered in 1989. It resulted from a cross between 'Guzal Kara' (Kurihara *et al.* 1976) and 'Neo Muscat'. It bears large (12 to 15 g) seedless white berries with crispy flesh and a neutral flavor after two GA applications. It is distinguished by a thin berry skin with no astringency resulting in ease of consumption without peeling. Its cultivation area reached 73 ha in 2012 (MAFF 2015).

Interspecific diploid breeding

Japanese consumers prefer large berries. 'Kyoho', whose berries average 12 g in weight, increased the standard for the desired berry size. This is a problem for breeders who attempt diploid cross breeding between *labruscana* and *vinifera* cultivars to obtain desirable characteristics such as suitability for Japan's climate, as *labruscana* cultivars generally have small berries compared with introduced *vinifera* table-use cultivars.

Inheritance of berry flesh texture in diploids is also quantitatively and additively controlled (Sato *et al.* 2006). Interspecific crosses between *labruscana* and *vinifera* cultivars mostly yield offspring whose berries have flesh that is intermediate between easy and not easy to masticate, and produce offspring whose berries have crispy flesh with a low probability.

Fig. 7. 'Shine Muscat' fruit cluster (seedless berries with gibberellic acid application).

Breeding to combine resistance to diseases and cracking and cold hardiness from *labruscana* with crispy flesh, a muscat flavor, and large berries from *vinifera* cannot be achieved by crosses among *vinifera* cultivars, but instead require interspecific crosses over multiple generations.

Grape breeding in the national institute has been based on a long-term strategy over generations for both diploid and tetraploid. The breeders have defined the muscat flavor as more desirable than the *labruscana* and neutral flavors. They obtained one offspring, Akitsu-21, with crispy flesh and a 7-g berry weight by crossing 'Steuben' (*V. labruscana*) with 'Muscat of Alexandria' (*V. vinifera*). The breeders crossed Akitsu-21 with various *vinifera* cultivars that had crispy flesh and large berries, and produced 'Shine Muscat' (**Fig. 7**) from Akitsu-21 × 'Hakunan' (Yamada *et al.* 2008) and 'Oriental Star' from Akitsu-21 × 'Ruby Okuyama' (Yamada *et al.* 2010); both have crispy flesh.

'Shine Muscat'

'Shine Muscat' produces large (12 g or more) white seedless berries after two GA applications to flower/fruit clusters and streptomycin spraying before flowering (Yamada *et al.* 2008). The berry has crispy flesh, a muscat flavor, no cracking, and no necrotic disorders. The fruit shelf life is longer than that of 'Kyoho'. Its berries have thin skin with no astringency resulting in being palatable without peeling, in

contrast to 'Kyoho' and *labruscana* cultivars, which have thick skins. The yield is appropriate for marketable fruit quality, at around 18 t/ha, versus 15 t/ha for 'Kyoho'. It is moderately tolerant to downy mildew and ripe rot, but sensitive to anthracnose (Kono *et al.* 2013, Shiraishi *et al.* 2007, Yamada *et al.* 2008). Its cold-hardiness is comparable to that of 'Kyoho'. 'Shine Muscat' cultivation has rapidly increased owing to its ease of cultivation and high fruit eating quality, and reached 463 ha in 2012 (MAFF 2015), only 5 years after the first sales of young plants in 2007.

'Oriental Star'

'Oriental Star' produces large (12 to 14 g) purple seedless berries after two GA applications and streptomycin spraying (Yamada *et al.* 2010). The berries have a neutral flavor, no cracking, and no necrotic disorders. The fruit shelf life is longer than that of 'Kyoho'. It is moderately resistant to ripe rot, but sensitive to anthracnose and downy mildew (Kono *et al.* 2013, Shiraishi *et al.* 2007, Yamada *et al.* 2010).

A survey of achievements and prospects

Thus far, cross-breeding has been based on parental phenotypes: cultivars with superior performance for a given trait are crossed. This approach has produced many promising cultivars. For populations derived from *vinifera* or *labruscana*, additive genes have been found that strongly control flesh DFP and firmness, berry weight, berry cracking, and resistance to powdery mildew (Eibach *et al.* 1989, Sato *et al.* 2006, Sato and Yamada 2004, Ueno *et al.* 2007). Resistance to downy mildew, anthracnose, and gray mold seems to be controlled by several oligogenes or by polygenes with considerable dominance effects (Eibach *et al.* 1989, Mortensen 1981). Recently, a few *vinifera* cultivars of Central Asian origin have been reported to have a gene resistant to powdery mildew (Coleman *et al.* 2009). 'Regent', a cultivar classified as *vinifera*, has a gene resistant to powdery mildew and downy mildew (Fischer *et al.* 2004), possibly derived from *V. rupestris* in its ancestor.

Hirakawa *et al.* (1998) showed that the muscat and labruscan flavors are inherited independently, and proposed a model for control by several genes with large dominant effects in agreement with Wagner (1967) and Reynolds *et al.* (1982).

The achievements of Japanese table grape breeding indicate the successful accumulation of useful genes for the above-mentioned traits.

The breeding target from 100 years ago, namely combining crispy flesh with a muscat or neutral flavor from *vinifera* with ease of cultivation (disease resistance, no cracking, no physiological disorders, and cold-hardiness) from *labruscana* has been largely achieved in 'Shine Muscat' through diploid interspecific crossing, and the production of seedless berries is available by means of GA application. However, breeding is not complete. 'Shine Muscat' is sensitive to anthracnose and only moderately resistant to downy mildew. Its berries are large, but they are smaller than those of 'Kyoho' and 'Pione'. Red and deeply purple berries are also attractive in markets. Crosses over generations among interspecific hybrids including 'Shine Muscat' are required for accumulating the genes to achieve the target completely (Yamada 2011). High productivity will also be an important breeding target, and will be realized by outbreeding. In addition, elucidating constituents related to eating quality other than flesh texture may promote the breeding (Shiraishi 1996, 2000, Shiraishi and Shiraishi 2002).

Tetraploid interspecific breeding succeeded by producing 'Kyoho' and related cultivars. The production of seedless berries by means of GA application is available. The target of crispy or nearly crispy flesh in GA-treated seedless fruit has been recently achieved in 'Queen Nina' and 'Sunverde'. Vine vigor in the tetraploid bud-sports, including 'Ishiharawase' and 'Centennial', is generally weak, but 'Kyoho' is very vigorous, although its productivity is not high. The mechanism of the phenomenon has not been elucidated. The periclinal chimera is possibly related to vine vigor. 'Kyoho' vigor may have resulted from heterozygosity caused by interspecific crossing. Tetraploid cultivars related to 'Kyoho' have generally been developed by inbreeding over multiple generations. Recently developed tetraploid cultivars are generally non-vigorous, suggesting that inbreeding depression has occurred. Further crossing based on parental phenotypes within a narrow gene pool may thus lead to serious inbreeding depression, unsuitable for commercial production.

The strategy of crossing among *vinifera* cultivars has not produced disease-resistant cultivars, especially for downy mildew and anthracnose. However, it has produced large berries with crispy flesh and a muscat flavor. This strategy and crossing 'Shine Muscat' with *vinifera* cultivars may lead to developing new cultivars that can be commercially grown under plastic covers on a small scale.

The size of the selection field has limited the number of offspring that breeders can evaluate. Marker-assisted selection (MAS) discards useless offspring in the initial stage, before planting in the field as seedlings, by DNA markers linked to important traits. This allows planting of only more promising offspring, thereby dramatically increasing the total number of offspring under selection. The use of DNA markers has been developed for berry skin coloration (Azuma *et al.* 2015, Ban *et al.* 2014). QTL analyses have been made for disease resistance in interspecific crosses (Akkurt *et al.* 2007, Fischer *et al.* 2004, Ramming *et al.* 2011, Riaz *et al.* 2011). Further use of marker-assisted selection will accelerate breeding.

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