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

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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 selling 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 selling 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’, ‘Fusakihari’, ‘Gold Nugget’, ‘Kusunoki’, Nagasaki No. 2, ‘Tanaka’, ‘Tsukumo’, and ‘Yougokou’ 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., 2000) 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, 2005). 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. Kamiunten (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 Group C. Only one cultivar, ‘Reigetsu’ (Terai et al., 2007), ‘Ryoho’ (Hiehata et al., 2008), and ‘Natsuyasari’ (Hiehata et al., 2010) are resistant to Group C. 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 ‘Natsuyasari’ (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
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, fruit was 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 Ca(NO₃)₂, 2 g NaHPO₄·12H₂O, 15 g sucrose, 5 g polypeptide, 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 ≈10⁸ 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’              | Seeding of an open-pollinated ‘Mogi’ seed irradiated with gamma rays | Resistant |
| ‘Mogi’                   | ‘Mizuhō’ × a seedling of a Chinese loquat | Susceptible |
| ‘Fusahikari’             | ‘Mizuhō’ × ‘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’ × ‘Honda wase’ | Susceptible |
| ‘Nagasaki No. 2’         | ‘Nagaski wase’ × ‘Guangdong’ | Susceptible |
| ‘Nagasaki No. 3’         | ‘Nagaski wase’ × ‘Obusa’ | Susceptible |
| ‘Taiho’                  | Bud mutant of an unknown loquat | Susceptible |
| ‘Tanaka’                 | Chance seedling | Susceptible |
| ‘Tsukumo’                | ‘Mogi’ × ‘Tanaka’ | Susceptible |
| ‘Yougyoku’               | ‘Mogi’ × ‘Morimoto’ | Susceptible |
| 75-142*                  | ‘Obusa’ × ‘Mogi’ | Susceptible |

*The 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. 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.

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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).

![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.](image-url)
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 (Apisporina morbosra) 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, ‘Taisho’, ‘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 | Expected ratio | $\chi^2$ | P |
|-------|-------------------|----------------|---------|---|
| 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 |

The 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.

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

*The 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.*

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’ × ‘Hondaawase’) is also assumed to have originated from ‘Mogi’, because ‘Hondaawase’ 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
‘Mogî’, 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). Resistat materials that are less closely related to ‘Mogî’ and ‘Shiromogi’ such as ‘Champagne’ 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.

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