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The Extent of Intersubgeneric Cross Compatibility between Japanese Plum (*Prunus salicina* Lindl.) and Peach (*P. percica* Batsch.)

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Intersubgeneric crosses between seven peach cultivars and 22 Japanese plum cultivars were carried out to produce intersubgeneric hybrid plants that were expected to have potential for new fruit cultivars and rootstocks for peach. No hybrid plants were derived from peach × plum crosses, whereas many hybrid plants were derived from the reciprocal intersubgeneric crosses. Among the plum cultivars pollinated with peach cultivars, 'Jinsanto', 'Formosa', 'Kasaharahatankyo', 'Oishiwase' and 'Manzaemon' showed high fruit set rates of more than 30%. The rates of harvested fruits in the nine crosses ranged from 5.4% to 25.4%. The rates of perfect seeds ranged from about 70% to 90% as observed in open-pollinated plum cultivars. In comparison between open pollination and pollination with 'Hakuho' pollen, the size of embryos was almost same in 'Yuko' and 'Oishiwase' and slightly small in 'Sordum' pollinated with 'Hakuho'. All of the perfectly developed embryos and some of the imperfectly developed embryos germinated and grew up to seedlings. The leaves of seedlings showed intermediate shapes between their parental peach and plum cultivars. Flower bud formation occurred in the intersubgeneric hybrid plants. However, most of the hybrid plants did not flower because of underdevelopment of the flower buds. All flowers developing in a few hybrids showed very abnormal morphology and dropped immediately after the anthesis. The meiotic products in the anthers were irregular and showed high sterility.

INTRODUCTION

Many cultivars of genus *Prunus* belong to three subgenera, *Microcerasus, Amygdalis* and *Prunophora*, which produce various interspecific hybrids within the subgenera (Layne and Sherman, 1986). Japanese plum (*Prunus salicina* Lndl.) belongs to *Prunophora* but the leading cultivars in Japan are complex intrasubgeneric hybrids between *P. salicina* located in Japan and *Prunus* species located in North American (e.g. *P. americana* Marsh.), southern east China (*P. simonii* Carr.) and Caucasus (e.g. *P. ceracifera* Ehrh.) (Yamaguchi, 1991). Almost all of these interspecific hybrid plum cultivars, except for those with *P. ceracifera* in their pedigree, are highly fertile and produce fruits with perfect seeds in open field (Wakana, 2005a), since the plum plants consisting of 24 species (Hedrich, 1911) are cross compatible and genetically very close in every aspects (Yoshida, 1984).

Peach cultivars consist of one species *P. percica* belonging to *Amygdalis* (Hesse, 1975), and is a major fruit tree in *Prunus*, because of the superior fruit characteristics such as high quality, very large size, long-term preservation and suitability for processing. However, cultivation of peach cultivars is relatively difficult in Japanese open field conditions because they are less tolerant to diseases and insects under humid Japanese conditions. Seedlings of local or native peach varieties such as 'Kataishimomo' and 'Ohatsumomo' are used for rootstocks of peach cultivars cultivated in Japan. These peach rootstocks show low water resisting property and low excess water tolerance as observed in scion preach cultivars. Compared with peach, Japanese plum cultivars including interspecific ones adapt to Japanese humid conditions and show high property and tolerance as to the two characters. Hence, the interspecific hybrid plants between the peach and Japanese plum are expected to be tolerant to the two characters and available as rootstocks for peach cultivars. In addition, interspecific hybrid plants between self-incompatible Japanese plum and self-compatible peach are highly expected to exhibit self-compatibility.

In spite of these superior characteristics expected for interspecific hybrids between peach and Japanese plum, there are only a few reports of the interspecific hybrids (Hesse, 1975; Bernhard *et al.*, 1979; Yoshida, 1984; Parfitt *et al.*, 1985), probably because of the difficulty of their hybridization and less useful hybrid characters such as variation of tree vigor and low fertility due to the unite of different two genomes by distant hybridization. With recent advances of micropropagation techniques in *Prunus* (Dimassi-Theriou, 1995; Fotopoulos and Sotiropoulos, 2005), however, establishment of appropriate interspecific rootstocks become possible. In addition to this, production of amphidiploids of the interspecific hybrids may increase the reproductive ability and tree vigor.

The objectives of this study are (1) to demonstrate the degree of reciprocal cross compatibility between various Japanese plum and peach cultivars, (2) to observe the degree of vigor in the hybrids and (3) to

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estimate the degree of reproductive ability in the interspecific hybrids

MATERIALS AND METHODS

Seven peach (*Prunus persica* Batsch.) cultivars and 28 plum cultivars listed in Table 1 were used for interspecific crossings between peach and plum. Of 28 plum cultivars, 10 are pure Japanese plum (*P. salicina* Lindl.), 15 are interspecific hybrids between *P. salicina* and North American species (*P.* spp.), two ('Mesley' and 'Hollywood') were those between *P. salicina* and European species (*P. ceracifera* Ehrh.) and one ('Ocelot') is myrobalan or cherry plum (*P. ceracifera* Ehrh.). 'Rose Plum' and 'Santa Rosa' are same cultivar with different name as well as 'Oishiwase' and 'Yoko'. All of these cultivars were ten– to fifteen–year–old trees grown in the Sasaguri orchard of the Kyushu University Farm, Fukuoka.

Table 1. Japanese plum cultivars used and their genetic backgrounds.

Plum and Hybrid group	Species background	Cultivar
Japanese	*P. salicina*	Jinsanto, Kasaharahatankyo, Manzaemon, Yonemomo, Yamaguchi, Honsumomo, Karari, Jinno-uchi, Ichinari, Nishida, Kelsey
Americana hybrid	*P. salicina* *P. americana* *P. simonii* *P. angustifolia*	Formosa, Oishiwase, Yoko, Beauty, Toward, Rose Plum, Santa Rosa, Summer King, Ozark Premier, White Queen.
Myrobalan	*P. ceracifera*	Ocelot
Myrobalan hybrid	*P. salicina* *P. ceracifera*	Methley, Hollywood
Unknown hybrid	*P. salicina* *P. simonii ?* *P. americana ?*	Sordum, Late Sordum, White Plum

Intersubgeneric crosses between peach and Japanese plum

Japanese plum × peach

To determine the plum cultivars that set fruits with high frequencies, thirty–one intersubgeneric crosses between twenty–two plum and two peach cultivars were carried out with plum cultivars as seed parents. Secondly, seven inter–subgeneric crosses between four peach and four plum cultivars were carried out with Japanese plum cultivars as seed parents to produce the hybrid seedlings. Before emasculation, flower buds were adjusted at the rate of one flower bud per about 25 leaves in each interspecific cross to enhance embryo development (Wakana *et al.*, 2005b). About 60 to 500 flower buds were emasculated one or two days before anthesis and pistils with wet stigma and normal morphology were chosen. Pollination was made with fresh pollen collected from just opened flowers of the pollen parents. Immediately after the pollination, the pollinated flowers were bagged to prevent further crosses.

The pollinated fruits were harvested at the ripening stage (June–July) in each cross. Seeds were excised from the fruits and their seed coats were removed. The embryos (seeds) derived were divided into three categories according to their development, i.e., perfectly developed (perfect seed), imperfectly developed (imperfect seed) and none (empty seed). All the embryos were planted on wet filter paper laid on the bottom of lidded plastic boxes and incubated under 25 °C conditions. Germinated embryos were planted and grew on the pot for one year under a green house, and then transplanted to open field. To certify the hybridity of plum–peach hybrid seedlings, leaf morphology was visually observed in the hybrids and their parents.

Peach × Japanese plum

Firstly, about 30 to 70 flower buds were emasculated in each of seven peach cultivars and pollinated with 'Oishiwase' just before anthesis. Second, 40 to 70 emasculated flowers of 'Hakuho' were use for each cross with 15 Japanese plum cultivars and Myrobalan plum 'Ocelot'. The pollen was collected from just–opened flowers that were bagged before anthesis. Fruit set was examined 35 days after pollination and at the maturation stage of peach.

Back crosses with a plum–peach hybrid

An interspecific hybrid plant SH8401 derived from 'Sordum' × 'Hakuho' was used as a pollen parent for crossing to three peach and eight Japanese plum cultivars. Pollination was carries out as described above. Fruits were harvested at the ripening stage and the seeds were examined similarly.

Cytological observation of meiosis in plum–peach hybrids

Flower buds of interspecific hybrids from Japanese plum × peach crosses were collected from February to March. They were immediately fixed acetic acid alcohol (3:1 v/v) for several hours, translated into 70% ethyl alcohol and stored in 4 °C until use. The anthers were excised from the flower buds, cut into small peaces on the glass slide with one drop of acetocarmin solution, covered with a small peace of glass cover and observed the meiosis and meiotic products with a microscope.

RESULTS

Fruit set rates in Japanese plum × peach crosses

The fruit set rates at 35 days after pollination ranged from 42% to 4% for plum × 'Hakuho' crosses and from 29% to 4% for plum × 'Rikaku' crosses (Fig. 1). Among the plum cultivars pollinated with 'Hakuho', 'Jinsanto', 'Formosa', 'Kasaharahatankyo' and 'Manzaemon' showed high fruit set rates of more than 30%, while 'Ocelot', 'Hollywood', 'Nishida', 'Kelsey', 'Rose Plum' and 'Santa Rosa' showed low rates of less than 7%. Among the plum cultivars pollinated with 'Rikaku', 'Formosa' and 'Oishiwase' showed high fruit set rates of about 30%, while 'Jinsanto', 'Ocelot' and 'Santa Rosa' showed less

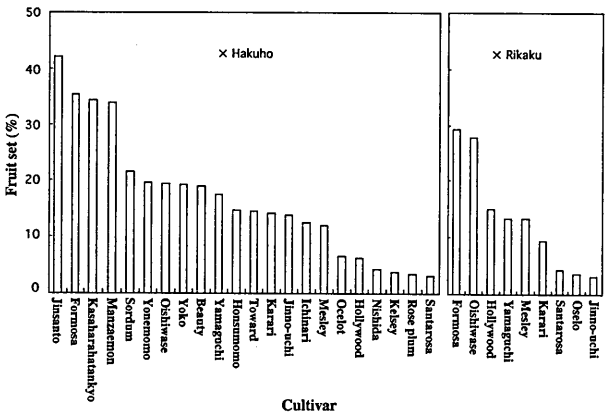

Fig. 1. The fruit set rates in Japanese plum cultivars pollinated with 'Hakuho' (left) and 'Rikaku' (right).

than 5% fruit set rates. The fruit set rates of the other cultivars ranged from 10% to 20% in the both crosses with 'Hakuho' and 'Rikaku'.

Based on the results of fruit set rates in Japanese plum × peach crosses, 'Jinsanto', 'Oishiwase', 'Sordum' and 'Yoko' were used for further nine crosses with four peach cultivars to produce interspecific hybrids. The rates of harvested fruits in the nine crosses ranged from 5.4% to 25.4% and those in 'Oishiwase' × 'Hakuho' and 'Yoko' × 'Hakuho' crosses showed year-to-year variation (Table 2).

Fruit set rates in peach × Japanese plum crosses

The fruit set rates of peach cultivars at 35 days after pollination with 'Oishiwase' were 31.8% for one cross with 'Sunagowase' and 0% for the other six crosses with six peach cultivars (Table 3). In the one cross, however, all the fruits dropped soon after the 35 days. The fruit set rates of 'Hakuho' at 35 days after pollination with 16 plum cultivars were 0% in 12 crosses and about 2% in four crosses with pollen of 'Jinno-uchi', 'Manzaemon', 'Toward' and 'Yonemomo' (Table 4). In the four crosses, however, all the fruits dropped soon after the 35 days.

Extent of embryo development in Japanese plum × peach crosses

In comparison between open pollination and pollination with 'Hakuho' pollen, the size of ripened fruits was almost same in 'Yuko', slightly small in 'Oishiwase' pollinated with 'Hakuho' and small in 'Sordum' pollinated with 'Hakuho' (Fig. 2). In all crosses, except for 'Sordum' × 'Hakuho' cross, the rates of perfect seeds ranged from about 70% to 90% as observed in open pollination and pollination with plum cultivars (Table 2). The 'Sordum' × 'Hakuho' cross produced about 50% of perfect seeds and also produced imperfect and empty seeds in relatively high frequencies. In comparison between open pollination and pollination with 'Hakuho' pollen, the size of embryos was almost same in 'Yuko' and 'Oishiwase' and slightly small in 'Sordum' pollinated with 'Hakuho' (Fig. 3). All of the perfectly developed embryos and some of the imperfectly developed embryos germinated and grew up to seedlings. The leaves of seedlings showed intermediate shapes between their parental peach and plum cultivars.

Fertility of plum-peach hybrid

Flower bud formation occurred in all the intersubgeneric hybrid plants. However, most of the hybrid plants did not flower, since almost all of the flower buds did not develop out of the scales and dropped at the flowering season (Table 5). All flowers developing in only seven hybrid plants showed very abnormal morphology such as bi-pistil with two short styles, pistilody of stamen and underdevelopment of anthers, and dropped immediately after the anthesis. Observation of

Table 2. The fruit set rates and the degree of embryo development in intersubgeneric crosses between Japanese plum and peach cultivars.

Cross	Year	No. of flowers pollinated	No. of fruits harvested (%)	No. of seeds in indicated degree of seed development			
				Perfect (%)	Imperfect	Empty	Total
Jinsanto × Hakuho	1986	100	13 (13.0)	12 (92.3)	0	1	13
Oishiwase × Akatsuki	1985	59	15 (25.4)	13 (86.7)	0	2	13
Oishiwase × Hakuho	1984	280	39 (13.9)	34 (87.2)	2	3	39
Oishiwase × Hakuho	1985	316	17 (5.4)	14 (82.4)	3	0	17
Oishiwase × Shuho	1985	400	26 (6.5)	20 (76.9)	2	4	26
Oishiwase × Saotome	1985	384	23 (6.0)	18 (78.3)	0	5	23
Sordum × Hakuho	1984	437	42 (9.6)	22 (52.4)	9	11	42
Yoko × Hakuho	1984	230	30 (13.0)	25 (71.4)	2	3	30
Yoko × Hakuho	1985	294	12 (4.1)	10 (83.3)	0	2	12
Jinsanto × Santa Rosa	1986	–	76	69 (90.8)	3	4	76
Jinsanto × open pollination	1986	–	57	41 (71.9)	16	1	58
Oishiwase × Elephant Heart	1986	–	24	21 (87.5)	0	3	100
Oishiwase × open pollination	1983	–	100	67 (67.0)	26	7	100
Oishiwase × open pollination	1984	–	100	73 (73.0)	21	6	100
Sordum × open pollination	1984	–	110	88 (80.0)	16	6	110
Yoko × open pollination	1984	–	100	88 (88.0)	12	0	100

Table 3. The rates of peach fruits setting 35 days after pollination with Japanese plum 'Oishiwase'.

Cultivar	No. of flowers pollinated	No. of fruits setting (%)	No. of fruits harvested
Saotome	32	0	0
Rikaku	50	0	0
Hakuho	49	0	0
Sunagowase	44	14 (31.8)	0
Kurakatawase	38	0	0
Hakuto	47	0	0
Minoshimahakuto	71	0	0

Table 4. The rates of 'Hakuho' fruits setting 35 days after pollination with Japanese plum cultivars.

Pollen parent	No. of flowers pollinated	No. of fruits setting (%)	No. of fruits harvested
Beauty	46	0	0
Hollywood	40	0	0
Honsumomo	54	0	0
Ichinari	48	0	0
Jinnouchi	49	1 (2.0)	0
Jinsanto	49	0	0
Manzaemon	56	1 (1.8)	0
Methley	27	0	0
Nishida	63	0	0
Oselo	52	0	0
Rose Plum	51	0	0
Santa Rosa	53	0	0
Sordum	45	0	0
Toward	70	1 (1.4)	0
Yamaguchi	62	0	0
Yonemomo	57	1 (1.8)	0

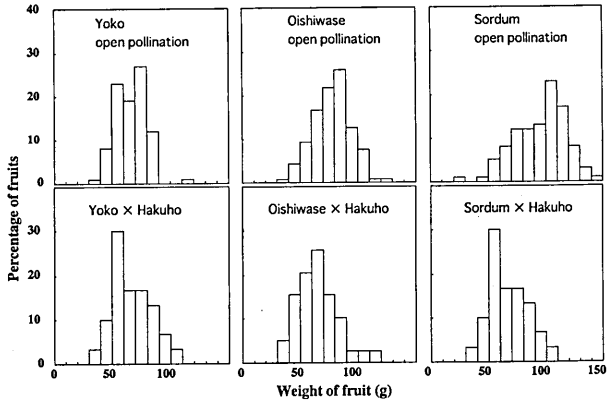

Fig. 2. Comparison of frequency distribution of fruit weight between fruits derived from open pollination and those from pollination with 'Hakuho' in three Japanese plum cultivars.

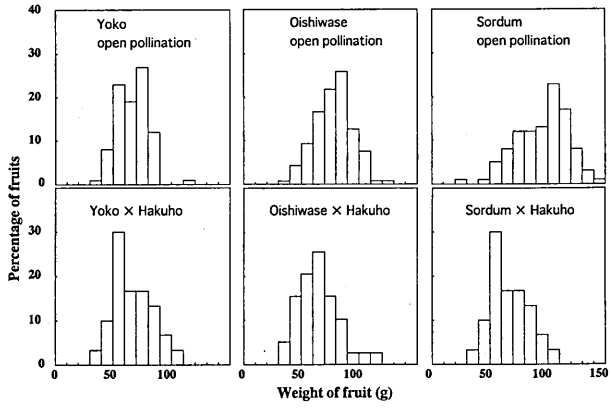

Fig. 3. Comparison of embryo length between embryos derived from open pollination and those from pollination with 'Hakuho' in Japanese plum cultivars.

Table 5. The degree of flower bud development and abnormality of flowers in interspecific hybrid seedlings derived from Japanese plum × peach cultivar crosses.

Cross	No. of seedlings examined	No. of seedlings flowering	No. of flowers and abnormal morphology of pistils
Yoko × Hakuho	11	1	a few small flowers with two short pistil
Oishiwase × Hakuho	19	1	many large flowers with one short pistil
		2	a few small flowers with two short pistil
Oishiwase × Saotome	11	0	
Oishiwase × Nunomewase	9	1	a few small flowers with two short pistil
Oishiwase × Miyako Hakuho	8	2	a few small flowers with two short pistil
Oishiwase × Shuho	3	0	
Oishiwase × Akatsuki	1	0	
Sordum × Hakuho	1	1	many small flowers with two short pistil
Beauty × Hakuho	1	1	many unopened flowers with undeveloped petals; pistilody of stamens
Jinsanto × Hakuho	1	0	
Jinsanto × Saotome	1	0	

Table 6. Frequency distribution of pollen mother cells dividing into different number of cells at the tetrad stage of meiosis in interspecific hybrid plants between Japanese plum and peach cultivars.

Hybrid seedling	No. of pollen mother cells (%) dividing into indicated cells at the tetrad stage of meiosis					
	4 (uniform)	4 (non-uniform)	5	6	7	Total
Sordum×Hakuho No. 1	27 (45.8)	7 (11.9)	3 (5.1)	10 (16.9)	0 (0)	59
Oishiwase×Hakuho No. 1	165 (64.5)	7 (2.7)	58 (22.7)	23 (9.0)	3 (1.2)	256

Table 7. Result of crosses of peach and Japanese plum cultivars with pollen of peach-plum hybrid SH-8401 (Sordum × Hakuho).

Seed parent	No. of flowers pollinated	No. of fruits obtained (%)	No. of seeds in indicated degree of seed development (%)			
			Perfect	Imperfect	Empty	Total
Peach						
Saotome	59	0 (0)	–	–	–	–
Shuho	72	1 (1.4)	0	0	1	1
Flavor Gold	56	0 (0)	–	–	–	–
Japanese plum						
Methley	24	1 (4.2)	0	0	1	1
Ozark Premier	8	0 (0)	–	–	–	–
Summer King	26	0 (0)	–	–	–	–
White Queen	54	0 (0)	–	–	–	–
Late Sordum	60	0 (0)	–	–	–	–
Yoko	30	2 (6.7)	0	0	2	2
Oishiwase	38	0 (0)	–	–	–	–
White Plum	50	0 (0)	–	–	–	–

meiosis in the pollen mother cells indicated frequent occurrence of univalent chromosomes and irregular meiotic products in the anthers (Table 6).

Only one fruit was harvested from crosses between three peach cultivars and peach–plum hybrids SH–8401 ('Sordum' × 'Hakuho') and only three fruits were harvested from the crosses between eight Japanese plum cultivars and SH–8401 (Table 7). However, all the seeds derived from the fruits were empty.

DISCUSSION

The present study indicates that no high intersubgeneric cross incompatibility exists in Japanese plum (including its interspecific hybrid cultivars) × peach crosses and that very high or perfect intersubgeneric cross incompatibility exists in the reciprocal crosses. In the peach × Japanese plum crosses, only a few fruits set 35 days after pollination, but they dropped immediately after the days and had not seeds. This suggests that the fruits were parthenocarpic and no fertilization occurred in the ovules. Unilateral interspecific cross incompatibility similar to the present crosses are known to occur in *Prunus* (Lewis and Crowe, 1958; Perez and Moore, 1985; Layne and Sherman, 1986; Kataoka *et al.*, 1988). Perez and Moore (1985) stressed that difference in pistil length and in pollen tube growth rate among species provide a sound basis for explaining the phenomenon of unilateral incompatibility in *Prunus*. On the other hand, Layne and Sherman (1986) emphasized that in attempting interspecific *Prunus* hybrids, it appears best to use the self-compatible species as the seed parents and the self-incompatible ones as the pollen parent, thereby avoiding unilateral interspecific incompatibility. In the present intersubgeneric crosses between peach and Japanese plum, however, neither relation of intersubgeneric cross incompatibility to self-incompatibility nor to pistil length and pollen tube growth rate is recognized. Pollen tube growth in both of the peach and plum styles are almost normal (data not presented), suggesting intersubgeneric barrier exits in the ovary of peach but not in the embryo sac. Arbeloa and Herrero (1987) suggested the importance of obturator in controlling of pollen tube entry into the ovary of peach, i.e., the pollen tubes reached to the obturator locating in the upper position of ovary stopped their growth for five days, since secretion from the obturator started five days after the pollen tube arrival. The starvation of pollen tubes for five days on the obturator should be especially lethal for those developing from small pollen grains of Japanese plum and its interspecific hybrid cultivars. The fact that there are no reports of success in intersubgeneric crosses with peach as seed parents strongly supports this hypothesis

The intersubgeneric hybrid seedlings derived from Japanese plum × peach crosses grew normally, but they showed very high degree of sterility and abnormality in reproductive behaviors. This result suggests that plum and peach genomes are very different each other and the intersubgeneric hybrid plants can not use directly

for breeding of cultivars producing new types of fruits, although effectiveness of them as root stocks for peach cultivars is unknown at present. In such cases, generally, amphidiploids of the intersubgeneric hybrid plants may recover their fertility and productivity. Hence, further studies on the estimation of ability of the hybrid plants as rootstocks and chromosome doubling of them are necessary for their usage in breeding and cultivation.

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