

Inheritance of Resistance to Loquat Canker (Group C) in Progenies Derived from ‘Shiromogi’ Loquat

Naofumi Hiehata⁵, Yoshihiko Sato¹, Shinji Fukuda, Yukiko Tominaga², Osamu Terai³, and Hirohisa Nesumi⁴

Fruit Tree Research Division, Agricultural and Forestry Technical Development Center, Nagasaki Prefectural Government, Omura, Nagasaki 856-0021, Japan

ADDITIONAL INDEX WORDS. *Eriobotrya japonica*, breeding, single gene, recessive trait, bacterial disease

ABSTRACT. Loquat canker (*Pseudomonas syringae* pv. *eriobotryae*) is a serious disease of loquat (*Eriobotrya japonica*), and no commercial cultivar in Japan is resistant to all strains of the disease. Loquat cultivar Shiromogi, which was selected from progeny seedlings of ‘Mogi’, is resistant to loquat canker Group C and has good fruit characteristics. This study was conducted to determine the inheritance of resistance to loquat canker Group C in ‘Shiromogi’. Seedlings produced from crosses between two resistant and 13 susceptible genotypes were classified as either resistant (R) or susceptible (S) based on the appearance of black–brown cankers ≈2 months after inoculation with a bacterial suspension of loquat canker Group C. Cross combinations between resistant parents ‘Champagne’ and ‘Shiromogi’ and selfing of ‘Shiromogi’ produced all resistant seedlings. Most crosses between ‘Shiromogi’ and susceptible parents either produced only susceptible seedlings or segregated for resistance in a ratio of 1 R:1 S. Seedlings produced by selfing two of the susceptible parents segregated in a ratio of 1 R:3 S. These results indicate that the resistance to loquat canker Group C of ‘Shiromogi’ is conferred by a single recessive gene, designated *pse-c*. Based on the crossing tests, we conclude that resistant parents ‘Shiromogi’ and ‘Champagne’ are homozygous for *pse-c*; the susceptible parents ‘Fukuharawase’, ‘Fusahikari’, ‘Gold Nugget’, ‘Kusunoki’, Nagasaki No. 2, ‘Tanaka’, ‘Tsukumo’, and ‘Yougyoku’ are homozygous for *Pse-c*; and the other susceptible parents in this experiment (‘Mogi’, ‘Nagasakiwase’, Nagasaki No. 3, ‘Taisho’, and 75-142) are heterozygous. Based on the pedigree of ‘Shiromogi’ and the results reported here, *pse-c* is probably derived from ‘Mogi’, a major cultivar in Japan.

Loquat canker, caused by *Pseudomonas syringae* pv. *eriobotryae*, attacks the buds, shoots, leaves, fruit, and underground parts of the loquat tree (Morita, 1988; Mukoo, 1952; Suga et al., 2007) and has a detrimental effect on vegetative growth and fruit production (Morita, 1991). It is the most serious disease of the loquat in Japan (Nesumi, 2006). The disease has also been reported in China, the United States, Australia, New Zealand, and Argentina (Alippi and Alippi, 1990; Lai et al., 1971; Lin et al., 1999; McRae and Hale, 1986; Wimalajeewa et al., 1978).

The pathogen has been classified into three groups (A, B, and C) based on the production of brown pigment and the pathogenicity to mesophyll (Morita, 1978). Group A strains produce no pigment and are not pathogenic to mesophyll, Group B strains produce no pigment and are pathogenic to mesophyll, and Group C strains produce brown pigment and are not pathogenic to mesophyll. Kamiuntan (1990, 1995) reported that the electrophoretic profiles of plasmid DNA obtained from the three groups were all different: a 52-MDa plasmid and an 82-MDa plasmid seemed to be associated with virulence in Groups A and C, respectively. No commercial cultivar in Japan is resistant to all three pathogen groups, although some have resistance to two of the three groups (Hiehata et al., 2007; Morita, 1988).

Improvement of loquat canker resistance is therefore one of the most important goals of loquat breeding in Japan. A screening assay based on inoculation and marker-assisted selection for loquat canker has been developed (Fukuda et al., 2005; Morita, 1988, 2005). This assay has been used to select resistant seedlings at the nursery stage in the loquat breeding program at the Agricultural and Forestry Technical Development Center, Nagasaki, Japan (Hiehata et al., 2002a).

Progress has been made in breeding for canker resistance to Groups A and B because many resistant materials have been identified (Hiehata et al., 2002b, 2007; Morita, 1988) and the resistance to these two groups is dominant (Hiehata et al., 2002b; Morita et al., 1985). Some of the authors of the present article have successfully developed cultivars resistant to both groups such as ‘Reigetsu’ (Terai et al., 2007), ‘Ryoho’ (Hiehata et al., 2008), and ‘Natsutayori’ (Hiehata et al., 2010). In contrast, there are only a few genetic resources with good fruit quality that are resistant to Group C such as ‘Shiromogi’ (Hiehata et al., 2003, 2007; Morita, 1988); most of the others have undesirable fruit characteristics. In addition, the mode of inheritance of resistance to Group C has not been elucidated until now. For these reasons, progress in breeding for resistance to Group C has lagged behind that for Groups A and B. New cultivars resistant to all three groups (A, B, and C) are highly desired for commercial loquat production in Japan.

The loquat cultivar Shiromogi, which is one of the few genetic resources resistant to Group C, originated from open-pollinated ‘Mogi’ seeds irradiated with gamma rays in 1961 (Ichinose et al., 1982), but it is unknown whether the gamma-ray treatment led to the resistance in this cultivar. ‘Shiromogi’ is a commercial cultivar in Japan with excellent fruit characteristics such as sweetness and tender texture, and it has often been used as breeding material for fruit quality at the

Received for publication 18 Jan. 2012. Accepted for publication 12 Apr. 2012. We thank Akira Morita and Masahiko Yamada for their continuous encouragement and technical advice.

¹Current address: National Institute of Fruit Science, Tsukuba, Ibaraki 305-8605, Japan.

²Current address: Central Nagasaki Development Bureau, Nagasaki Prefectural Government, Saikai, Nagasaki 851-3305, Japan.

³Retired.

⁴Current address: National Agricultural Research Center for Western Region, Zentsuui, Kagawa 765-8508, Japan.

⁵Corresponding author. E-mail: nhiehata@pref.nagasaki.lg.jp.

Agricultural and Forestry Technical Development Center. The objective of this study was to determine the inheritance of the resistance to loquat canker Group C derived from ‘Shiromogi’, which is currently the most valuable source of resistance to Group C.

Materials and Methods

PLANT MATERIALS. ‘Shiromogi’ and ‘Champagne’ were selected as parents resistant to loquat canker Group C, and 13 other cultivars and selections were used as susceptible parents (Table 1). Three seedling populations were derived from the two resistant parents: two from reciprocal crosses between ‘Champagne’ and ‘Shiromogi’ and one from selfing of ‘Shiromogi’. Six of the susceptible parents were used as the pollen parent in crosses with ‘Shiromogi’, six were used as the seed parent in crosses with ‘Shiromogi’, and one (‘Nagasakiwase’) was crossed with ‘Shiromogi’ in both directions. Two selfings and five crosses, including one set of reciprocal crosses, were made between susceptible genotypes. The crosses and selfings were made in 1987, 1996, 1998, and 2003 at the Fruit Tree Research Division, Agricultural and Forestry Technical Development Center, Nagasaki, Japan, using standard techniques.

Fruit from the crosses and selfings were harvested at full maturity (i.e., May to June). The seeds were extracted and sown in plastic flats filled with a mixture containing an equal volume of peatmoss and *kanuma-tsuchi* (Japanese pumice widely used for horticulture) after rinsing without stratification. Seedlings at the second- or third-leaf stage were potted individually in plastic pots (0.6 L) containing the same medium. The next spring, the plants were transplanted to bigger plastic pots (5.7 L) containing the same medium. Compound fertilizer (18N–4.8P–

9.1K) was added to the pots every month during seedling growth in the plastic pots. All seedlings were placed in a greenhouse from the time of sowing to inoculation and were watered as needed.

INOCULUM PREPARATION AND INOCULATION TESTS. We performed inoculation with *P. syringae* pv. *eriobotryae* (Group C) as described previously (Hiehata et al., 2002b) with some modifications. Specifically, strain CG001 of *P. syringae* pv. *eriobotryae* Group C was isolated from cankers on loquat leaves at the Fruit Tree Research Division. CG001 had been identified as a Group C strain based on its production of a brown pigment during culture and avirulence to mesophyll. The bacteria were cultured at 25 °C on to PSA agar medium [decoction of 300 g potato in 1 L water, 0.5 g $\text{Ca}(\text{NO}_3)_2$, 2 g $\text{NaH}_2\text{PO}_4 \cdot 12\text{H}_2\text{O}$, 15 g sucrose, 5 g polypeptone, 15 g agar, pH 7.0] for 2 d before inoculation. Immediately before inoculation, the bacteria were collected and suspended in sterile distilled water to give a concentration of $\approx 10^8$ cfu/mL, and 0.02% Tween 20 was added as the surfactant.

The loquat seedlings were inoculated in the greenhouse to avoid infection by other pathogens. Two actively growing, half-expanded leaves were selected from each seedling. The bacterial suspension was needle-inoculated at six to nine sites per leaf at the midribs on the abaxial surface of the selected leaves. The inoculated leaves were covered with a polyethylene bag for 24 h to maintain high humidity. Canker incidence was evaluated ≈ 2 months after inoculation. Seedlings could be classified as either resistant or susceptible according to the absence or presence of black–brown cankers (Fig. 1A–D) because the response to the inoculation of loquat canker is qualitative (Hiehata et al., 2002b, 2003). Small or unclear cankers that were difficult to classify in appearance were sliced off and evaluated based on the presence of lesions in midrib tissue (Figs. 1B and D).

Table 1. Parental cultivars and selections used to produce progenies in various crosses for determining the inheritance of the resistance to loquat canker Group C.

Cultivars and selections	Origin	Evaluation
‘Champagne’	Selected and introduced to California ≈ 1908	Resistant
‘Shiromogi’	Seedling of an open-pollinated ‘Mogi’ seed irradiated with gamma rays	Resistant
‘Fukuharawase’	‘Mizuho’ \times a seedling of a Chinese loquat	Susceptible
‘Fusahikari’	‘Mizuho’ \times ‘Tanaka’	Susceptible
‘Gold Nugget’	Introduced into Japan from the United States ≈ 1952	Susceptible
‘Kusunoki’	Chance seedling	Susceptible
‘Mogi’	Chance seedling of a Chinese loquat	Susceptible
‘Nagasakiwase’	‘Mogi’ \times ‘Hondawase’	Susceptible
Nagasaki No. 2 ^a	‘Nagasakiwase’ \times ‘Guangdong’	Susceptible
Nagasaki No. 3 ^a	‘Nagasakiwase’ \times ‘Obusa’	Susceptible
‘Taisho’	Bud mutant of an unknown loquat	Susceptible
‘Tanaka’	Chance seedling	Susceptible
‘Tsukumo’	‘Mogi’ \times ‘Tanaka’	Susceptible
‘Yogyoku’	‘Mogi’ \times ‘Morimoto’	Susceptible
75-142 ^a	‘Obusa’ \times ‘Mogi’	Susceptible

^aNagasaki No.2, Nagasaki No.3, and 75-142 have been selected at Fruit Tree Research Division, Agricultural and Forestry Technical Development Center, Nagasaki Prefectural Government, Japan.

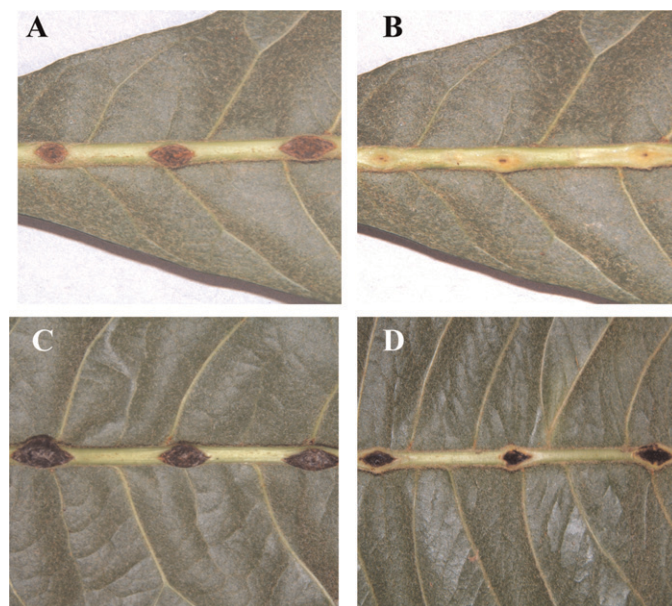


Fig. 1. Reactions to loquat canker Group C after midrib inoculation of resistant [(A) in appearance, (B) inside midrib] and susceptible [(C) in appearance, (D) inside midrib] loquat seedlings. No canker was produced inside and out even if brown scabs were produced on the cortical layer (A) and needle wounds remained inside midrib (B) for resistant seedlings. Whereas, for susceptible seedlings, black–brown cankers were produced at inoculated sites (C) and recognized inside the midribs when the cortical layer were sliced off (D).

STATISTICAL ANALYSIS. Chi-square analysis was used to test the fit of observed-to-expected segregation ratios for each cross that segregated for resistant and susceptible seedlings and to determine the inheritance of loquat canker resistance.

Results

The reciprocal crosses between resistant cultivars Champagne and Shiromogi and the selfing of 'Shiromogi' produced all resistant seedlings (Table 2). The crosses between 'Shiromogi' and susceptible pollen parents resulted in two types of segregation in the progeny: all susceptible seedlings or both resistant and susceptible seedlings. Progeny seedlings from crosses in which 'Fusahikari', Nagasaki No. 2, or 'Yougyoku' was used as the susceptible parent were all susceptible, whereas crosses in which 'Nagasakiwase', Nagasaki No. 3, 'Taisho', or 75-142 was the susceptible parent segregated for both resistant and susceptible seedlings. The susceptible × 'Shiromogi' crosses (i.e., in which the susceptible genotype was used as the seed parent) also resulted in two types of segregation, like in the case of the 'Shiromogi' × susceptible crosses. When 'Fukuharawase', 'Gold Nugget', 'Kusunoki', 'Tanaka', or 'Tsukumo' was used as the susceptible parent, all progeny seedlings were susceptible. Crosses in which 'Mogi' or 'Nagasakiwase' was used as the

susceptible parent segregated for both resistant and susceptible seedlings. The progeny of self-pollinated 'Mogi' and 'Taisho' segregated for both resistant and susceptible seedlings, although five crosses between susceptible parents (including 'Taisho') produced no resistant progeny.

The observed segregation fitted a ratio of 1 R:1 S in chi-square test in four crosses among six crosses between 'Shiromogi' and susceptible parents in which both resistant and susceptible seedlings were produced, although significant segregation distortion was observed in two crosses ('Mogi' × 'Shiromogi' and 'Nagasakiwase' × 'Shiromogi') (Table 2). The 1 R:3 S ratio hypothesis for the segregation ratio was not significantly declined in all two selfings of 'Mogi' and 'Taisho'.

Discussion

Three crosses or selfings of parents resistant to loquat canker Group C yielded all resistant seedlings, suggesting that both 'Champagne' and 'Shiromogi' are homozygous for the resistance gene(s). The crosses between 'Shiromogi' and susceptible parents provided evidence that the resistance in 'Shiromogi' is inherited as a single-gene recessive trait. This mode of inheritance is similar to that of other disease resistance genes such as that of fireblight (*Erwinia amylovora*) in pear [*Pyrus communis* (Thompson et al., 1975)], black spot (*Alternaria kikuchiana*) in Japanese pear [*Pyrus pyrifolia* (Kozaki, 1973)], alternaria blotch (*Alternaria mali*) in apple [*Malus pumila* (Saito and Takeda, 1984)], and black knot (*Apisorina morbosa*) in plum [*Prunus* sp. (Norton and Boyhan, 1991)]. We propose the name *pse-c*, which is derived from the scientific name of the pathogenic bacterium, as the designation for the loquat canker Group C resistance gene. Furthermore, we conclude that the genotypes of the parental individuals used in this experiment are as follows: resistant parents 'Shiromogi' and 'Champagne', *pse-c pse-c*; susceptible parents 'Mogi', 'Nagasakiwase', Nagasaki No. 3, 'Taisho', and 75-142, *Pse-c pse-c*; and susceptible parents 'Fukuharawase', 'Fusahikari', 'Gold Nugget', 'Kusunoki', Nagasaki No. 2, 'Tanaka', 'Tsukumo', and 'Yougyoku', *Pse-c Pse-c* (Table 3).

Because a set of crosses used in this study was not for only genetic materials but mainly for the practical breeding, consequently, we could not reveal whether the inheritance was controlled cytoplasmically as a result of the lack of reciprocal crosses. However, our conclusion is supported by the result that most of crosses among 24 crosses, which were derived from many parental cultivars and selections, fitted the expected ratios.

Table 2. Segregation of resistance to loquat canker Group C in progenies of various loquat crosses.

Cross	Observed frequency ^z		Expected ratio	χ^2	<i>P</i>
	Resistant	Susceptible			
Resistant × resistant					
‘Champagne’ × ‘Shiromogi’	24	0	1: 0	—	—
‘Shiromogi’ × ‘Champagne’	38	0	1: 0	—	—
‘Shiromogi’ × ‘Shiromogi’	42	0	1: 0	—	—
‘Shiromogi’ × susceptible					
‘Shiromogi’ × ‘Fusahikari’	0	54	0: 1	—	—
‘Shiromogi’ × ‘Nagasakiwase’	12	14	1: 1	0.154	0.695
‘Shiromogi’ × Nagasaki No. 2	0	13	0: 1	—	—
‘Shiromogi’ × Nagasaki No. 3	9	13	1: 1	0.727	0.394
‘Shiromogi’ × ‘Taisho’	5	9	1: 1	1.143	0.285
‘Shiromogi’ × ‘Yougyoku’	0	21	0: 1	—	—
‘Shiromogi’ × 75-142	77	79	1: 1	0.026	0.873
Susceptible × ‘Shiromogi’					
‘Fukuharawase’ × ‘Shiromogi’	0	54	0: 1	—	—
‘Gold Nugget’ × ‘Shiromogi’	0	16	0: 1	—	—
‘Kusunoki’ × ‘Shiromogi’	0	111	0: 1	—	—
‘Mogi’ × ‘Shiromogi’	52	32	1: 1	4.762	0.029
‘Nagasakiwase’ × ‘Shiromogi’	22	43	1: 1	6.785	0.009
‘Tanaka’ × ‘Shiromogi’	0	88	0: 1	—	—
‘Tsukumo’ × ‘Shiromogi’	0	34	0: 1	—	—
Susceptible × susceptible					
‘Fukuharawase’ × ‘Nagasakiwase’	0	21	0: 1	—	—
‘Fusahikari’ × ‘Taisho’	0	27	0: 1	—	—
‘Gold Nugget’ × ‘Nagasakiwase’	0	12	0: 1	—	—
‘Mogi’ × ‘Mogi’	13	49	1: 3	0.538	0.463
‘Nagasakiwase’ × ‘Fusahikari’	0	25	0: 1	—	—
‘Taisho’ × ‘Fusahikari’	0	26	0: 1	—	—
‘Taisho’ × ‘Taisho’	7	20	1: 3	0.012	0.912

^zThe number of resistant or susceptible seedlings in each progeny for the inoculation test of strain CG001. The bacterial suspension was needle-inoculated at six to nine sites per leaf at the midribs on the abaxial surface of actively growing, half-expanded leaves. Seedlings were classified as either resistant or susceptible according to the absence or presence of black-brown cankers about 2 months after inoculation (Fig. 1).

In the progeny of most crosses between ‘Shiromogi’ and susceptible genotypes, the observed segregation fit the expected ratio, but significant distortion was observed in the progeny of two crosses: ‘Mogi’ × ‘Shiromogi’ and ‘Nagasakiwase’ × ‘Shiromogi’. There are at least two possible explanations for the unexpected segregation ratios. One is that minor genes affecting the reaction to Group C might be present in addition to the *pse-c* gene. Both major and minor genes that control resistance to pear scab (*Venturia nashicola*) were reported in pear (Abe et al., 2000). Similarly, it has been suggested that resistance to Group C derived from ‘Champagne’ is controlled by genes at several loci (Hiehata et al., 2003). Another possibility is that inbreeding affects the expression of resistance in the progeny seedling populations. ‘Mogi’ × ‘Shiromogi’ is a backcross and ‘Nagasakiwase’ × ‘Shiromogi’ is a half-sib cross; thus, the parents in each of these crosses are related.

Table 3. Putative loquat genotypes for resistance to loquat canker Group C based on the crossing tests.^z

Evaluation	Genotype	Cultivars and selections
Resistant	<i>pse-c pse-c</i>	‘Shiromogi’—‘Champagne’
Susceptible	<i>Pse-c pse-c</i>	‘Mogi’—‘Nagasakiwase’—Nagasaki No. 3—‘Taisho’—75-142
Susceptible	<i>Pse-c Pse-c</i>	‘Fukuharawase’—‘Fusahikari’—‘Gold Nugget’—‘Kusunoki’—Nagasaki No. 2—‘Tanaka’—‘Tsukumo’—‘Yougyoku’

^zThe resistance to loquat canker Group C of ‘Shiromogi’ is conferred by a single recessive gene, designated *pse-c*, which is derived from the scientific name of the pathogenic bacterium.

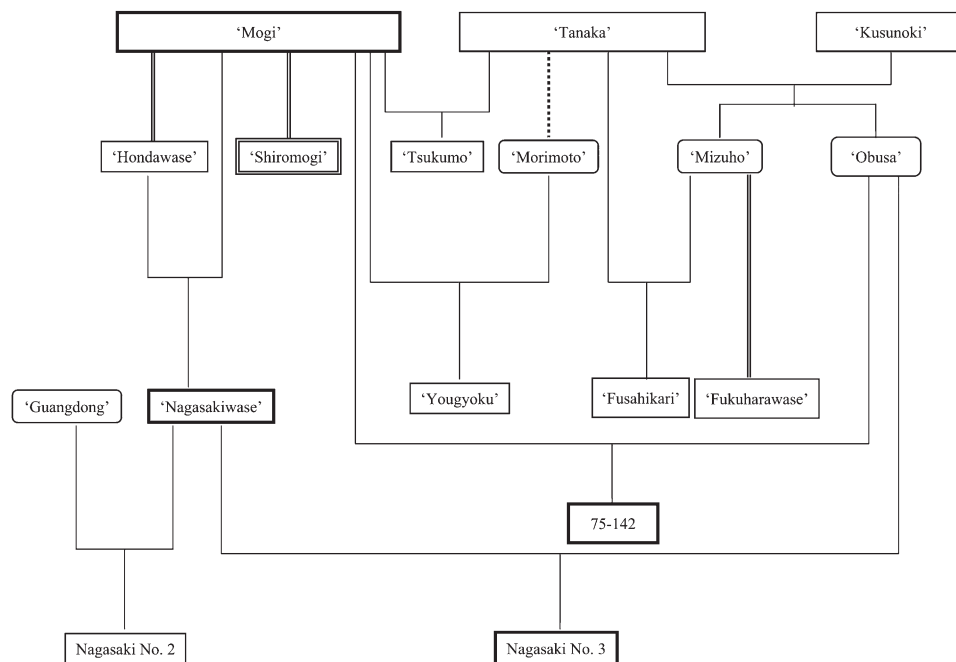


Fig. 2. Pedigree of loquat cultivars and selections in Japan. Rectangles outlined with double lines, bold lines, and single lines represent homozygous recessive (*pse-c pse-c*), heterozygous (*Pse-c pse-c*), and homozygous dominant (*Pse-c Pse-c*) genotypes, respectively. Rectangles with rounded corners indicate genotypes that have not been tested for resistance. Broken vertical line indicates progeny derived after mutagenesis of the parent. Double vertical lines indicate that only the seed parent of the progeny cultivar is known.

Although it has been more difficult to breed cultivars resistant to loquat canker Group C than to Groups A and B, for which the resistance is dominant (Hiehata et al., 2002b; Morita et al., 1985), it should now be possible to introgress resistance to all three groups into existing cultivars. 75-142 has both *Pse-a*, which is a dominant gene for resistance to loquat canker Group A (Hiehata et al., 2002b), and *pse-c*. Thus, this selection is expected to produce progeny resistant to both Groups A and C if it is selfed or crossed with another loquat carrying *pse-c*. Consequently, 75-142 should be valuable material for breeding resistance against loquat canker.

Although breakdown of resistance conferred by major single genes has been reported for some diseases (Kiyosawa, 1982; Parisi et al., 1993), we think that the possibility of this occurring with Group C resistance is low for the following reasons. First, a total of 109 canker strains collected from orchards throughout Japan have been classified into Groups A to C (Morita, 1978), and the reaction of several cultivars, which were inoculated with 10 different strains of each group, was consistent within a given group (Morita, 1988). This result suggests that new strains of this pathogen do not develop rapidly. Second, resistant loquat cultivars would not replace existing ones for some time because loquat is a perennial crop; consequently, genetic variation of this bacterium resulting from strong selection pressure by the resistance gene *pse-c* would hardly change.

‘Shiromogi’, which has two *pse-c* genes, was selected from seedlings of ‘Mogi’, and thus it is either the progeny of ‘Mogi’ and an unknown loquat or a self-derived seedling of ‘Mogi’. Unless the gamma rays have affected the resistance of ‘Shiromogi’, at least one of the two *pse-c* genes is assumed to be derived from ‘Mogi’ (Fig. 2). ‘Obusa’, which is the seed parent of 75-142, does not carry *pse-c*; it was selected from progeny of a cross between ‘Tanaka’ and ‘Kusunoki’, both of which are homozygous for *Pse-c*. Hence, the *pse-c* gene in 75-142 is also derived from ‘Mogi’, its pollen parent. The *pse-c* gene in ‘Nagasakiwase’ (‘Mogi’ × ‘Hondawase’) is also assumed to have originated from ‘Mogi’, because ‘Hondawase’ does not carry *pse-c* (S. Fukuda, Y. Tominaga, and H. Nesumi, unpublished data). In addition, the *pse-c* gene in Nagasaki No. 3 (‘Nagasakiwase’ × ‘Obusa’) also came from ‘Nagasakiwase’ because the parents of ‘Obusa’ do not carry *pse-c*. For all of these reasons, we conclude that the *pse-c* genes of the loquats used in this study (except possibly for ‘Champagne’ and ‘Taisho’, which are of unknown parentage) are derived from ‘Mogi’.

Because they carry a copy of *pse-c*, heterozygotes can be used as a source of resistance in breeding programs. However, the *pse-c* genes in ‘Nagasakiwase’, Nagasaki No. 3, and 75-142 are apparently derived from

‘Mogi’, as is the case with ‘Shiromogi’; in addition, ‘Shiromogi’ and the five heterozygotes used in this study appear to be very closely related genetically (Fukuda et al., 2006). If these parents are used repeatedly in breeding for Group C resistance, inbreeding depression might be a concern, as has been reported in rabbiteye blueberry [*Vaccinium ashei* (Lyrene, 1983)], persimmon [*Diospyros kaki* (Yamada, 1993)], and Japanese pear (Sato et al., 2008). Resistant materials that are less closely related to ‘Mogi’ and ‘Shiromogi’ such as ‘Cham-pagne’ and ‘Xia lou bai mi’ should therefore be actively used as parents for breeding resistance to Group C, although they have fewer desirable fruit traits than ‘Shiromogi’ and the heterozygotes in this study.

Literature Cited

- Abe, K., K. Kotobuki, T. Saito, and O. Terai. 2000. Inheritance of resistance to pear scab from European pears to Asian pears. *J. Jpn. Soc. Hort. Sci.* 69:1–8.
- Alippi, A.M. and H.E. Alippi. 1990. Stem canker of loquat: A new disease in Argentina. *Rev. Argent. Microbiol.* 22:155–158.
- Fukuda, S., N. Hiehata, T. Yamamoto, O. Terai, and H. Nesumi. 2005. Development of DNA markers linked to the resistance gene (*Pse a*) to loquat canker. *J. Jpn. Soc. Hort. Sci.* 74:345–349.
- Fukuda, S., T. Yamamoto, S. Ohta, C. Nishitani, Y. Tominaga, and H. Nesumi. 2006. Genetic diversity of loquat varieties by SSR markers. *J. Jpn. Soc. Hort. Sci.* 75(suppl. 1):70 (Abstr.).
- Hiehata, N., S. Fukuda, and O. Terai. 2007. Evaluation of loquat canker resistance in new loquat cultivars released in Japan and introduced from foreign countries. *Bul. Nagasaki Fruit Tree Expt. Sta.* 10:14–21.
- Hiehata, N., S. Fukuda, Y. Tominaga, O. Terai, H. Nesumi, K. Asada, J. Nagato, Y. Sato, H. Nakayama, and T. Nakao. 2010. A new loquat cultivar ‘Natsutayori’. *Bul. Nagasaki Agr. For. Tech. Dev. Ctr.* 1:83–100.
- Hiehata, N., Y. Sato, S. Fukuda, and O. Terai. 2002a. Selection at juvenile age for resistance to loquat canker in loquat breeding. *Bul. Nagasaki Fruit Tree Expt. Sta.* 9:27–37.
- Hiehata, N., Y. Sato, S. Fukuda, and O. Terai. 2002b. Inheritance of resistance to loquat canker (*Pseudomonas syringae* pv. *eriobotryae*, Group A) in loquat (*Eriobotrya japonica*). *J. Jpn. Soc. Hort. Sci.* 71:255–261.
- Hiehata, N., Y. Sato, S. Fukuda, and O. Terai. 2003. Inheritance of resistance to Group C of loquat canker (*Pseudomonas syringae* pv. *eriobotryae*). *J. Jpn. Soc. Hort. Sci.* 72(suppl. 2):534 (Abstr.).
- Hiehata, N., O. Terai, S. Fukuda, Y. Tominaga, H. Nesumi, A. Morita, J. Nagato, I. Ichinose, Y. Sato, K. Asada, M. Hashimoto, T. Nakao, and T. Yoshida. 2008. New loquat cultivar ‘Ryoho’. *Bul. Nagasaki Fruit Tree Expt. Sta.* 11:1–15.
- Ichinose, I., H. Muramatsu, K. Hamaguchi, O. Terai, J. Ikeda, K. Asada, and M. Hashimoto. 1982. New loquat cultivar ‘Shiromogi’ [in Japanese]. *Abstr. Jpn. Soc. Hort. Sci. Spring Mtg.* p. 58–59 (Abstr.).
- Kamiuntun, H. 1990. Loss of a plasmid in *Pseudomonas syringae* pv. *eriobotryae* is correlated with change of symptoms. *Ann. Phytopathological Soc. Jpn.* 56:645–650.
- Kamiuntun, H. 1995. Improvement of a plasmid in the expression of virulence in *Pseudomonas syringae* pv. *eriobotryae*. *Ann. Phytopathological Soc. Jpn.* 61:376–380.
- Kiyosawa, S. 1982. Genetics and epidemiological modeling of breakdown of plant disease resistance. *Annu. Rev. Phytopathol.* 20: 93–117.
- Kozaki, I. 1973. Black spot disease resistance in Japanese pear. I: Heredity of the disease resistance. *Bul. Hort. Res. Sta. A* 12:17–27.
- Lai, M., W.O. McCartney, and C.W. Morin. 1971. Canker of loquat caused by *Pseudomonas* sp. *Phytopathology* 61:248–249.
- Lin, S., R.H. Sharpe, and J. Janick. 1999. Loquat: Botany and horticulture. *Hort. Rev.* 23:233–276.
- Lyrene, P. 1983. Inbreeding depression in rabbiteye blueberries. *HortScience* 18:226–227.
- McRae, E.M. and C.N. Hale. 1986. New plant disease record in New Zealand: Loquat canker. *N. Z. J. Agr. Res.* 29:547–550.
- Morita, A. 1978. Studies on the loquat canker caused by *Pseudomonas eriobotryae* (Takimoto) Dowson. II: Grouping of the bacterial isolates on the basis of their pigment producibility and pathogenicity. *Ann. Phytopathological Soc. Jpn.* 44:6–13.
- Morita, A. 1988. Studies on the grouping of the *Pseudomonas syringae* pv. *eriobotryae* and the varietal resistance against loquat canker. *Spec. Bul. Nagasaki Fruit Tree Expt. Sta.* 1–58.
- Morita, A. 1991. Effect of the inoculation of *Pseudomonas syringae* pv. *eriobotryae* at seedling stage upon its growth and fruit-productivity. *Ann. Phytopathological Soc. Jpn.* 57:629–633.
- Morita, A. 2005. Studies of loquat canker. *Spec. Bul. Nagasaki Fruit Tree Expt. Sta.* 2:1–145.
- Morita, A., I. Ichinose, and K. Asada. 1985. Analysis of resistant gene in loquat canker. I. *Kyushu Agr. Res.* 47:101.
- Mukoo, H. 1952. Studies on the causal bacteria of the loquat canker (1). *Bul. Natl. Inst. Agr. Sci. C-1*:1–190.
- Nesumi, H. 2006. Loquat (biwa), p. 85–95. In: *Horticulture in Japan 2006*. Shoukadoh Publication, Kyoto, Japan.
- Norton, J.D. and G.E. Boyhan. 1991. Inheritance of resistance to black knot in plums. *HortScience* 26:1540.
- Parisi, L., Y. Lespinasse, J. Guillaumes, and J. Krüger. 1993. A new race of *Venturia inaequalis* virulent to apples with resistance due to the *Vf* gene. *Phytopathology* 83:533–537.
- Saito, K. and K. Takeda. 1984. Genetic analysis of resistance to alternaria blotch (*Alternaria mali* Roberts) in apple: Studies on the breeding of the apple. VIII. *Jpn. J. Breeding.* 34:197–209.
- Sato, A., Y. Sawamura, N. Takada, and T. Hirabayashi. 2008. Relationship between inbreeding coefficients and plant height of 1-year-old seedlings in crosses among Japanese pear (*Pyrus pyrifolia* Nakai) cultivars/selections. *Sci. Hort.* 117:85–88.
- Suga, Y., S. Fukuda, Y. Tominaga, and H. Nesumi. 2007. Characteristics of isolated bacterium from canker symptom(s) observed in the underground parts of loquat seedlings for rootstock. *Bul. Nagasaki Fruit Tree Expt. Sta.* 10:30–40.
- Terai, O., N. Hiehata, S. Fukuda, J. Nagato, Y. Sato, K. Asada, A. Morita, T. Nakao, Y. Tominaga, I. Ichinose, T. Yoshida, and M. Hashimoto. 2007. New loquat cultivar ‘Reigetsu’. *Bul. Nagasaki Fruit Tree Expt. Sta.* 10:1–13.
- Thompson, J.M., R.H. Zimmerman, and T. van der Zwet. 1975. Inheritance of fire blight resistance in *Pyrus*. *J. Hered.* 66:259–264.
- Wimalajeewa, D.L.S., I.G. Pascoe, and D.L. Jones. 1978. Bacterial stem canker of loquat. *Australas. Plant Pathol.* 7:33.
- Yamada, M. 1993. Persimmon breeding in Japan. *Jpn. Agr. Res. Qrtly.* 27:33–37.