

Shanghai Suimitsuto, One of the Origins of Japanese Peach Cultivars

Toshiya Yamamoto^{1*}, Kohei Mochida² and Tateki Hayashi¹¹National Institute of Fruit Tree Science, Fujimoto, Tsukuba, Ibaraki 305–8605²Faculty of Agriculture, Tokyo University of Agriculture and Technology, Saiwaicho, Fuchu, Tokyo 183–8509

Summary

Almost all peaches grown in Japan supposedly originated from ‘Hakuto’ by crossbreeding, so that they are closely related to it. For example, ‘Hakuho’ and ‘Akatsuki’, offsprings of ‘Hakuto’, were obtained by controlled hybridization. There is a possibility that many cultivars are chance seedlings or bud sports of ‘Hakuto’. However, the genetic origin of ‘Hakuto’ has not yet been identified. In this study, genetic relationships between ‘Hakuto’ and other peaches with different origins were analyzed, using 10 SSR markers. The results indicate that a close relationship exists between ‘Shanghai Suimitsuto’ and ‘Hakuto’ as well as a possible parent–offspring relationship. Contrarily, the peach ‘Kinto’ showed a close relationship to ‘Hakuto’ but not that of a parent–offspring because of a discrepancy of genotypes for the SSR loci. Parentage analysis of ‘Hakuto’ and ‘Shanghai Suimitsuto’ that was analyzed by 43 SSR loci, revealed that all SSR alleles were inherited by ‘Hakuto’ without any discrepancy from the putative parent ‘Shanghai Suimitsuto’. These results indicate the very high possibility that ‘Shanghai Suimitsuto’ is a parent of ‘Hakuto’ and one of the original germplasm of the Japanese peaches.

Key Words: genetic origin, Hakuto, *Prunus persica*, Shanghai Suimitsuto, simple sequence repeat (SSR).

Introduction

The peach (*Prunus persica* (L.) Batsch) is one of the most important fruit species adapted to temperate and subtropical zones in the world (Scorza and Sherman, 1996). Peaches, which were introduced several times into Japan from their center of origin in China, have been cultivated for 1500–2000 years for fresh consumption and for ornamental purposes. The present peach cultivars in Japan having large fruit size and high fruit quality were generated by the introduction of germplasms from China, U.S.A., and Europe about 100–150 years ago (Takenaka, 1884; Namikawa and Mizutani, 1989; Scorza and Okie, 1990). More than 20 cultivars including ‘Shanghai Suimitsuto’ (also called ‘Chinese Cling’), ‘Tenshin Suimitsuto’, ‘Banto’ and ‘Yuto’ were introduced from China (Takenaka, 1884). Among them, ‘Shanghai Suimitsuto’ has the best fruit quality and adaptability and its offsprings eventually replaced the native peaches leading to the modern true-to-type peaches in Japan. However, no detailed descriptions of the origin of cultivated peaches have been documented, and the cultivar pedigree of ‘Shanghai Suimitsuto’ has not yet been identified.

Today, more than two-thirds of Japanese peach cultivars are thought to be derived from offsprings or

related cultivars of ‘Hakuto’. The 10 leading cultivars in Japan and their percent production are as follows: ‘Hakuho’ (20.2%), ‘Akatsuki’ (12.6%), ‘Kawanakajima Hakuto’ (9.8%), ‘Hikawa Hakuho’ (8.0%), ‘Asama Hakuto’ (5.0%), ‘Yamane Hakuto’ (3.6%), ‘Shimizu Hakuto’ (3.6%), ‘Nagasawa Hakuho’ (3.2%), ‘Yahata Hakuho’ (3.0%) and ‘Takei Hakuho’ (2.8%). ‘Hakuho’ is a F₁ progeny of ‘Hakuto’ and ‘Tachibana Wase’ (Togashi and Kawaguchi, 1936a, b), whereas ‘Akatsuki’ is one between ‘Hakuto’ and ‘Hakuho’ (Kanato et al., 1980). ‘Kawanakajima Hakuto’, ‘Asama Hakuto’, ‘Yamane Hakuto’, ‘Shimizu Hakuto’, ‘Hikawa Hakuho’, ‘Nagasawa Hakuho’, ‘Yahata Hakuho’ and ‘Takei Hakuho’ are thought to be related to ‘Hakuto’, however, the exact relationships are unknown. Therefore, almost all widely grown cultivars are descendants of ‘Hakuto’.

There are reports that ‘Hakuto’ was found and selected as a chance seedling by Jugoro Ohkubo in Okayama prefecture in 1899. However, its parents are unknown (Togashi, 1933; Yoshida, 1980; Namikawa and Mizutani, 1989; Yoshida, 1991, 2002). Based on morphological characteristics of the tree and fruit, ‘Shanghai Suimitsuto’ and/or ‘Kinto’ might be the parent of ‘Hakuto’ (Namikawa and Mizutani, 1989; Yoshida, 1980; Yoshida, 2002). Therefore, identification of a genetic relationship between ‘Shanghai Suimitsuto’ or ‘Kinto’ and ‘Hakuto’ will establish that relationship.

Recently, SSRs (simple sequence repeats, also known as microsatellites) have become markers of choice in

Received; June 18, 2002. Accepted; September 24, 2002.

*Corresponding author

Contribution No. 1273 of the National Institute of Fruit Tree Science.

both animal and plant species because of their abundance, high degree of polymorphism, and suitability for automated analysis (Weber and May, 1989). The SSR marker provides a more reliable method for parentage analysis because of its co-dominant inheritance and large number of alleles per locus. In peach, SSR markers have been developed (Cipriani et al., 1999; Sosinski et al., 2000; Testolin et al., 2000; Yamamoto et al., 2002) and used to analyze European cultivars (Testolin et al., 2000).

In this study, we first investigated the genetic relationship between 'Hakuto' and the other 17 peach cultivars by using 10 SSR markers, including 'Shanghai Suimitsuto'. Both native and foreign accessions were, likewise, tested. Then, a parent-offspring relationship of 'Shanghai Suimitsuto' vs. 'Hakuto' was analyzed by using 43 SSR markers. Based on the SSR analysis, the origin of Japanese peach cultivars was examined.

Materials and methods

Plant materials and DNA extraction

The eighteen peach cultivars examined in this study were: 'Hakuto', 'Kinto', 'Shanghai Suimitsuto', 'Tenshin Suimitsuto', 'Feichangtao', 'Redhaven', 'Nectared 1', 'Independence', 'Ohatsumomo', 'Nagano Yaseito', 'Oucho Yuto', 'Kuto 1', 'Thai Yaseito', 'Akabana Banto', 'Kikumomo', 'Houkimomo', 'Swatow', and 'Juseito' (Table 4). 'Shanghai Suimitsuto', 'Tenshin Suimitsuto', and 'Feichangtao' are true-to-type Chinese peaches that were introduced into Japan. 'Redhaven' peach and 'Nectared 1' and 'Independence' nectarines originated in USA, whereas 'Ohatsumomo', 'Nagano Yaseito', and 'Oucho Yuto' are wild peaches grown in Japan. 'Kuto 1' and 'Thai Yaseito' are wild

peaches that originated in Taiwan and Thailand, respectively. 'Akabana Banto', 'Kikumomo', 'Houkimomo', 'Swatow' and 'Juseito' are ornamental flowering peaches; the first 3 cultivars originated in Japan. The other 2 were introduced from China. The Japanese peach cultivar 'Kinto' might be related to 'Hakuto' (Yoshida, 1980).

Plant materials were obtained from the National Institute of Fruit Tree Science (Tsukuba, Japan). Genomic DNA was isolated from fresh young peach leaves by using the modified CTAB protocol, described by Yamamoto et al. (2001a, b).

SSR analysis

Of the 43 SSR markers used in this study (Table 1), 12 SSRs, M1a, M2b, M3b, M4c, M5a, M6a, M7a, M9a, M11c, M12a, M13b and M15a were derived from cDNA libraries of mature or young fruits of 'Akatsuki'

Table 1. SSR markers used in this study.

Source	SSR name
Fruit cDNAs	M1a, M2b, M3b, M4c, M5a, M6a, M7a, M9a, M11c, M12a, M13b, M15a
	MA004b, MA005c, MA006b, MA007a, MA009b, MA010a, MA013a, MA014a, MA015a, MA016b, MA017a, MA019a, MA020a, MA021a, MA023a, MA024a, MA026a, MA027a, MA030a, MA031a, MA035a, MA039a, MA040a, MA042a ^z , MA044a ^z , MA045a ^z , MA046a ^z , MA051a ^z , MA053a ^z , MA056a ^z , MA058a ^z
Genomic DNAs	

^zCharacteristics are denoted in Table 2. The other SSR markers were described in Yamamoto et al. (2002).

Table 2. Eight newly developed microsatellite loci derived from an enriched genomic library of 'Akatsuki'. Motifs and PCR product size refer to sequenced alleles.

Locus	Primer sequence (5'–3')	Motif	PCR product size (bp)	Annealing temperature (°C)
MA042a	F: GCAGAGCAAGCAAGCAAGCA R: CTCTCACTTCTCAGACCCTC	(AG) _{12.5}	295	55
MA044a	F: CAGAGATTCTGGGCTTACA R: CCACCTCCTCTTTCTATTCT	(AG) ₅	411	55
MA045a	F: ACTAAAGGCACGGATAACT R: TAATAAGATGGAGAAGCGAC	(GA) _{17.5}	323	55
MA046a	F: GCTGAAAGCGATAACCACTA R: TGTACCAAACAGGGCCTAAG	(GT) ₈ (GA) ₁₇	238	55
MA051a	F: ACATCATAAACATCGCAGTA R: TTTGGAGCTAAATGGGTATC	(GA) _{26.5}	219	55
MA053a	F: TCACTCTCCAGTAAACACTATG R: AGCCACTACAATGATAGCAA	(GA) _{13.5}	234	55
MA056a	F: GTCTTGTCTCCATTAGTCCC R: GAACCTTGATGGATTGGTTTG	(GA) ₃₀	283	55
MA058a	F: ATGTGGCAGATGGCGATTGT R: TCTCCTATGTCCGCAAGCA	(AG) _{4.5} T(AG) _{5.5}	285	55

(Yamamoto et al., 2002). The remaining 31 were developed from an enriched genomic library of 'Akatsuki' (Yamamoto et al., 2002, Table 1). Characteristics of 8 newly developed SSR markers are summarized in Table 2.

PCR amplification was performed in a 20 μ l solution of 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 1.5 mM MgCl₂, 0.01 % gelatin, 0.2 mM of each dNTP, 10 pmoles of forward primer, labeled with a fluorescent chemical (FAM or TET or HEX), and unlabelled reverse primer for each combination, 10 ng of genomic DNA, and 0.5 unit of Taq polymerase (Life Technologies, USA). Amplification of 40 SSR fragments (excluding MA004b, MA015a and MA039a) was performed with 35 cycles at 94 °C for 1 min, 55 °C for 1 min and 72 °C for 2 min, for denaturation, annealing and primer extension, respectively. The loci of MA004b and MA039a were annealed at 50 °C, whereas that for MA015a was conducted at 52 °C. The PCR products were separated and identified by using a PRISM 377 DNA sequencer (PE Applied Biosystems, USA). The size of the amplified bands was calculated, based on an internal standard DNA (GeneScan-350TAMRA, PE Applied Biosystems, USA) with GeneScan software (PE Applied Biosystems, USA).

Data analysis

Genetic identities were calculated, based on the fraction of alleles commonly observed between 'Hakuto' and other cultivars at the 10 SSR loci, according to Nei's genetic identity (Nei, 1972) by using the NTSYS-pc, ver. 2.01 (Rolf, 1998).

The parent-offspring relationship between 'Shanghai

Suimitsuto' and 'Hakuto' was examined by using 43 SSR loci. The parentage analysis was conducted based on the appearance of one allele at a single SSR locus transmitted from the putative parent 'Shanghai Suimitsuto' to its offspring 'Hakuto'. A parent-offspring relationship is questionable if one or more discrepancies exist on the appearance of SSR alleles.

Results and Discussion

Genetic similarity between Hakuto and other cultivars

The 10 SSR markers, M1a, M4c, M12a, M15a, MA007a, MA009b, MA010a, MA013a, MA014a, and MA015a, used to trace the genetic background of 'Hakuto', produced 1 or 2 discrete amplified fragments for 18 peach cultivars (Table 3). Segregation of alleles at the 10 SSR loci was evaluated in the 126 F₂ progenies derived from an intraspecific cross between 'Akame' and 'Juseito'. Five SSR markers, M12a, M15a, MA007a, MA010a and MA013a, segregated according to the Mendelian ratio of 1:2:1 in the F₂ progenies (data not shown). The other 5 SSR markers, evaluated by using 2 to 3 sets of cultivars with parent-offspring relationships, showed that one allele was transmitted from the parents to their offsprings without any discrepancies indicating that the SSRs are controlled by a single locus.

Ten SSR loci are distinguishable in 18 peach cultivars (Table 3). The genetic identities (similarities) between 'Hakuto' and the other 17 peach cultivars were evaluated, based on the commonly observed SSR alleles (Table 4). The values of genetic identity ranged from 0 in 'Oucho Yuto' and 'Juseito' to 0.73 in 'Shanghai

Table 3. Genotypes of 18 peach cultivars analyzed using 10 SSR loci. SSR genotypes are denoted by a combination of 2 putative alleles indicated as their size (bp).

Cultivar name	SSR loci									
	M1a	M4c	M12a	M15a	MA007a	MA009b	MA010a	MA013a	MA014a	MA015a
Hakuto	80/80	78/94	195/195	136/136	121/133	130/130	124/124	197/213	163/167	178/263
Kinto	73/84	80/94	195/195	136/136	133/135	130/130	124/124	211/213	165/167	178/263
Shanghai Suimitsuto	80/84	80/94	195/195	136/136	121/135	130/130	124/124	211/213	163/167	263/263
Tenshin Suimitsuto	84/84	78/88	189/189	116/147	131/131	130/132	110/110	211/211	160/160	180/185
Feichangtao	84/84	80/80	177/177	116/136	111/111	161/161	110/126	207/209	150/160	185/185
Redhaven	84/84	90/94	197/197	116/136	111/111	132/132	124/124	197/207	150/163	185/187
Nectared 1	84/84	80/90	177/177	132/147	111/111	132/132	124/124	197/207	150/150	185/185
Independence	84/84	90/90	195/195	136/136	111/111	132/132	124/126	197/197	160/160	185/185
Ohatsumomo	84/84	80/80	177/177	147/147	111/111	130/130	122/122	207/207	175/175	184/184
Nagano Yaseito	73/80	80/88	177/177	147/147	131/131	130/161	110/122	207/207	150/150	184/185
Oucho Yuto	84/84	88/88	177/177	132/132	111/111	132/132	110/110	209/209	150/150	176/176
Kuto 1	84/84	88/88	185/185	136/138	131/131	132/132	110/110	213/213	150/150	184/184
Thai Yaseito	80/80	88/88	183/183	147/147	129/129	132/132	110/110	195/195	160/160	168/168
Akabana Banto	80/80	88/88	183/183	132/136	121/121	130/130	116/124	207/207	150/160	263/263
Kikumomo	80/86	88/88	179/183	132/132	131/133	130/132	120/120	207/207	160/160	185/185
Houkimomo	80/80	88/88	179/179	132/132	133/133	132/132	122/122	207/207	150/150	184/184
Swatow	84/84	84/84	185/185	147/147	127/127	130/130	124/124	197/197	167/167	184/184
Juseito	84/84	88/88	177/177	132/132	117/117	132/132	112/112	211/211	160/160	187/187

Suimitsuto', with an average of 0.23. The genetic identities of 'Shanghai Suimitsuto' and 'Kinto' are 0.73 and 0.65, respectively, thus are larger than those of the others. Because genetic identity is related to the ratio of common alleles, 'Shanghai Suimitsuto' and 'Kinto' have a very close genetic relationship to 'Hakuto'.

Native or very old introduced peaches 'Ohatsumomo', 'Nagano Yaseito' and 'Oucho Yuto' have the genetic identities of 0.08, 0.13 and 0 to 'Hakuto', respectively, indicating that no relationship exists between the 3 cultivars and 'Hakuto'. The ornamental flowering peaches, such as 'Akabana Banto', 'Kikumomo', 'Houkimomo', 'Swatow' and 'Juseito' are not closely related with 'Hakuto' because their genetic identities are less than 0.43. 'Tenshin Suimitsuto' and 'Feichangtao', which were chosen as representatives of different fruit peach groups in China, also did not show a close relationship with 'Hakuto'. 'Redhaven' peach and 'Nectared 1' and 'Independence' nectarines with values between 0.14 to 0.33 with 'Hakuto', indicate no close relationship. These data reveal that 'Shanghai Suimitsuto'

and 'Kinto' are genetically very close to 'Hakuto', whereas the other cultivars are not.

When SSR alleles of 'Hakuto' were compared with those of the other cultivars, the number of alleles shared with 'Hakuto' ranged from 0 in 'Oucho Yuto' and 'Juseito' to 10 in 'Shanghai Suimitsuto'. Only 'Shanghai Suimitsuto' possessed the same alleles as those of 'Hakuto' for all tested loci, suggesting a parent-offspring relationship between them. 'Kinto' shared 9 alleles in the 10 loci with 'Hakuto', indicating that it is genetically very close to 'Hakuto' but a parent-offspring relationship between them is questioned because of a discrepancy at the SSR M1a and the other 3 SSR loci (MA006b, MA027a and MA035a; data not shown).

Parentage analysis of Hakuto and Shanghai Suimitsuto

A total of 43 SSR markers, including 10 markers tested for 'genetic similarity between Hakuto and other cultivars', was used to determine whether a parent-offspring relationship exists between 'Hakuto' and 'Shanghai Suimitsuto'. Twenty SSR markers were poly-

Table 4. Peach cultivars used in this study and relationship between Hakuto and other 17 cultivars assessed by 10 SSR loci.

Cultivar name	Nature	Origin	Genetic identity with 'Hakuto'	Number of putative alleles shared with 'Hakuto'
Hakuto	cultivated fruit peach	Japan	—	—
Kinto	cultivated fruit peach	Japan	0.65	9
Shanghai Suimitsuto	cultivated fruit peach	China	0.73	10
Tenshin Suimitsuto	cultivated fruit peach	China	0.14	2
Feichangtao	cultivated fruit peach	China	0.07	1
Redhaven	cultivated fruit peach	USA	0.33	5
Nectared 1	cultivated fruit peach, nectarine	USA	0.14	2
Independence	cultivated fruit peach, nectarine	USA	0.31	4
Ohatsumomo	native peach	Japan	0.08	1
Nagano Yaseito	native peach	Japan	0.13	2
Oucho Yuto	native peach, nectarine	Japan	0.00	0
Kuto 1	native peach	Taiwan	0.15	2
Thai Yaseito	native peach	Thailand	0.08	1
Akabana Banto	flowering peach	Japan	0.43	6
Kikumomo	flowering peach	Japan	0.21	3
Houkimomo	flowering peach	Japan	0.16	2
Swatow	flowering peach	China	0.33	4
Juseito	flowering peach	China	0.00	0

Table 5. Genotypes of 'Hakuto' and 'Shanghai Suimitsuto' at 20 polymorphic or heterozygous SSR loci. Genotype at each locus is denoted as the size of 2 putative alleles (bp). Putative alleles of 'Hakuto' transmitted from its putative parent 'Shanghai Suimitsuto' are written in *italy*.

Cultivar name	M1a	M4c	M6a	MA004b	MA006b	MA007a	MA013a	MA014a	MA015a	MA017a
Hakuto	80/80	78/ <i>94</i>	193/197	85/87	295/295	121/133	197/213	163/167	178/263	165/165
Shanghai Suimitsuto	80/84	80/ <i>94</i>	193/197	85/85	295/297	121/135	211/213	163/167	263/263	165/173

Cultivar name	MA019a	MA020a	MA024a	MA026a	MA027a	MA030a	MA040a	MA051a	MA053a	MA056a
Hakuto	108/108	180/180	245/245	195/197	160/191	238/238	220/222	219/223	249/249	285/287
Shanghai Suimitsuto	106/108	172/180	234/245	197/199	153/191	236/238	220/222	219/223	234/249	275/285

morphic or heterozygous between the 2 peach cultivars. The other 23 SSR markers produced monomorphic discrete amplified fragments of the same size. The parentage of 'Hakuto' was analyzed, based on the inheritance of SSR alleles, assuming 'Shanghai Suimitsuto' to be its putative parent (Table 5). One allele was commonly observed in these 2 cultivars for all 20 polymorphic SSR markers. For example, the 80 bp allele at M1a, the 94 bp allele at M4c, the 85 bp allele at MA004b, the 295 bp allele at MA006b, and the 121 bp allele at MA007a were found in both 'Shanghai Suimitsuto' and 'Hakuto'. These results indicate that they have a strong parent-offspring relationship.

In humans, the probability for paternity (parentage) is based on the allele inheritance and frequency; less than 10 SSR markers are enough to confirm parentages (Hummel, 1971; Hashiyada et al., 1997; Katsumata et al., 2001). The parentages of several wine grapes, e.g., 'Cabernet Sauvignon', 'Chardonnay', and 'Gamay', have been identified by SSR analysis (Bowers and Meredith, 1997; Sefc et al., 1997; Bowers et al., 1999). In this study, the 20 polymorphic SSR markers (a total of 43 SSRs) used to examine the parentage between 'Shanghai Suimitsuto' and 'Hakuto' are sufficient to identify parent-offspring relationships.

The genetic diversity of cultivated peaches is very small as indicated by morphological characteristics, as well as its assessment by molecular markers such as RAPD (Random Amplified Polymorphic DNA), RFLP (Restriction Fragment Length Polymorphism) and AFLP (Amplified Fragment Length Polymorphism) (Chaparro et al., 1994; Rajapakse et al., 1995; Shimada et al., 2000). In our preliminary experiments, RAPD, RFLP and AFLP markers did not produce enough polymorphic bands between 'Shanghai Suimitsuto' and 'Hakuto' (data not shown). In contrast, about half of the SSR markers generated polymorphisms among the 2 cultivars so that they can be effectively utilized for parentage analysis in peach.

Origin of Japanese fruit peaches

The names of many fruit and ornamental peach cultivars were documented in the Edo period. Although these peaches were probably replaced by cultivars introduced from China and Europe about 100–150 years ago (Namikawa and Mizutani, 1989; Yoshida, 1991), their genetic relationships were not investigated. In this study, we used SSR markers to reveal that 'Hakuto' and not the native or ornamental ones is the parent or a closely related ancestor of the present Japanese peaches. 'Shanghai Suimitsuto' by its parent-offspring relationship to 'Hakuto' has the highest probability that it is the putative parent of the current peach cultivars out of a large number of introduced cultivars. This information will be utilized in the breeding programs for *Prunus persica*.

Acknowledgements

The authors are grateful to Drs. M. Yamaguchi, M. Yoshida, N. Matsuta and I. Ogiwara for their valuable suggestions. We are also grateful to T. Haji, H. Yaegaki, T. Imai, T. Kimura, I. Nakajima and T. Iida for their useful discussions and technical assistance.

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‘上海水蜜桃’は日本の生食用モモの起源品種の1つである

山本俊哉¹・持田耕平²・林 建樹¹

¹ 農業技術研究機構果樹研究所 305–8605 茨城県つくば市藤本

² 東京農工大学農学部 183–8509 東京都府中市幸町

摘 要

‘白鳳’、‘あかつき’を初め日本の生食用モモ品種のほとんどが、‘白桃’の子供もしくは‘白桃’に関連すると考えられている。しかしながら、‘白桃’の起源については不明であった。そこで本研究では、‘白桃’及び起源の異なるモモ品種について、10種類のSSRマーカーを用いて遺伝的類縁性の解析を行った。その結果、‘上海水蜜桃’と‘白桃’が遺伝的に近く、両品種に親子関係がある可能性が示唆された。一方、他の親候補である‘金桃’は、‘白桃’と遺伝的に近いことが示された

が、SSR対立遺伝子の遺伝子型に矛盾が観察されたことから両者間の親子関係は否定された。次に、‘白桃’と‘上海水蜜桃’の親子関係を43種類のSSRマーカーを用いて分析した。‘上海水蜜桃’を‘白桃’の親とした場合、すべてのSSR対立遺伝子が矛盾なく仮定親から子供に遺伝していた。これらの結果から、‘上海水蜜桃’が‘白桃’の親である可能性と、‘上海水蜜桃’が現在の日本の生食用モモの起源品種の1つであることが示唆された。