

## GENETIC RELATIONSHIPS OF JAPANESE POTATO CULTIVARS ASSESSED BY RAPD ANALYSIS

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### Abstract

Seventy-three breeding lines and cultivars, which included all Japanese cultivars, were assessed by random amplified polymorphic DNA (RAPD) analysis. Thirty-one of 40 decamer primers revealed 84 scorable RAPDs. Using these RAPDs, 67 of 73 cultivars were distinguished from each other. One of the cultivars released as a protoclonal variant was able to distinguish from the parent by increasing the number of primers surveyed. Based on the number of different RAPDs between each pair of accessions, cluster analysis was performed to exploit genetic diversity in Japanese cultivars. Closely related cultivars deduced from their pedigrees were clustered closely, indicating that similarities based on the presence vs. absence of RAPDs were reflections of genetic similarities. Old Japanese cultivars, as suggested by their similarity of chloroplast DNA to *S. tuberosum* ssp. *andigena*, were indeed clustered with ssp. *andigena* accessions, supporting these were relic cultivars of early European potatoes. The present study suggests that Japanese potatoes are an interesting mass of genetic diversity including North American, European, and Andean germplasm and relic potatoes.

### Compendio

Setenta y tres líneas de mejoramiento y cultivares, que incluyen a todos los cultivares japoneses, fueron determinados por el análisis del DNA polimórfico amplificado al azar (RAPD). Treinta y uno de 40 imprimadores decámeros revelaron 84 RAPDs posibles de marcar. Utilizando estos RAPDs, 67 de 73 cultivares fueron distinguidos unos de los otros. Uno de los cultivares liberados como una variante protoclonal fue distinguido del progenitor incrementando el número de imprimadores estudiados. Basándose en el número de diferentes RAPDs entre cada par de entradas, se llevó a cabo un análisis de grupos para aprovechar la diversidad genética en los cultivares japoneses. Los cultivares muy relacionados a juzgar por sus genealogías se encontraban bien agrupados, indicando que las similitudes basadas en la presencia o ausencia de RAPDs eran un reflejo de las simili-

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tudes genéticas. Los viejos cultivares japoneses, a juzgar por la similitud del DNA de sus cloroplastos a *S. tuberosum* ssp. *andigena*, estaban de hecho agrupados con las entradas de la ssp. *andigena*, apoyadas por los viejos cultivares de las primeras papas europeas. Este estudio sugiere que las papas japonesas son una masa interesante de diversidad genética incluyendo germoplasmas norteamericanos, europeos y andinos, y papas muy antiguas.

### Introduction

Genetic identities of cultivars and relationships among them are essential in maintaining germplasm and breeding new cultivars. Potato is widely adapted and thousands of cultivars have been released. Historically, many exotic germplasms were used in potato breeding to confer various disease resistances (24, 26). However, parentages of most cultivars could be traced back to Early Rose or its parental clone, Garnet Chili (24) and genetic variation might not be as broad as expected (18).

The potato was first brought into Japan in the early 17th century (16), but soon after, Japan closed its borders to the outer world for approximately two hundred years. In mid-19th century when it opened its doors again, North American and European cultivars were successively introduced (22). The present leading cultivars in Japan, *i.e.* Irish Cobbler and May Queen, are the result of early introductions. Potato breeding programs have been publicly organized in Japan since 1902. Inter-varietal and inter-specific hybridizations were first made in 1916 and in 1939, respectively. Until the present, approximately 40 cultivars have been officially released (19).

Hosaka (7) surveyed chloroplast DNA (ctDNA) of these released cultivars and those of unknown origin and found that Japanese potatoes had a similar history to European potatoes in terms of chloroplast DNA. And an interesting group of old Japanese cultivars, Murasaki-imo, Nemuro-murasaki, Rankoku 3 and Rankoku 5, were found to have A type ctDNA (7). The A type ctDNA is typically found in *Solanum tuberosum* ssp. *andigena*, an immediate ancestor of the potato, and was found in only the oldest European cultivar analyzed, Myatt's Ashleaf (8). Thus, the old Japanese cultivars were suggested to be relic potatoes of the early European introductions (7).

Random amplified polymorphic DNAs (RAPDs) (36) are PCR-based DNA markers detected by simple procedures, and have wide applicability in breeding and genetics (25). RAPD analysis has been used for cultivar identification in various crops including broccoli and cauliflower (11), rice (5), cocoa (33), celery (37), apple (14), and potato (1). Mori *et al.* (21) successfully identified all potato cultivars registered in Japan by the presence or absence of 13 RAPDs amplified by five decamer primers.

In the present study, all available Japanese potato cultivars including some breeding lines and some North American and European cultivars were analyzed by RAPD analysis and their genetic relationships are discussed.

## Materials and Methods

### *Cultivars Used*

Seventy-three cultivars and breeding lines including two accessions of *S. tuberosum* ssp. *andigena*, *i.e.* CIP 701624 (Amaccaya, Cuzco, Peru) and CIP 704082 (Malula, Potosi, Bolivia), were used in this study (Fig. 3). All cultivars registered in Japan were included except for Nemurobeni which was not available to this study. Red Echo and Yellow Shark were recently commercialized by Sakata Seed Co., and their parentages were not available. Shirobana-danshaku and Bansei-danshaku have been considered to be a white-flowered and a late-matured sport of Irish Cobbler (called Danshaku-imo in Japan), respectively. Neodelicious is an unregistered triploid cultivar originated from a cross between Early Rose and *S. phureja* (30). Red Andes is supposedly a synonym of Neodelicious. Jaga Kids Red '90 and Jaga Kids Purple '90 are protoclonal variants of Neodelicious (23). The above four cultivars are referred to as a Neodelicious series in this paper.

### *DNA Isolation, PCR and Electrophoresis*

Genomic DNA was isolated by the method of Doyle and Doyle (3). The procedures to obtain reproducible RAPD patterns have been optimized (10). Amplification reactions were performed in volumes of 10  $\mu$ l consisting of 10 ng of genomic DNA, 0.2  $\mu$ M primer, 10 mM Tris-Cl buffer (pH 8.3), 50 mM KCl, 2 mM MgCl<sub>2</sub>, 0.001% gelatin, 100  $\mu$ M each of dATP, dCTP, dGTP and dTTP (Takara, Kyoto, Japan), and 0.2 unit *Taq* DNA polymerase (TOYOBO, Osaka, Japan). Thermal cycling was carried out by a BioOven III (Biotherm Corporation, Arlington, VA, USA) set for one cycle of 1 min at 91.5 C, then 45 cycles of 5 sec at 91.5 C, 1 min at 36 C and 2 min at 72 C, followed by one cycle of 2 min at 72 C. Decamer primers used were listed in Table 1. Amplified DNA products were electrophoresed in 1.6% agarose (LO3, Takara) gels in TAE buffer (40 mM Tris-acetate and 1 mM EDTA) containing ethidium bromide. After electrophoresis, the gel was further stained by ethidium bromide (0.08  $\mu$ g/ml) for 30 to 40 min and photographed over UV light. Observations were made from photographs.

## Results

Seventy-three cultivars including named varieties, breeding lines, and two ssp. *andigena* cultivars were tested with 40 decamer primers. There was extensive variation in RAPD patterns among the accessions, in which amplified DNA fragments varied for presence vs. absence and also in their intensities (Fig. 1). Among them, the bands clearly segregating (presence vs. absence) in at least two accessions were regarded as RAPDs in the following text and scored (arrows in Fig. 1). Nine primers did not generate any scorable bands because of either monomorphic or complicated band-

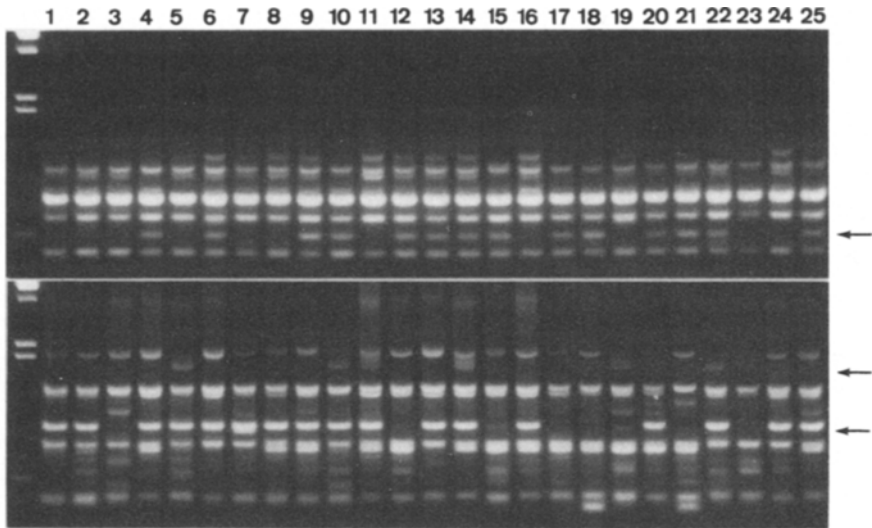


FIG. 1. RAPD patterns by the primers, No. 116 (upper panel) and No. 118 (lower panel). Lane 1 Early Rose, 2 Russet Burbank, 3 Bintje, 4 Irish Cobbler, 5 May Queen, 6 Tunika, 7 Benimaru, 8 Myojo, 9 Hokkaishiro, 10 Bifukashiro, 11 Bifukabeni, 12 Norin 1, 13 Norin 2, 14 Chitose, 15 Oojiro, 16 Unzen, 17 Tachibana, 18 Yoraku, 19 Niseko, 20 Rishiri, 21 Shimabara, 22 Eniwa, 23 Yukijiro, 24 Chijiwa, 25 Hokkai-aka. Scored bands are indicated by arrows. The left lane in each panel contains *Hind*III digested lambda DNA.

ing patterns. Each of the remaining 31 primers generated 1 to 6 scorable bands, or RAPDs, which totaled 84 RAPDs (Table 1).

Even using these 84 RAPDs, some cultivars were not discriminated from each other: Irish Cobbler and Shirobana-danshaku, Nemuro-murasaki and Murasaki-imo, and Rankoku 3 and Rankoku 5, and among the Neodelicious series. All others were clearly identified with at least six differences (between Early Rose and Russet Burbank). A further analysis using a total of 74 primers, however, did reveal a specific band which discriminated Jaga Kids Purple '90 from the parental clone, Neodelicious (Fig. 2).

The presence/absence of each RAPD was examined for the cultivars related as parent-progeny, *i.e.* Hokkaikogane, 70169-93, and 70169-115 (all from Toyoshiro x Hokkai 51), Konafubuki (Toyoshiro x WB66201-10), Oojiro (Irish Cobbler x Norin 1), Hatsufubuki (Irish Cobbler x WB61037-4), Kita-akari (Irish Cobbler x Tunika), and Toyo-akari (Tunika x WB61037-4). For example, 25 of 84 RAPDs were polymorphic among Toyoshiro, Hokkai 51, Hokkaikogane, 70169-93, and 70169-115 (Table 2, only scores of polymorphic RAPD bands are presented). Twenty-one RAPD bands were segregating in the  $F_1$ 's, while 2 RAPD bands were present in one of the parents, but not in the  $F_1$ 's. Thus, at least 23 RAPDs were of a heterozygous

TABLE 1.—*Decamer primers used and number of RAPDs scored.*

Primer No.	Sequence (5' to 3')	Source <sup>a</sup>	No. of RAPDs scored
1	TGGTCACTGA	1)	3
16	TTGTCACTGA	2)	1
21	TGGTCACCGA	2)	4
22	TGGTCACGGA	2)	2
27	TGGTCACTGC	2)	3
35	TGGTGAATGA	2)	1
38	TTGAGCCAG	3)(OPC-01)	4
39	GTGAGCGTC	3)(OPC-02)	3
41	CCGCATCTAC	3)(OPC-04)	2
46	CTCACCGTCC	3)(OPC-09)	3
51	TGCGTGCTTG	3)(OPC-14)	2
61	TCTGGTGAGG	3)(OPD-04)	2
68	AGCGCCATTG	3)(OPD-11)	2
72	CATCCGTGCT	3)(OPD-15)	3
73	AGGGCGTAAG	3)(OPD-16)	2
84	AGATGCAGCC	3)(OPE-07)	3
86	CTTCACCCGA	3)(OPE-09)	4
93	GGTGACTGTG	3)(OPE-16)	2
95	GGACTGCAGA	3)(OPE-18)	3
99	CAGGCCCTTC	4)(=OPA-01)	2
108	GGGTAACGCC	3)(OPA-09)	2
109	GTGATCGCAG	3)(OPA-10)	3
115	AGCCAGCGAA	3)(OPA-16)	3
116	GACCGCTTGT	3)(OPA-17)	3
118	CAAACGTCCG	3)(OPA-19)	2
121	TGATCCCTGG	3)(OPB-02)	2
123	GGACTGGAGT	3)(OPB-04)	6
125	TGCTCTGCCC	3)(OPB-06)	1
131	CCTTGACGCA	3)(OPB-12)	4
193	ACCAGGTTGG	3)(OPH-14)	4
231	GTCCCGTGGT	3)(OPJ-12)	3

<sup>a</sup>Primers were commercially synthesized by 1) Akitsu Keisoku and 2) TOYOBO, purchased from 3) Operon Technologies Inc. (primer identities given in parentheses), or 4) synthesized by Dr. K. Kosuge, Faculty of Science, Kobe University.

nature in the parents. Bands lacking in the parents were in no case present in their F<sub>1</sub>'s.

Russet Burbank and Irish Cobbler have been recorded as being descended from Early Rose via somatic mutations and/or line selections (24). However, these three varieties were quite distinct from each other (Table 2). Compared with Early Rose, 2 of 6 different RAPD bands were additional in Russet Burbank, and 4 of 15 different RAPD bands were additional in Irish Cobbler.

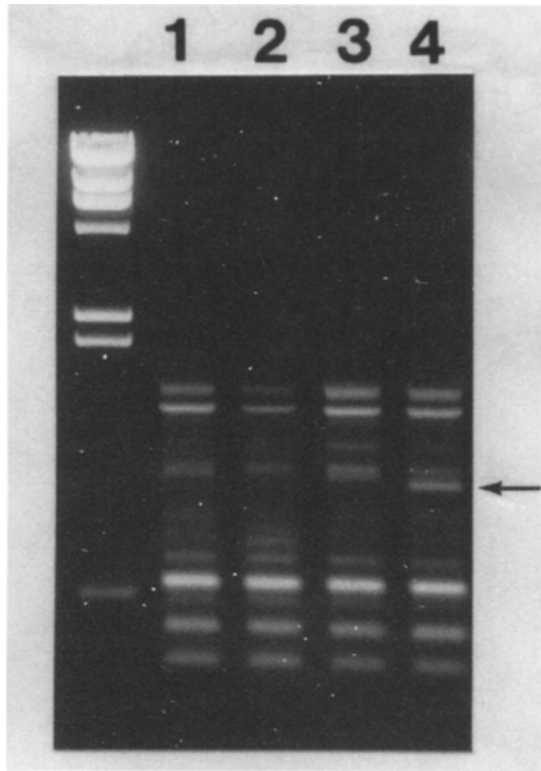


FIG. 2. RAPD patterns of clonally related cultivars by the primer No. 68. Lane 1 Neodelicious, 2 Red Andes, 3 Jaga Kids Red '90, 4 Jaga Kids Purple '90. The band indicated by the arrow distinguished a protoclonal variant, Jaga Kids Purple '90, from the source cultivar, Neodelicious. The left lane contains *Hind*III digested lambda DNA.

Based on the number of differences between each pair of accessions, cluster analysis was performed using Ward's method (32) (Fig. 3).

The cultivars used could be differentiated into three main groups. Group 1 (upper branch in Fig. 3) consisted of mainly Japanese cultivars, but also including Irish Cobbler and ND860-2. Group 2 (middle branch) consisted of many Japanese cultivars and most foreign varieties. Group 3 (lower branch) consisted of two subgroups; a Neodelicious series, Tunika and Musamaru were grouped in one subgroup. In the second subgroup, old Japanese cultivars, Murasaki-imo, Nemuro-murasaki, Rankoku 3 and Rankoku 5, were first clustered together and then clustered with *ssp. andigena* accessions.

The progenies with parent - progeny relationships (described above) were closely clustered together with either one of immediate parents. In many cases, the cultivars with close pedigrees clustered closely: for example,

TABLE 2.—RAPD scores of *Toyoshiro*, *Hokkai 51* and their  $F_1$ 's, and those of *Early Rose*, *Russet Burbank* and *Irish Cobbler*. Only those showing polymorphisms among given cultivars are presented.

Cultivars	Score of RAPDs <sup>a</sup>
<i>Toyoshiro</i> ( <i>Female parent</i> )	1001111101011111011111100
<i>Hokkai 51</i> ( <i>Male parent</i> )	1110111111110001100010011
<i>Hokkaikogane</i> ( $F_1$ )	1111110011010011010011111
70169-93 ( $F_1$ )	0000001110001101010010000
70169-115 ( $F_1$ )	1110011111001110011100100
<i>Early Rose</i>	01111110110110111011
<i>Russet Burbank</i>	01111101110001111001
<i>Irish Cobbler</i>	10000010001111000110

<sup>a</sup>presence (1) or absence (0).

Unzen and Tachibana (Norin 1 x Katahdin), Dejima (Hokkai 31 x Unzen), Setoyutaka (Saikai 10 x Unzen), and Nishiyutaka (Dejima x Choukei 65) were clustered together.

## Discussion

### *Cultivar Identification*

Eighty-four RAPDs were able to differentiate 67 of 73 accessions used in this study. Mori *et al.* (21) identified 39 Japanese potatoes by as few as 13 RAPDs amplified using 5 primers. Thirty-six North American cultivars were successfully identified using only two primers (1). These results suggest that RAPD analysis is a powerful tool for cultivar identification in potato.

Natural somatic mutations commonly occur in potato and selection for the new characteristics has given rise to clonal variants. This study supported that Shirobana-danshaku was truly a sport of Irish Cobbler, since no differences were found between them. But, Bansei-danshaku, also recorded as a sport of Irish Cobbler, was apparently different from Irish Cobbler. This was probably misrecorded, as open-pollinated berries are often found in potato fields either by selfing or natural hybridization. Since some of RAPD bands present in Bansei-danshaku were not found in Irish Cobbler and the latter is pollen sterile, selfing is not a likely explanation for the deviation of Bansei-danshaku from Irish Cobbler. Alternatively, hybrid origin could be proposed for Bansei-danshaku.

Russet Burbank has been recorded as a sport of Burbank which was derived by line selection from open-pollinated berries of Early Rose. Irish Cobbler has been recorded as a sport of Early Rose (24). However, Douches

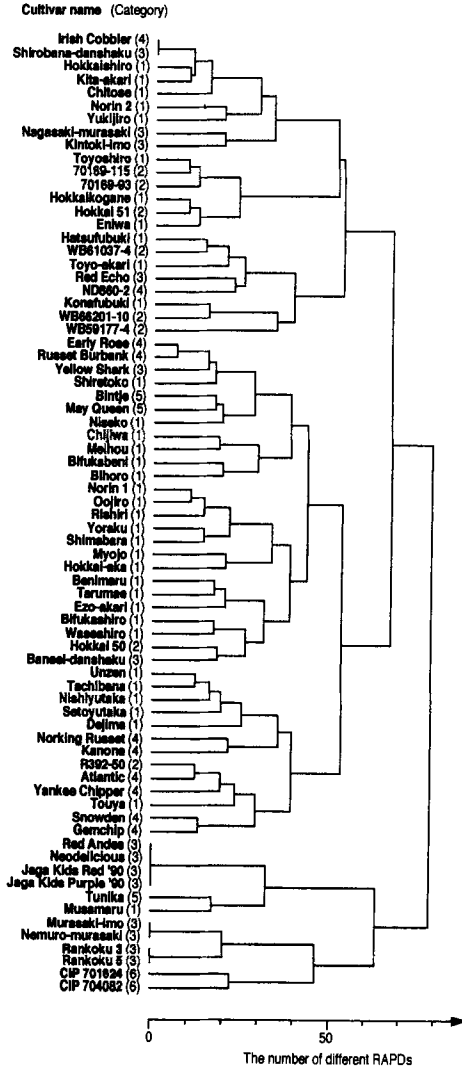


FIG. 3. Relationships among potato varieties and breeding lines disclosed by cluster analysis based on the number of different RAPDs. Cultivars are categorized as; (1) varieties officially released in Japan, (2) breeding lines in Japan, (3) others in Japan, (4) North American varieties, (5) European varieties, and (6) *Solanum tuberosum* ssp. *andigena*.



*et al.* (2) found quite distinct electrophoretic patterns of isozymes for Irish Cobbler, and thus, concluded its origin to be unknown. They also found additional allozymes in Burbank when compared with Early Rose and proposed its hybrid origin with an unknown cultivar (2). Their proposals are strongly supported by the present study, since some additional bands were identified in Russet Burbank and Irish Cobbler.

Neodelicious was not discriminated from Red Andes and its protoclonal variants, even using the 84 RAPDs. This confirmed that Red Andes is synonymous with, or a sport of Neodelicious. Demeke *et al.* (1) reported that some of clonal variants were discriminated from the parental clones by increasing the number of primers surveyed. In fact, further detail comparisons between Neodelicious and Jaga Kids Purple '90 disclosed a polymorphic band, which demonstrated a high sensitivity of RAPD analysis for cultivar discrimination.

#### *Genetic Diversity in Japanese Potatoes*

As shown by a dendrogram in Fig. 3, genetically related cultivars according to the pedigrees were generally clustered closely together. The closest relationships were found among cultivars with almost identical genetic background, *i.e.* synonyms, sports and protoclonal variants, which showed similar RAPD patterns. Cultivars selected by line selections or those derived by hybridization were closely clustered with each other. Therefore, similarities based on the presence vs. absence of RAPDs reflect genetic similarities and are useful for estimating genetic relationships, as demonstrated in *Allium* species (34), *Brassica* species (15), cereal crop species (4), papaya (28), spring barley (29), tomato (35), and diploid and tetraploid wheat (13, 31).

Recent North American cultivars, except ND 860-2, were all clustered in one branch in Group 2, suggesting their close relationships. This might partly result from the small number of samples and may even be biased by sampling only from processing potatoes. Mendoza and Haynes (18) indicated poor genetic diversity in North American potatoes. Recently released U.S. cultivars all contain to some extent exotic germplasm in their pedigrees (24); however, at least for processing potatoes, their genetic diversity seems to be less broad.

Although recent North American cultivars were in a single branch, they were not distinct from Japanese cultivars, as preliminarily reported by Hosaka and Ogawa (9). Group 1 and Group 2 in Fig. 3 are unable to be uniquely characterized according to the pedigrees because their genetic backgrounds are considerably intermixed. Cultivars once released were then used as parental lines and foreign cultivars were also prominently used in Japanese

breeding programs. Among 36 released cultivars, the foreign cultivars used as immediate parents are as follows: Irish Cobbler (in 8 cultivars), Pepo (5), Tunika (4), Hochprozentige (2), Katahdin (2), L. F. Rosen (1), Deodara (2), Mirabilis (1), Gineke (1), Kennebec (1), and Priekulsky Ranny (1). Further, wild germplasm has been successively incorporated into breeding lines (12), broadening genetic diversity of Japanese cultivars.

The third main group, Group 3, seems to be a more consistent group. According to the pedigree, one-third of genetic information in Neodelicious was derived from Andean cultivated diploid species, *S. phureja* (30). Tunika was introduced recently from Germany, and registered for the area suffering severe damage by cyst nematode (20), because it has the cyst nematode resistant gene (H1) derived from *S. tuberosum* ssp. *andigena* (26). Musamaru was bred by Tunika x Kon-iku 20 (17). Old Japanese cultivars, as discussed later, could be immediate descendants of ssp. *andigena*; thus, Group 3 could be characterized by introgression from Andean cultivated potatoes.

Therefore, it is suggested that Japanese potatoes, as a whole, are an interesting mass of genetic diversity including early European or relic potatoes to the most advanced cultivars harboring Andean germplasm, and those featured by the 19th century cultivar, Irish Cobbler.

#### *Old Japanese Cultivars*

The potato first brought from South America to Europe was ssp. *andigena* (6, 8, 27), which was introduced to Japan in the early 17th century (16). Based on chloroplast DNA analysis, four old cultivars, Murasaki-imo, Nemuro-murasaki, Rankoku 3 and Rankoku 5, were proposed to be derived from the early Japanese potatoes because of their ctDNA type having a typical ssp. *andigena* type, A type ctDNA (7). These old cultivars were clearly separated by RAPD analysis from the other cultivars and showed close relationships with ssp. *andigena*. This strongly supports that these cultivars are relic potatoes of early European introduction, having characteristics of ssp. *andigena* in common. Speculating from their cultivar names of Rankoku 3 and Rankoku 5, they might be selfed progenies from the same parent, siblings, or even sports. This was supported by the RAPD data showing no difference between them. Murasaki-imo and Nemuro-murasaki, collected as local varieties from central Japan and Hokkaido, respectively, were indistinguishable by RAPDs. All four cultivars have purple skin tubers in common. Morphological observations indicated that Rankoku 3 resembled Rankoku 5 and Murasaki-imo resembled Nemuro-murasaki. All these data might indicate that these old cultivars could be all descended from a few clones, or maybe one, introduced from Europe in early 17th century. It is likely that subsequent cultivar differentiation in Japan before the introduction of foreign cultivars in mid-19th century resulted from line selection of open-pollinated selfed berries or from somatic mutations.

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