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Diversity and breeding of flowering cherry in Japan

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Abstract: In early spring, the flowering of cherry trees is taken as a good sign for farmers to initiate rice cultivation in Japan. In the era before calendars, the timing of cultivation was very important for growing rice plants in temperate regions. Nine native species of flowering cherry (*Prunus* subgenus *Cerasus*) are present in Japan and they are classified into three groups: Yamazakura, Miyamazakura, and Edohigan. More than 250 cultivars of Japanese flowering cherry have been selected or bred from these wild species. Two species, Oshimazakura and Edohigan, have specially contributed to the breeding of flowering cherry cultivars. While Edohigan is distributed in most areas of Japan, Oshimazakura (of the Yamazakura group) is an endemic species found around the Izu and Boso Peninsulas. 'Somei-yoshino,' *Prunus* × *yedoensis*, is the most popular cultivar and now comprises 80-90% of all flowering cherry trees planted in Japan. 'Somei-yoshino' was probably created through hybridization between Edohigan and Oshimazakura in the Edo era. In this paper, the diversity and breeding of Japanese flowering cherry, including the origin of 'Somei-yoshino,' are described along with the political and horticultural backgrounds.

1. Introduction

At the end of March, the flowering of Chinese plum has been taken as a sign to initiate the plowing of paddy fields for rice cultivation in China. Therefore, Chinese people take an interest in looking at plum flowers, which is the reason why many cultivars of Chinese plum have been developed. The Chinese plum blooms in early February in Japan. Japanese farmers pay attention to the flowering of flowering cherry because it blooms at the end of March (Fig. 1). As Japan is located at the northern limits of the rice cultivation area, without a calendar, the timing to start rice cultivation was very important to identify the cultivation period and secure the best yield for farmers. Rice cultivation started by plowing paddy fields, then about a month later sowing rice seeds on the paddy. Growth of rice plants was restricted to the period between May and October (*ca*. 160 days) both in China and Japan. Farmers had to harvest the rice grains before snow at the end of October. As the rice yield was the basis of Japanese hierarchy, everyone in Japan, not only farmers, has been interested in the flowering of flowering cherry. More than 250 cultivars of flowering cherry have been selected or bred from wild *Cerasus* species in Japan (Kawasaki, 1991).

Farmers both in China and Japan started rice cultivation by ploking paddy fields at the end of march (yellow circle).

'Somei-yoshino'

A single cultivar, *Prunus yedoensis* (Matsum.) A.V. Vassil. 'Somei-yoshino' (Iketani *et al*., 2006), comprises more than 80-90% of flowering cherry trees planted in parks, and along roads and rivers across Japan, except in Okinawa and Hokkaido Islands. As *Cerasus* species have complete self-incompatibility, 'Somei-yoshino' has been propagated as a clone using grafting techniques. This paper discusses three topics in terms of the origin of

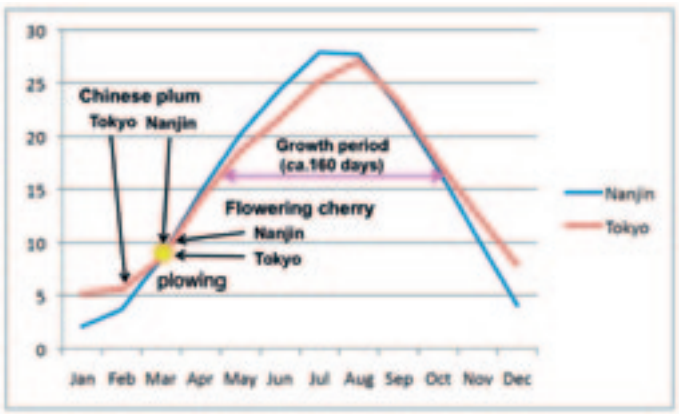

Fig. 1 - Changes of average temperature in Nanjin (China) and Tokyo (Japan).

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'Somei-yoshino': 1. Genetic variations of *Cerasus* species in Japan, 2. Political and horticultural backgrounds, 3. DNA analysis to reveal the origin of 'Somei-yoshino' (Fig. 2).

Fig. 2 - Flowering cherry 'Somei-yoshino'. Image credit: http://iko4wd.blog.so.net.ne.jp/2008-03-25.

2. Genetic variations of flowering cherry in Japan

Wild Cerasus *species in Japan*

The subgenus *Cerasus* of the genus *Prunus* includes more than 50 species, most of which are distributed in temperate areas in the Northern Hemisphere, especially in China, where 33 wild species occur (Yu and Li, 1986). In Japan, nine native species have been recorded (Table 1): Yamazakura (*P. jamasakura* Sieb. ex Koidz.), Oyamazakura (*P. sargentii* Rehder), Kasumizakura [*P. verecunda* (Koidz,) Koehne], Mamezakura (*P. incisa* Thumb. ex Murray), Takanezakura (*P. nipponica* Matsum.), Chojizakura [*P. apetala* (Sieb. et Zucc.) Fr. et Sav.], Oshimazakura [*P. lannesiana* (Carr.) Wilson var. *speciosa* (Koidz.) Makino], and Edohigan [*P. pendula* f. *ascendens* (Makino) Ohwi]. In addition, three wild species, Karamizakura (*P. pseudo-cerasus* Lindl.), Himarayazakura (*P. cerasoides* D. Don) and Kanhizakura (*P. campanulata* Maxim.), have been popularly cultivated since their introductions from China, Taiwan, and Nepal, respectively (Kawasaki, 1991) (Fig. 3).

Table 1 - Wild species of the subgenus *Cerasus* in Japan

Yamazakura group	Yamazakura	*P. jamazakura*
	Ooyamazakura	*P. sargentii*
	Kasumizakura	*P. verecunda*
	Oshimazakura	*P. Iannesiana*
Mamezakura group	Mamezakura	*P. incisa*
	Takanezakura	*P. nipponica*
Chojizakura group	Chojizakura	*P. apetala*
Edohigan group	Edohigan	*P. pendula*
Miyamazakura group	Miyamazakura	*P. mazimowiczii*
Karamizakura group	Karamizakura	*P. pseudo-cerasus (China)*
Kanhizakura group	Kanhizakura	*P. campanulata (Taiwan)*
Himarayazakura group	Himarayazakura	*P. cerasoides (Nepal)*

Fig. 3 - *Cerasus* species. Flowering of different cultivars. Top left 'Edohigan', Top middle 'Yamazakura', Top right 'Oshimazakura', bottom left 'Chojizakura', bottom right 'Kanhizakura'. Courtesy of Mr. Makoto Tsuruta.

Distribution of wild Cerasus *species in Japan*

Two wild species, Yamazakura and its close relative Oyamazakura, are broadly distributed throughout Japan (Fig. 4). While Edohigan is distributed from Kyushu Island to the Tohoku region (northern area of mainland Japan), this species is absent from some large peninsulas, such as Kii, Noto and Boso. As Edohigan blooms faster than Yamazakura and other Japanese *Cerasus* species, it was possibly spread by farmers along with rice cultivation from the south to the north of Japan. Mamezakura and its variant Kinki-Mamezakura are restricted to the mountainous area in the middle of the mainland. The wild population of Oshimazakura is endemic to the Izu and Boso Peninsulas and to Oshima Islands. As the flowers of Os-

Fig. 4 - Distribution of wild *Cerasus* species in Japan (Kawasaki, 1991).

himazakura have large white petals with a pleasant fragrance, it has been used as a parent to develop various cultivars of flowering cherry. Its green leaves are also used to decorate cakes. The flowers of Edohigan bloom faster than its leaves extrude. In contrast, flowers and leaves appear at the same time in Yamazakura and other species. Wild Edohigan and Yamazakura trees reach a height of 20-25 m, while Mamezakura and Oshimazakura have a relatively short stature (*ca.* 10 m).

Cultivars of flowering cherry

The history of the breeding of flowering cherry in Japan can be classified into three phases: Selection phase (Ancient to Azuchi-Momoyama era), Mutant phase (first half of Edo era), and Cross-hybridization phase (last half of Edo era to present). Two important incidents, the establishment of the Tokugawa Government (1603) and the practice of the Kyoho Reforms (1716), are related in the division of the three phases (Fig. 5). Before the Azuchi-Momoyama era, about 20 cultivars were selected from the native population of flowering cherry. 'Ukon,' with yellowish petals, and 'Shidare zakura,' with droopy branches, were representative cultivars in the Selection phase. During the first half of the Edo era, because Shoguns, especially the 3rd Shogun Tokugawa Iemitsu, asked Daimyos to donate fantastic or unusual flowers and trees, many ornamental cultivars of more than 100 species were brought together at Edo Castle. About 30 cultivars of flowering cherry with mutant phenotypes, such as many petals 'Ito kukuri' and dwarf stature 'Asahiyama' were collected in the Mutant phase. During the last half of the Edo era, flowering cherry cultivars were developed using natural or artificial cross-hybridization. In the Cross-hybridization phase of the last half of the Edo era, more than 80 cultivars, such as 'Ichiyo' with a leafy stigma and 'Surugadai-nioi' with a fragrance, were created by hybridization with Oshimazakura as parent (Fig. 6).

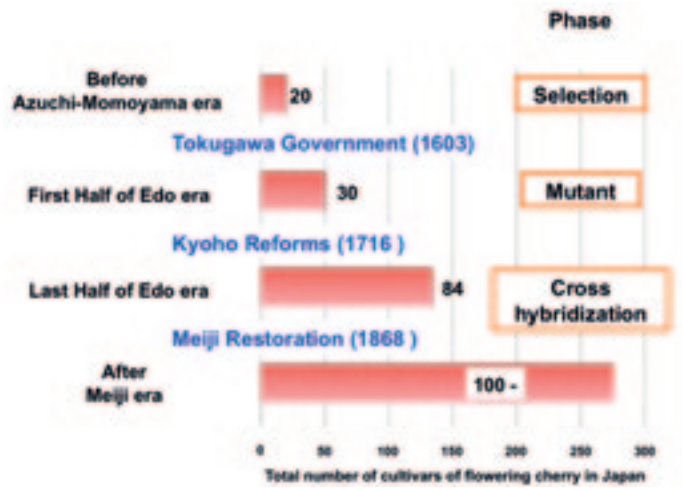

Fig. 5 - Three phases in the breeding of flowering cherry.

Fig. 6 - Cultivars (Cross hybridization phase) during last half of Edo era. Courtesy of Mr. Makoto Tsuruta..

3. Political and horticultural backgrounds

260-year peace during Edo period

Ieyasu Tokugawa (1542-1616), who was the 1st Shogun, struggled to establish the Tokugawa Government (1603-1868). It is thought to be the longest period of peace in the world at that time. The 260 years of peace under the Tokugawa Government was an important background to the development of various cultures, including horticulture. Takatora Todo (1556-1630) was probably a key person for the establishment of the Tokugawa Government and for the basis of the origin of 'Somei-yoshino.' He constructed more than 20 castles, including Edo Castle. And he once owned Kisyu Kokawa-Han and visited Mt. Yoshino, which was famous for its large Yamazakura population. Later, Takatora moved to Ise-Han where both Iga and Koga Ninja lived. Thus, Takatora organized the Ninja into a CIA (Central Intelligence Agency, USA)-like 'Onmitsu' system in order to keep an eye on the behavior of Daimyos for the Tokugawa Government. His house was located in 'Somei' village of Edo city and the name of his gardener was Ito Ihei, who was probably a secret manager of 'Onmitsu' under the control of the Todo clan. After Ieyasu died, Takatora constructed 'Kan-eiji' temple for Ieyasu's grave in 1625. Iemitsu Tokugawa (3rd Shogun) and Takatora directed the transplantation of wild Yamazakura trees from Mt. Yoshino to 'Kan-eiji' temple. As a result, 'Kan-eiji' temple became a famous 'Hanami' place in Edo city. Note: 'Hanami' means looking at blossoms whilst eating and drinking

Collection of cultivars and mutants

During the lifetime of Iemitsu Tokugawa (1623-1651) of the 3rd Shogun of the Tokugawa Government, most social systems, including transport and the economy, were established. Iemitsu, who was rather eccentric and an enthusiast of ornamental flowers and trees, asked Daimyos to donate fantastic or unusual plants, and as a result many mutant cultivars of more than 100 plant species were brought to Edo Castle. These collected plants were later

given to the Ito Ihei clan through the Todo clan. Hybridizations among the collected genetic resources led to the development of many horticultural cultivars, such as morning glory, Japanese azalea, camellia, orchid, and fern, by the Ito Ihei clan (gardeners) and people in Edo city. They frequently held competitive exhibitions of the cultivars that they had developed. For example, an unusual phenotype 'Shiro saizaki botan' of morning glory appeared at a frequency (one out of 20,000 seeds), corresponding to recombination among 6-7 recessive alleles. Thus, Japanese gardeners and others might have recognized a principle of inheritance before Mendel (1865) (Fig. 7).

Fig. 7 - 'Shiro saizaki botan', Morning glory (6-7 recessive allele). Courtesy of Dr Yoshiaki Yoneda http://protist.i.hosci.ac.jp/Asago/Yoneda_DB/J/menu.html.

Accumulation of horticultural knowledge

During the period of peace, not only gardeners but also enthusiasts in Edo city enjoyed breeding ornamental flowers and trees. Much knowledge and many horticultural techniques were accumulated during the process of developing the new cultivars of ornamental plants. Many books and illustrations describing the knowledge and developed cultivars were published during the last half of the Edo era. For example, Kan-En Iwasaki published a book 'Somoku sodate-gusa' (Plant Breeding) in 1818. In this book, he illustrated six different grafting, four cutting and three layering techniques, which are comparable to the present horticultural techniques. In those days, as more than 80 cultivars of flowering cherry had been developed by using natural or artificial cross-hybridization, this horticultural knowledge and these techniques must have contributed to the development of new cultivars of flowering cherry (Fig. 8, 9).

'Ippon-zakura' to 'Gun-zakura'

Yoshimune Tokugawa (1684-1751) used to be a Daimyo in Wakayama, close to Mt. Yoshino, which was famous for its beautiful scenery covered with Yamazakura trees. After he became the 8th Shogun, he enacted the 'Kyoho Reforms' to rebuild the finances of the Tokugawa Government. Also he opposed the powers of the Todo clan and Kan-eiji temple. Yoshimune abolished 'Onmitsu' under the control of the Todo clan and then organized his subordinates into the 'Oniwaban,' which was also a CIA-like system. This change meant that Ito Ihei might lose his salary as a secret manager of the 'Onmitsu.' Against the Kan-eiji temple, Yoshimune tried to develop new 'Hanami' places because 'Kan-eiji' was the famous 'Hanami' place in Edo city. He wanted to reconstruct the scenes of flowering cherries on Mt. Yoshino in Edo city. Therefore, he directed transplantation of a group of wild Yamazakura trees, propagated by grafting in Edo Castle, to several new 'Hanami' places, such as Shinagawa, Sumida-gawa and Asuka-yama. Then, he encouraged people to eat and drink under blossoms because he knew the starting time of rice cultivation was very important for farmers to achieve the best rice yield.

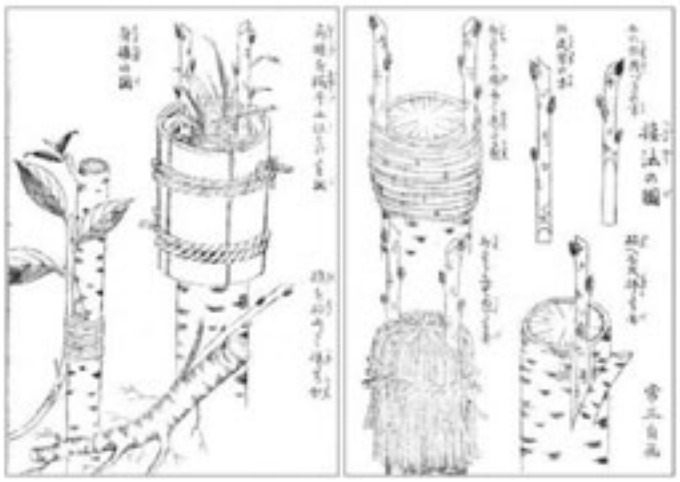

Fig. 8 - Illustrations of six different grafting techniques. Image credit: http://dl.ndl.go.jp/info:ndljp/pid/2569455.

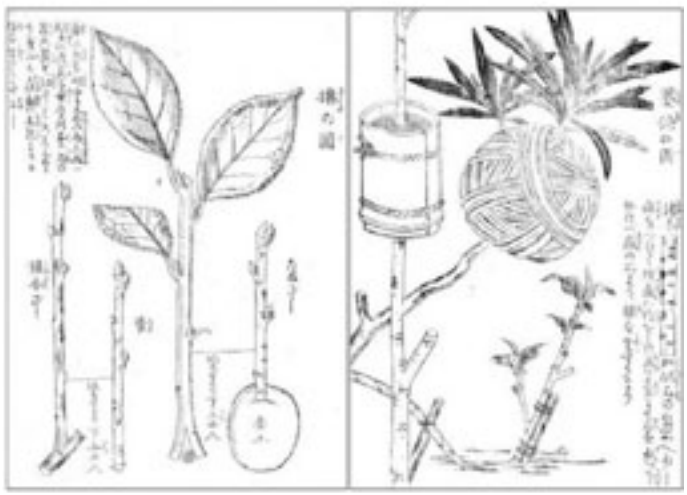

Fig. 9 - Illustrations of 4 cutting (left) and 3 layering (right).

During the first five to ten years, people probably enjoyed 'Hanami' under blossoms but after 15 years, the wild Yamazakura trees grew to be over 15 m high. Yoshimune did not realize that the tree height of flowering cherry was so important because people were able to look at flowers closely in spite of the height of the trees on the slopes on Mt. Yoshino (Fig. 10). In flat places of Edo city, the wild trees of Yamazakura grew too high to look at the blossoms

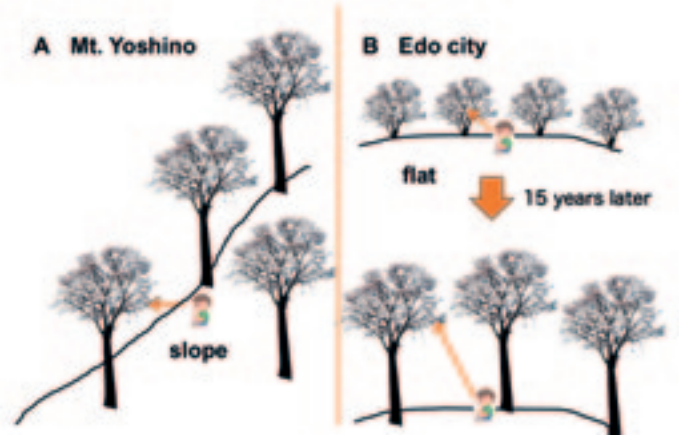

Fig. 10 - Sitting person's view of flowering cherry on the slopes of Mt. Yoshino (A) and on flat places in Edo city (B).

closely from under the trees but no one complained for fear that Yoshimune would punish them. Nowadays, all Yamazakura trees, planted by Yoshimune, have been replaced by 'Somei-yoshino.'

Before the mid-Edo era, people enjoyed seeing a distant scene of a single big flowering cherry 'Ippon-zakura.' On the contrary, Yoshimune introduced the concept of a group of flowering cherry 'Gun-zakura' to people in Edo city.

Involvement of Masatake Ito Ihei

Masatake (1676-1757) of 4th Ito Ihei and his father Sannojo (?-1719) were excellent plant breeders who developed many ornamental cultivars, Japanese azalea, camellia and sweet flag. As the Ito Ihei clan probably earned a salary from the Todo clan as managers of the 'Onmitsu,' they enjoyed plant breeding and gardening as a hobby. Sannojo and Masatake wrote many horticultural books, such as 'Kadan-chikin-syo' (1695) and 'Koeki -chikin-syo' (1719). Sannojo illustrated 120 plant species of ornamental flowers and trees including 46 cultivars of flowering cherry. Masatake also illustrated 197 species of ornamental plants, however, there was no description of flowering cherry. It is very unlikely that Masatake was uninterested in the breeding of flowering cherry. He probably excluded descriptions of flowering cherry from his books in order to avoid conflict with Yoshimune who initiated the 'Kyoho Reforms' in 1716. Masatake might have found that wild Yamazakura trees were not suitable to 'Gun-zakura' but he could not blame Yoshimune because Yoshimune might not just punish Masatake, he might wipe out the entire Todo clan. Thus, Masatake may have tried to develop a new cultivar for 'Gun-zakura' in secret within Kan-eiji temple.

4. DNA analysis to reveal the origin of 'Somei-yoshino'

'Somei-yoshino' was first identified and named by Yorinaga Fujino in 1900 and Dr. Jinzo Matsumura of Tokyo University registered it as *Prunus* x *yedoensis* at 1901. Dr. Ernest H. Wilson (1916) proposed, through morphological observations, the hypothesis that 'Somei-yoshino' is a hybrid of Oshimazakura and Edohigan. Dr. Kaname Takenaka (1962, 1965) confirmed Wilson's hypothesis by observing morphologies of the hybrids, Izu-yoshino and Amagi-yoshino, produced through artificial hybridization between the two species. However, these hybrids show higher stature and whiter petals compared with 'Somei-yoshino.'

Analyses of restriction fragment length polymorphism of chloroplast DNA (Kaneko *et al*., 1986) and plastid subtype identity sequence (Ohta *et al*., 2006) clearly indicate that the maternal lineage of 'Somei-yoshino' is Edohigan. In contrast, nuclear DNA analysis of flowering cherry is difficult because *Cerasus* species have complete self-incompatibility. We found that sequence variations of *PolA1* gene are useful for analyzing phylogenetic relationships in rice and wheat (Takahashi *et al*., 2009; Rai *et al*., 2012). *PolA1* is a single copy nuclear gene encoding the largest subunit of RNA polymerase I complex. Thus, DNA fragments containing intron 19 and exon 20 sequences of *PolA1* gene were amplified by PCR using template DNAs from wild strains of *Cerasus* species in Japan (Fig. 11). PCR products were purified and analyzed by direct sequencing technique. Sequence analysis of exon 20 indicates that

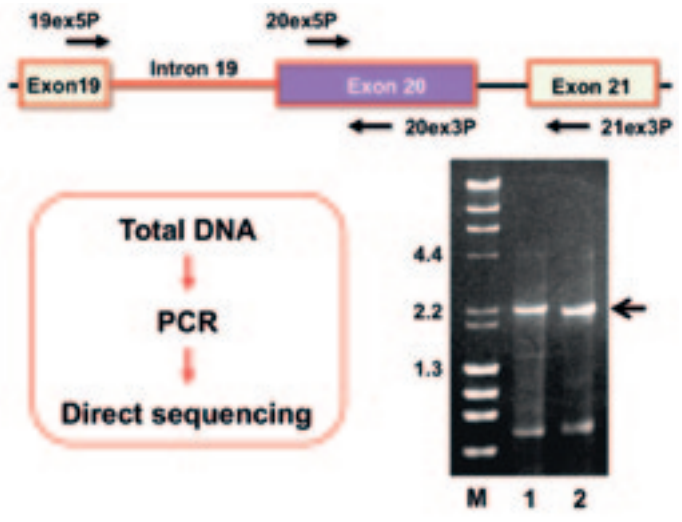

Fig. 11 - Sequence analyses of intron 19 and exon 20 of *PolA1* gene in *Cerasus* species.

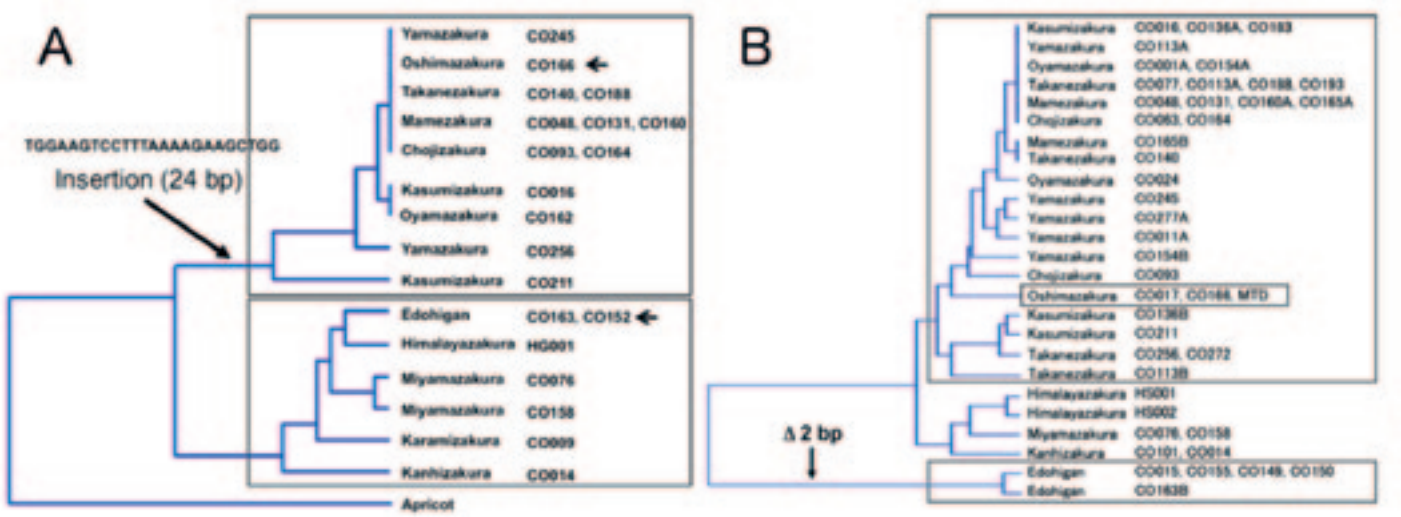

Fig. 12 - Relationships of exon 20 (A) and intron 19 (B) sequences of *PolA1* gene among *Cerasus* species, in Japan.

	25	36	38	43	101	128	131	146	171	174	178	199	298	305	309	349 - 350	392	416	457	477	492	500
'Somei-yoshino'	A	T	T	T	A	A	C	A	C	T	G	A	T	C	T	del (2)	A	A	C	A	C	G
	T	C	C	A	T	G	T	G	A	C	A	C	C	T	G	AA	C	T	A	G	T	A
Edohigan	A	T	T	T	A	A	C	A	C	T	G	A	T	C	T	del (2)	C	A	C	A	C	G
	A	T	T	T	A	A	C	A	C	T	G	A	T	C	T	del (2)	C	A	C	A	C	G
'Komatsuotome'	A	T	T	T	A	A	C	A	C	T	G	A	T	C	T	del (2)	C	A	C	A	C	G
	A	T	T	T	A	A	C	A	C	T	G	A	T	C	T	del (2)	A	A	C	A	C	G
Oshimazakura	T	C	C	A	T	G	T	G	A	C	A	C	C	T	G	AA	C	T	A	G	T	A
	T	C	C	A	T	G	T	G	A	C	A	C	C	T	G	AA	C	T	A	G	T	A
Yamazakura	A	C	C	A	A	G	T	G	C	C	A	C	C	T	G	AA	C	T	A	G	T	A
	A	C	C	A	A	G	T	G	C	C	A	C	C	T	G	AA	C	T	A	G	T	A

Fig. 13 - Comparison of two allelic intron 19 sequences within *PolA1* gene among 'Somei-yoshino,' Edohigan, 'Komatsuotome,' Oshimazakura, and Yamazakura.

Yamazakura and Edohigan can be clearly distinguished (Fig. 12). A particular insertion of 24 bp was found in the Yamazakura group including Oshimazakura as well as Mamezakura and Chojizakura groups (Table 1). This data indicates that these three groups share the same ancestor. The sequence analysis of intron 19 shows a similar result to that of exon 20 (Fig. 12), however Oshimazakura is clearly distinguished by three single nucleotide polymorphisms (SNPs) from Yamazakura and other species.

Sequence analysis of intron 19 shows that 'Somei-yoshino' contains a haplotype containing the three SNPs at the positions of 25 101, and 171, which are specific to Oshimazakura (Fig. 13). This result is very important for considering the origin of 'Somei-yoshino' because Oshimazakura is an endemic species to the Izu and Boso Peninsulas (Fig. 4). Another haplotype of 'Somei-yoshino' is identical to that of the wild Edohigan except for one SNP at the position of 392. The same SNP was found in a haplotype of 'Komatsu-otome.' 'Komatsu-otome' is a cultivar of Edohigan with a short stature (*ca*. 6 m) and is found as an original tree in Ueno Park, which was in the precincts of Kan-eiji temple in the Edo era. These results suggest that 'Somei-yoshino' originates from hybridization between a maternal parent, a semi-dwarf cultivar closely related to 'Komatsu-otome,' and a paternal parent, a cultivar of Oshimazakura (Fig. 14). Also 'Somei-yoshino' could originate from hybridization between hybrids containing each haplotype.

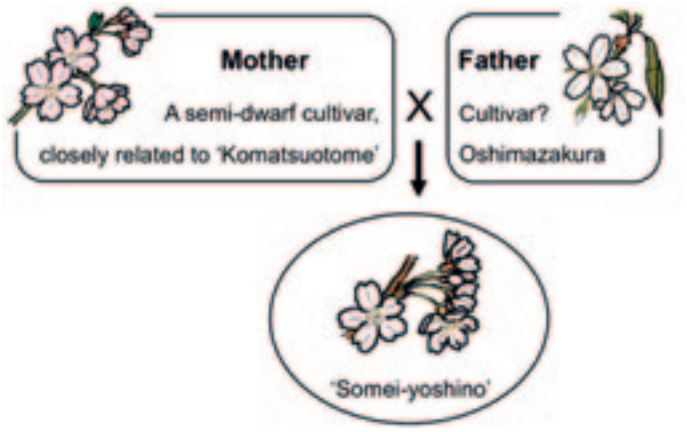

Fig. 14 - Schematic representation of the origin of 'Somei-yoshino' (Nakamura *et al*., 2007).

'Komatsu-otome' (tree No. 135, assigned by Ueno Park) was grown around the ruins of the Bell Tower in Kan-eiji temple (Fig. 15). Now, a total of ten trees related to Edohigan grow around the Bell Tower. Four trees (133, 134, 136, 138) have been identified as 'Somei-yoshino.' Sequence analysis of chloroplast DNA shows that the maternal lineage of all ten trees is Edohigan. And sequence analysis of the *PolA1* gene indicates that three trees (141, 142, 144) and 'Somei-yoshino' contain a haplotype (O) specific to Oshimazakura. One tree (145) is homozygous of the haplotype (K), which is shared by 'Komatsu-otome' and 'Somei-yoshino.' In addition, one haplotype (T) found to be specific to the chloroplast DNA of 'Some-yoshino' (Ando *et al*., unpublished) is shared with another tree (142). These results suggest that flowering cherry trees around the Bell Tower were developed by artificial hybridizations between Edohigan and Oshimazakura, and that there were sufficient genetic resources to develop 'Somei-yoshino' and 'Komatsu-otome.' DNA analysis of offshoots of four 'Somei-yoshino' clones revealed that these clones were propagated by using layering or grafting with a weak stock. This result suggests the action of a professional gardener. The purpose of planting the four clones together might be related to the evaluations of the 'Gun-zakura' by Buddhists of the Kan-eiji temple.

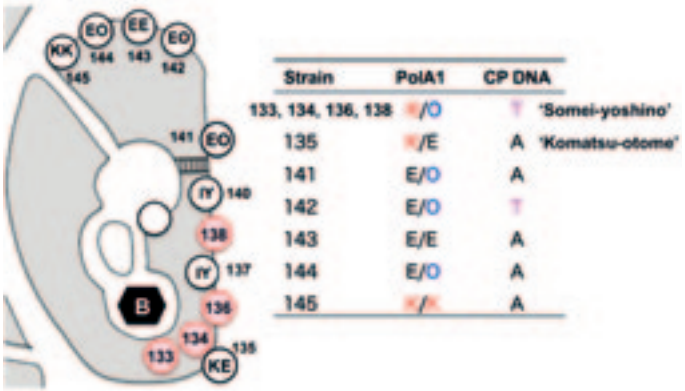

Fig. 15 - Haplotypes of intron 19 in *PolA1* gene and of chloroplast (CP) DNA analyzed for ten trees around the ruins of the Bell Tower (B) in Kan-eiji temple.

Masatake Ito Ihei (1676–1757) lived at the same time as Yoshimune Tokugawa (1684–1751). Masatake had the ability to develop 'Somei-yohsino' because he had developed many ornamental cultivars of various plant species (Iwasaki, 1989, 1991). Masatake might be the person who planted hybrids of flowering cherry around the Bell Tower because Kan-eiji temple had a close relationship with the Todo clan and because the precinct of Kan-eiji was an extraterritorial place from the Tokugawa Government. Except for Masatake, there was no reason why anyone would record the origin of 'Somei-yoshino.'

After the Meiji Restoration

Ken-eiji temple was destroyed during the 'Boshin' war (1868) and the temple grounds were established as Ueno Park (1873). The Meiji Government held Japanese industrial exhibitions several times in Ueno Park in order to promote Japanese industry. 'Somei-yoshino' shoots were massively propagated using grafting with a strong stock by gardeners in 'Somei' village, and then the shoots were probably sold in the exhibitions. The oldest known 'Somei-yoshino' tree is one of the 1,000 shoots that were planted within Hirosaki Castle in 1882, the year after the 2nd Japan Industry Exhibition (1881). As no one could buy the 1,000 shoots without seeing the real 'Somei-yoshino,' it was probably planted within Ueno Park at that time. At present, many 'Somei-yoshino' trees are beginning to show gaps in their stems, which seems to support the idea that 'Somei-yoshino' has a 60-year life span. As these gaps are caused by imbalanced growth between the scion and stock after grafting, if clones of 'Somei-yoshino' are propagated using grafting with a weak stock, they would be able to survive for hundreds of years.

5. Conclusions

There is no record of the origin of 'Somei-yoshino' but the results presented in this paper suggest that Ito Ihei Masatake, or someone else, developed 'Somei-yoshino' in secret as a suitable cultivar for 'Gun-zakura' within the grounds of Kan-eiji temple. 'Somei-yoshino' was created by horticultural techniques developed during the long period of peace and economic stability of the Edo era. 'Somei-yoshino' has been a parent of more than 100 cultivars since the Meiji Restoration. Dr. Yozaburo Shirahata (2000) suggested that 'Hanami' consisting of 'Gun-zakura,' ('Eating and drinking', and 'Mass gathering') is a popular culture unique to Japan, and the Japanese love of 'Hanami' is showing no sign of diminishing.

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