Quantitative Inheritance of Resistance to Loquat Canker (Pseudomonas syringae pv. eriobotryae, Group C) in Loquat Progenies from Crosses between a Resistant Cultivar, ‘Champagne’, and Susceptible Cultivars

Naofumi Hiehata5, Shinji Fukuda1, Yoshihiko Sato2, Yukiko Tominaga3, and Osamu Terai4

Abstract. Loquat canker, caused by Pseudomonas syringae pv. eriobotryae, is a serious disease of loquat [Eriobotrya japonica (Thunb.) Lindl.] in some countries such as Japan. Therefore, improved canker resistance is an important objective for loquat breeding. The resistance to loquat canker Group C in descendants of ‘Shiromogi’ was expressed only in homozygotes with a recessive gene at a single locus, which was designated pse-c/pse-c. ‘Champagne’, which is distantly related to ‘Shiromogi’, is another cultivar with resistance to Group C. The inheritance of this resistance in progenies of crosses between ‘Champagne’ and susceptible cultivars was examined. The offspring seedlings from 14 crosses between ‘Champagne’ (pse-c/pse-c) and 12 susceptible cultivars (Psc-c/Psc-c or Psc-c/pse-c) were classified into two types of resistant and susceptible. All of the hybrid progenies between ‘Champagne’ (pse-c/pse-c) and Psc-c/pse-c parents showed two types of resistant and susceptible. The proportion of resistant offspring showed great differences significantly, depending on the hybrid combinations. It ranged from 0.203 to 0.596 with an average of 0.407. It indicated that the resistance was controlled by one or more additional genes or loci other than the Psc-c (pse-c) locus. In addition, the proportion of resistant offspring from crosses between ‘Champagne’ (pse-c/pse-c) and Psc-c/pse-c parents ranged from 0.463 to 0.701 (and averaged 0.601), which seriously deviated from the segregation of 1:1, indicating that the segregation was both Mendelian and polygenic in a threshold character. The proportion of resistant seedlings cannot be predicted by the phenotype and the genotype in the Psc-c (pse-c) locus. Therefore, the general combining ability of ‘Champagne’ resulting from the additional gene effect was estimated, which was 0.407 and 0.101 for ‘Champagne’ × Psc-c/Psc-c and ‘Champagne’ × Psc-c/pse-c cultivars, respectively. The gene effect of susceptible cultivars ranged from –0.204 (‘Yougyoku’), to +0.189 (‘Togoshi’) for ‘Champagne’ × Psc-c/pse-c cultivars and from –0.138 (‘Taisho’) to +0.089 (‘Nagasakiwase’) for ‘Champagne’ × Pse-c/pse-c cultivars.

Loquat canker, caused by Pseudomonas syringae pv. eriobotryae, is a bacterial disease that has been reported for nearly a century in Japan (Ikata, 1927; Nakata, 1934). The disease has also been reported in China (Lin et al., 1999), the United States (Lai et al., 1971), Australia (Wimalajeewa et al., 1978), New Zealand (McRae and Hale, 1986), and Argentina (Alippi and Alippi, 1990). The disease attacks the buds, shoots, leaves, and fruit of the loquat tree (Morita, 1988; Muko, 1952), and it has a detrimental effect on vegetative growth and fruit production (Morita, 1991). It is currently the most serious disease of the loquat in Japan (Nesumi, 2006). The disease attacks not only the above-ground parts of the loquat, but also its below-ground parts, leading to seedling production decline in nurseries (Suga et al., 2007).

Because there were no completely resistant varieties grown commercially in Japan, bactericides were widely used in loquat orchards. However, controlling the disease in this way was difficult because of the high labor requirements and cost. Therefore, improvement of canker resistance of loquat in Japan is one of the most important goals in loquat breeding. In addition, requirements for disease-resistant cultivars continue to increase as a result of increasing public concerns of environmental responsibility. To support resistance breeding, a screening assay based on inoculation and marker-assisted selection for loquat canker resistance has been developed (Fukuda et al., 2005; Morita, 1988). 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).

The pathogen has been classified into three groups (A, B, and C) based on the presence of a brown pigment and pathogenicity in mesophyll tissue (Morita, 1978). Group A strains produce no pigment and are not pathogenic, Group B strains produce brown pigment and are pathogenic, and Group C strains produce brown pigment and are not pathogenic. Progress has been made in breeding for 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 based on a single dominant gene (Hiehata et al., 2002b; Morita et al., 1985). We have successfully developed three cultivars that are resistant to both groups: ‘Reigetsu’ (Terai et al., 2007), ‘Ryoho’ (Hiehata et al., 2008), and ‘Natsutayori’ (Hiehata et al., 2010). In contrast, there are not enough genetic resources that are resistant to Group C (Hiehata et al., 2007; Morita, 1988); ‘Shiromogi’ and ‘Champagne’ are resistant to Group C and have moderate or larger fruit size and good edible fruit quality. Therefore, they are important cultivars with high potential as cross-parents in breeding, which combine high fruit quality and large fruit size with resistance to loquat canker Group C.

Hiehata et al. (2012) elucidated the inheritance of the resistance to Group C derived from ‘Shiromogi’. ‘Shiromogi’ originated as a seedling derived from an open-pollinated ‘Mogi’ seed irradiated with gamma rays (Ichinose et al., 1982). The resistance to Group C in ‘Shiromogi’ is currently the most valuable source of resistance to Group C among loquat cultivars, which is inherited with complete dominance at a single locus and expressed only in a recessive homozygote (pse-c/pse-c; Hiehata et al., 2012). The gene pse-c was probably derived from ‘Mogi’ (Hiehata et al., 2012), which is currently a major Japanese cultivar and it was a chance seedling found and selected in Japan.

Seedlings resistant to Group C with the pse-c gene have been produced by the breeding program at the Agricultural and Forestry Technical Development Center, Nagasaki, Japan. However, inbreeding depression might be a concern in breeding for Group C resistance because the number of resistant parent materials that contain pse-c (e.g., ‘Mogi’, ‘Shiromogi’) is limited, and there are close relationships among these materials (Fukuda et al., 2013). Although their descendants could be crossed or back-crossed with parents to produce a high proportion of homozygous-recessive seedlings (pse-c/pse-c) that are resistant to Group C, these crosses involve inbreeding and were therefore likely to exhibit inbreeding.
depression with lower tree vigor or yield. Resistant materials which are less closely related to ‘Mogi’ and ‘Shirromogi’ should therefore be actively used as parents to improve the effectiveness of breeding for resistance to Group C.

‘Champagne’, which is of unknown parentage, is one of the few genetic resources that are resistant to Group C. It was selected and introduced to California in 1908 (Morton, 1987) and was introduced to Japan in 1952. The particular usefulness of this loquat is its complete resistance to Groups A, B, and C (Morita, 1988). ‘Champagne’ is distantly related to ‘Moji’, ‘Shirromogi’, and Japanese cultivars (Fukuda et al., 2013). Thus, it has high potential as a cross-parent for preventing inbreeding depression in breeding for loquat canker resistance, and especially resistance to Group C. The genotype of ‘Champagne’ has been estimated to be homozygous-recessive (pse-c/pse-c) for the locus (Hiehata et al., 2012), but the resistance of ‘Champagne’ may be controlled by additional genes at another locus different from the pse-c locus (Hiehata et al., 2003). The objective of the present study was to clarify the inheritance of the resistance to loquat canker Group C derived from ‘Champagne’ through crosses between ‘Champagne’ and susceptible genotypes.

Materials and Methods

Plant materials. ‘Champagne’ was crossed with 12 cultivars susceptible to loquat canker Group C (Table 1). The genotype of susceptible cultivars is Pse-c/Pse-c or Pse-c/Pse-c, and eight of the 12 cultivars have been characterized at this locus (Table 1; Hiehata et al., 2012). The genotype of the other four cultivars was estimated as follows: ‘Oubasa’ and ‘Morimotou’ were estimated as Pse-c/Pse-c because ‘Oubasa’ was an offspring from ‘Tanaka’ (Pse-c/Pse-c) × ‘Kusunoki’ (Pse-c/Pse-c), and ‘Morimotou’ is a late-maturing bud sport from ‘Tanaka’ (Pse-c/Pse-c). ‘Suzukaze’ and ‘Togoshi’ were estimated as Pse-c/Pse-c because a cross of ‘Suzukaze’ with 87-222, which has the genotype Pse-c/pse-c, and selfing of ‘Togoshi’ both produced no resistant seedlings (N. Hiehata, S. Fukuda, and O. Terai, unpublished data).

The crosses were performed in 1996, 1999, and 2002 at the Fruit Tree Research Division, Agricultural and Forestry Technical Development Center, Nagasaki, Japan, using standard techniques. Nine of the susceptible parents were used as the male parent and five were used as the female parent in crosses with ‘Champagne’, including two sets of reciprocal crosses (Tables 2 and 3).

Fruit from the crosses were harvested at full maturity. The seeds were extracted and sown in plastic flats filled with a mixture containing an equal volume of peat moss and kanuma-tsuhi (Japanese pumice that is widely used for horticulture) after rinsing but without stratification. Seedlings at the second- or third-leaf stage were potted individually in plastic pots (0.6 L) containing the same medium. The following spring, the plants were transplanted into 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. Seven hundred thirty-six seedlings were produced from 14 crosses between ‘Champagne’ and the 12 susceptible genotypes.

Inoculum preparation and inoculation tests. We inoculated 2-year-old seedlings with P. syringae pv. eribiotryae (Group C). The inoculum source, methods, and evaluation for pathogenicity of loquat canker Group C were the same as in Hiehata et al. (2012). The number of resistant or susceptible seedlings in each progeny was determined using an inoculation test with strain CG001. The bacteria were cultured at 25°C on potato sucrose agar medium [decoction of 300 g potato in 1 L of water, 0.5 g Ca(NO₃)₂, 2 g NaHPO₄·12 H₂O, 15 g sucrose, 5 g poly-peptide, 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 10⁶ colony-forming units/mL and 0.02% Tween 20 was added as a 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 approximately 2 months after inoculation. Seedlings could be classified as either resistant or susceptible according to the absence or presence of black–brown cankers because the response to the inoculation of loquat canker is qualitative (Hiehata et al., 2002b, 2012). Small or unclear cankers that were difficult to classify in appearance were sliced off and evaluated based on the presence of lesions in the midrib tissue.

Statistical analysis. We used the χ² test to compare the observed and expected segregation ratios for each cross that produced both resistant and susceptible seedlings and to determine the inheritance of the loquat canker resistance. Because the proportion of resistant seedlings can be approximated as a binomial distribution, we calculated confidence limits for the obtained proportion of resistant seedlings (pᵢ for cross i) at P = 0.95 as pᵢ ± 1.96√pi(1-pi)/nᵢ (Snedecor and Cochran, 1967). Homogeneity of the proportion of resistant seedlings over the crosses was tested using the χ² test for each of the ‘Champagne’ × Pse-c/Pse-c and ‘Champagne’ × Pse-c/pse-c groups (Snedecor and Cochran, 1967).

Results and Discussion

Segregation for the resistance to loquat canker Group C in seedlings from 10 crosses between ‘Champagne’ (pse-c/pse-c) and Pse-c/Pse-c cultivars. All the seedlings from crosses between ‘Champagne’ (pse-c/pse-c) and Pse-c/Pse-c cultivars were expected to have no segregation; that is, all would have a susceptible Pse-c/pse-c genotype (Hiehata et al., 2012). However, the phenotype of the seedlings segregated into both resistant and susceptible offspring for all crosses between ‘Champagne’ and the Pse-c/Pse-c cultivars (Table 2).

The proportion of resistant seedlings varied widely among the crosses, ranging from 0.203 (‘Youyoku’ as the male parent) to 0.596 (‘Togoshi’ as the male parent) and averaged 0.407 (Table 2). ‘Fusahikari’ was used in reciprocal crosses with ‘Champagne’, and the proportions of resistant seedlings were 0.256 and 0.414 when ‘Fusahikari’ was used as the male parent and the female parent, respectively. These proportions were not significantly different (χ² test).

The proportion of resistant seedlings differed significantly between different crosses (χ² test, P < 0.001; Table 2). We calculated the confidence interval for the proportion of resistant seedlings for each cross at P = 0.95 based on a binomial distribution (Table 2). We assumed a significant difference when the confidence interval did not overlap for a pair of crosses. The proportions of resistant seedlings in crosses with ‘Youyoku’ and ‘Fusahikari’ as the male parents and ‘Suzukaze’ as the female parent were lower than 0.26 and were significantly lower than those of ‘Kusunoki’ and ‘Togoshi’ as male parents; both of them had proportions higher than 0.52. Furthermore, the proportion of resistant seedlings with ‘Youyoku’ as the male parent was significantly lower than those of ‘Fukuharawase’ and ‘Morimotou’ as the male parents and ‘Tanaka’ as the female parent.

The unexpectedly produced resistant seedlings in all of these crosses clearly indicated that the inheritance of resistance to loquat canker Group C was controlled by one or more additional genes or loci other than the Pse-c (pse-c) locus. The large difference in the proportion of resistant seedlings from cross to cross suggested that the inheritance was controlled by unknown factors that were
not evident phenotypically in the parents, possibly with additive and/or dominant effects. Genetic control by some oligogenes or polygenes indicates that the resistance to loquat canker Group C, which is a qualitative reaction based on the absence or presence of black–brown cankers (Hiehata et al., 2012), may exhibit threshold characteristics (Falconer, 1981). Thus, the proportion of resistant seedlings can only be estimated by observing the offspring of the crosses, and breeders must choose parents and crosses that yield a high proportion of resistant seedlings based on the combining ability of the parents in each cross.

The proportion of the resistant seedlings from ‘Champagne’ × ‘Fusahikari’ (0.256) did not differ significantly from that in the reciprocal cross, ‘Fusahikari’ × ‘Champagne’ (0.414). It suggested that the inheritance is not controlled cytoplasmically, but rather is controlled by nuclear genes.

Segregation for the resistance to loquat canker Group C in seedlings from four crosses between ‘Champagne’ (pse-c/pse-c) and Pse-c/pse-c cultivars. If we assume that the genetic control of Group C resistance is solely associated with the Pse-c (pse-c) locus, the seedlings from crosses between ‘Champagne’ (pse-c/pse-c) and susceptible heterozygous (Pse-c/pse-c) cultivars should segregate into resistant (pse-c/pse-c) and susceptible (Pse-c/pse-c) offspring with a 1:1 ratio (i.e., a proportion of 0.50) for the resistant seedlings. The actual proportion of resistant seedlings from these four crosses ranged from 0.463 (with ‘Taisho’ as the male parent) to 0.701 (with ‘Mogi’ as the pollen parent) and averaged 0.601 (Table 3). The observed segregations in two of the four crosses fit the expected 1:1 ratio of resistant to susceptible seedlings, but in ‘Champagne’ × ‘Mogi’ and ‘Nagasakiwase’ × ‘Champagne’, the proportions of resistant seedlings were significantly higher than 0.5, and the segregation therefore did not fit the expected ratio. In addition, the proportions of resistant seedlings differed significantly among the four crosses ($\chi^2$ test, $p < 0.001$ by $\chi^2$ test).

Table 1. Parental cultivars used to produce progenies for determining the inheritance of the resistance to loquat canker Group C of ‘Champagne’ and their origin, evaluation, and genotype.

| Cultivars   | Origin               | Evaluation | Genotype     |
|------------|----------------------|------------|--------------|
| Champagne  | Selected and introduced to California ≈1908 | Resistant | pse-c/pse-c  |
| Fukuharawase | ‘Mizubo’ × a seedling of an unknown Chinese loquat | Susceptible | Pse-c/Pse-c  |
| Fusahikari  | ‘Mizubo’ × ‘Tanaka’ | Susceptible | Pse-c/Pse-c  |
| Kusunoki    | Derived from a seedling of an unknown Chinese loquat | Susceptible | Pse-c/Pse-c  |
| Mogi        | Derived from a seedling of an unknown Chinese loquat | Susceptible | Pse-c/Pse-c  |
| Morimoto    | Bud mutant of ‘Tanaka’ | Susceptible | Pse-c/Pse-c  |
| Nagasakiwase | ‘Mogi’ × ‘Hondaewase’ | Susceptible | Pse-c/Pse-c  |
| Obusa       | ‘Tanaka’ × ‘Kusunoki’ | Susceptible | Pse-c/Pse-c  |
| Suzukaze    | ‘Kusunoki’ × ‘Mogi’ | Susceptible | Pse-c/Pse-c  |
| Taisho       | Bud mutant of ‘Mogi’ | Susceptible | Pse-c/Pse-c  |
| Tanaka      | Derived from a seedling of an unknown Chinese loquat | Susceptible | Pse-c/Pse-c  |
| Togoshi    | ‘Mogi’ × ‘Tanaka’ | Susceptible | Pse-c/Pse-c  |
| Yougyoku    | ‘Mogi’ × ‘Morimoto’ | Susceptible | Pse-c/Pse-c  |

1Hiehata et al. (2012).
2It is likely that ‘Morimoto’ is homozygous-dominant because it is a bud mutant of ‘Tanaka’, which is homozygous-dominant.
3The genotype of ‘Obusa’ seems to be homozygous-dominant because it is a F1 of ‘Tanaka’ × ‘Kusunoki’, both of which are homozygous-dominant.
4It has been confirmed that genotypes of ‘Suzukaze’ and ‘Togoshi’ are homozygous-dominant by progeny tests (N. Hiehata, S. Fukuda, and O. Terai, unpublished data).

Table 2. Segregation of resistance to loquat canker Group C in the progenies between ‘Champagne’ (pse-c/pse-c) and susceptible cultivars with homozygous-dominant genotype (Pse-c/Pse-c) for the locus controlling the resistance of ‘Shiromogi’.

| Cross                      | No. of seedlings evaluated ($n_i$) | No. of seedlings | Proportion of resistant seedlings ($p = a/n_i$) | Confidence limit ($P = 0.95^{22}$) |
|----------------------------|-----------------------------------|-----------------|-----------------------------------------------|----------------------------------|
|                            | i                                 | Resistant ($a_i$) | Susceptible ($n_i$)                           | Lower                            | Upper                            |
| Champagne × Yougyoku       | 1                                 | 69              | 14                                             | 0.203 a                          | 0.108                            | 0.298                           |
| Suzukaze × Champagne       | 2                                 | 29              | 7                                              | 0.241 ab                         | 0.086                            | 0.397                           |
| Champagne × Fusahikari     | 3                                 | 43              | 11                                             | 0.256 ab                         | 0.125                            | 0.386                           |
| Champagne × Obusa          | 4                                 | 51              | 19                                             | 0.373 abc                        | 0.240                            | 0.505                           |
| Fusahikari × Champagne     | 5                                 | 58              | 24                                             | 0.414 abc                        | 0.287                            | 0.541                           |
| Champagne × Fukuharawase   | 6                                 | 72              | 31                                             | 0.431 bc                         | 0.316                            | 0.545                           |
| Tanaka × Champagne         | 7                                 | 53              | 24                                             | 0.453 bc                         | 0.319                            | 0.587                           |
| Champagne × Morimoto       | 8                                 | 61              | 30                                             | 0.492 bc                         | 0.366                            | 0.617                           |
| Champagne × Kusunoki       | 9                                 | 70              | 37                                             | 0.529 c                          | 0.412                            | 0.646                           |
| Champagne × Togoshi        | 10                                | 47              | 28                                             | 0.596 c                          | 0.455                            | 0.736                           |
| Total                     | 553 (N)                           | 225 (4)         | 328                                            |                                   |                                  |                                  |

Average $\chi^2$ (9 df) = ($\Sigma a_i p_i - \Sigma n_i p_i$)/[$\Sigma n_i (1-p_i)$] = 33.21***

1Confidence limit of proportion of resistant seedlings at $P = 0.95$ calculated as $p_i \pm 1.96\sqrt{[p_i (1-p_i)/n_i]}$.
2It is significant that $\chi^2$ test.

Table 3. Segregation of resistance to loquat canker Group C in progenies between ‘Champagne’ (pse-c/pse-c) and susceptible cultivars with heterozygous genotype (Pse-c/pse-c) for the locus controlling the resistance of ‘Shiromogi’.

| Cross                      | No. of seedlings evaluated ($n_i$) | No. of seedlings | Proportion of resistant seedlings ($p = a/n_i$) | Confidence limit ($P = 0.95^{22}$) |
|----------------------------|-----------------------------------|-----------------|-----------------------------------------------|----------------------------------|
|                            | i                                 | Resistant ($a_i$) | Susceptible ($n_i$)                           | Lower                            | Upper                            |
| Champagne × Taisho         | 1                                 | 41              | 19                                             | 0.220                            | 0.639                            | 0.463                           |
| Mogi × Champagne           | 2                                 | 46              | 24                                             | 0.087                            | 0.768                            | 0.522                           |
| Nagasakiwase × Champagne   | 3                                 | 29              | 20                                             | 4.172                            | 0.041                            | 0.690                           |
| Champagne × Mogi           | 4                                 | 67              | 47                                             | 10.881                           | 0.001                            | 0.701                           |
| Total                     | 183 (N)                           | 110 (4)         | 73                                             |                                   |                                  |                                  |

Average $\chi^2$ (3 df) = ($\Sigma a_i p_i - \Sigma n_i p_i$)/[$\Sigma n_i (1-p_i)$] = 8.21*

1Data tested for goodness-of-fit to a 1:1 ratio.
2Confidence limit of proportion of resistant seedlings at $P = 0.95$ calculated as $p_i \pm 1.96\sqrt{[p_i (1-p_i)/n_i]}$.
3*Significant at $P < 0.05$ by $\chi^2$ test.
of the seedlings have the genotype between ‘Champagne’ and susceptible cultivar specific combining ability for each cross beestimated by performing the crosses and the expected proportion of resistant seedlings from inheritance controlled solely by the additive and dominance gene effects, respectively.

Estimation of the combining abilities of crosses between ‘Champagne’ and the Pse-c/Pse-c cultivars. First, we observed the expected proportion of resistant seedlings for each cross between ‘Champagne’ and susceptible cultivar $i$ (PRS). Second, we assumed that PRS$S_i$ was zero for crosses between ‘Champagne’ and the Pse-c/Pse-c cultivars. Third, we estimated GCA as the value that remains after subtracting the expected proportion of resistant seedlings (PRS$S_i$ = 0.000) from the average proportion of resistant seedlings for all crosses between ‘Champagne’ and the Pse-c/Pse-c cultivars weighted by the number of seedlings in each cross; the weighted average for all cultivars combined was 0.407 (Table 4). We included the results of the reciprocal crosses between ‘Champagne’ and ‘Fusuhikari’ in this calculation and estimated the weighted average, because they did not differ significantly. Fourth, we estimated the total combining ability (GCA + SCA), which cannot be separated into GCA and SCA based on the available data. Fortunately, GCA + SCA is sufficient to guide breeders to choose superior crosses.

GCA (0.407) differed greatly from PRS$S_i$ (0.000). However, GCA + SCA was not large, ranging from −0.204 to +0.189 (Table 4), indicating a minor modification of the proportion of resistant seedlings, although there were significant differences among the crosses (Table 2).

GCA + SCA was high for ‘Champagne’ × ‘Togoshi’ and ‘Champagne’ × ‘Kusunoki’ at 0.189 and 0.122, respectively. In contrast, ‘Champagne’ × ‘Yougyoku’ and ‘Suzukaze’ × ‘Champagne’ had low GCA + SCA, at −0.204 and −0.166, respectively. GCA + SCA did not differ greatly among the other crosses. We should note that the GCA + SCA estimates contain an error component that results from the number of evaluated seedlings in each cross (sampling error).

Table 4. GCA + SCA estimates of susceptible cultivars with Pse-c/Pse-c and Pse-c/pse-c for the locus controlling the resistance of ‘Shiromogi’ to loquat canker Group C in crossing with ‘Champagne’.

| Cultivar                  | No. of seedlings | Proportion of resistant seedlings (PRS$S_i$) | GCA  | GCA + SCA |
|--------------------------|------------------|---------------------------------------------|------|----------|
| Pse-c/Pse-c cultivar     |                  |                                             |      |          |
| Fukuharawase             | 72               | 0.431                                       | 0.000| 0.407    |
| Fushihikari              | 101              | 0.347                                       | 0.000| 0.407    |
| Kusunoki                 | 70               | 0.529                                       | 0.000| 0.407    |
| Morimoto                 | 61               | 0.492                                       | 0.000| 0.407    |
| Obusa                    | 51               | 0.373                                       | 0.000| 0.407    |
| Suzukaze                 | 29               | 0.241                                       | 0.000| 0.407    |
| Tanaka                   | 53               | 0.453                                       | 0.000| 0.407    |
| Togoshi                  | 47               | 0.596                                       | 0.000| 0.407    |
| Yougyoku                 | 69               | 0.203                                       | 0.000| 0.407    |
| Weighted average         |                  |                                             | 0.407|          |
| Pse-c/pse-c cultivar     |                  |                                             |      |          |
| Mogi                     | 113              | 0.628                                       | 0.500| 0.101    |
| Nagasakisawase           | 29               | 0.690                                       | 0.500| 0.101    |
| Taisho                   | 41               | 0.463                                       | 0.500| 0.101    |
| Weighted average         |                  |                                             | 0.601|          |
to downy mildew (Plasmopara viticola) in grapevine (Vitis spp.; Brown et al., 1999), necrotic scab (Venturia nashicola) in Japanese pear [Pyrus pyrifolia (Burm. f.) Nakai] and Chinese pear (Pyrus bretschneideri Rehder; Abe and Kotobuki, 1998), and scab (Venturia inaequalis) in apple (Malus pumila Mill.; Williams and Kuc, 1969). In our previous study, the observed segregation in most crosses between ‘Shiromogi’ (pse-c/pse-c) and the Pse-c/pse-c cultivars fit the expected ratio (one resistant:one susceptible), but we observed significant segregation distortion in two crosses (Hiehata et al., 2012). This bad fit may be explained by the existence of one or more quantitative trait loci in addition to the Pse-c (pse-c) locus.

Therefore, we conclude the resistance to loquat canker Group C is polygenic or controlled by one or more oligogenes in addition to pse-c. The inheritance of one or more recessive genes and of one or more polygenes has been reported in the resistance to fusarium wilt (Fusarium oxysporum f. sp. melonis) in melon (Cucumis melo L.; Nakazumi and Hirai, 2004), which is similar to the results obtained in the present study. There were some reports that resistance to scab in apple and pear is controlled by both a dominant major gene and polygenes (Abe et al., 2000; Lamb et al., 1985).

There were many reports about the inheritance of resistance to pathogens of Pseudomonas syringae in several crops besides loquat. Resistance controlled by major genes has been described in tomato (Solanum lycopersicum L.; Martin et al., 1993) to P. syringae pv. tomato, in soybean [Glycine max (L.) Merrill; Keen and Buzzell, 1991] to P. syringae pv. glycinea, in maize (Zea mays L.; Xu et al., 2009) to P. syringae pv. syringae and in cucumber (Cucumis sativus L.; Olczak-Wolmam et al., 2009) to P. syringae pv. lachrymans. In contrast, resistance of bean (Phaseolus vulgaris L.; Yaish et al., 2006) to P. syringae pv. phaseolicola and of pea (Pisum sativum L.; Fondevilla et al., 2012) to P. syringae pv. syringae is under polygenic control. On the other hand, Taylor et al. (1996) reported that race-specific resistance to P. syringae pv. phaseolicola in bean was controlled by major genes, whereas non-race-specific resistance exhibited quantitative inheritance. Considering that ‘Champagne’ exhibits resistance to all three groups of loquat canker, it might have non-race-specific resistance.

Implications for breeding for resistance to loquat canker. Because the resistance to loquat canker Group C from ‘Shiromogi’ is a recessive trait, it was more difficult to breed cultivars resistant to Group C than that of Groups A and B, for which the resistance is dominant (Hiehata et al., 2002b; Morita et al., 1985). In the present study, we found that ‘Champagne’ had a high GCA and consequently produced resistant plants in all crosses with homozygous-dominant cultivars, even for cultivars that did not produce resistant seedlings in crosses with ‘Shiromogi’ (Hiehata et al., 2012). However, the proportion of resistant seedlings varied among the crosses, as was the case for scab in apple (Kellerhals et al., 1993). This information will facilitate the breeding of resistant cultivars because ‘Champagne’ could produce resistant seedlings through a single cross, even crossed with cultivars that did not produce resistant seedlings in crosses with ‘Shiromogi’.

The quality of fruit produced by ‘Champagne’ is not as good as that of accessions that possess pse-c derived from ‘Mogi’ (e.g., ‘Shiromogi’, ‘Nagasakiwase’). However, the fruit maturity stage of ‘Champagne’ is earlier than that of these cultivars derived from ‘Mogi’ (Nagato et al., 1996). Because ‘Champagne’ is homozygous-dominant for Pse-c (Hiehata et al., 2002b), it is a valuable breeding material to produce cultivars with precocious character. Also, ‘Champagne’ is less closely related genetically to the mentioned materials that possess pse-c derived from ‘Mogi’ (Fukuda et al., 2013), it may help breeders to avoid the inbreeding depression that has been reported in fruit bushes and trees such as rabbit-eye blueberry (Vaccinium ashei Reede; Lyrene, 1983), persimmon (Diophysys kaki Thunb.; Yamada, 1993), and Japanese pear (Sato et al., 2008). In addition, introgression of the resistance from ‘Champagne’ into existing cultivars would decrease the possibility of breakdown of the Group C resistance conferred by a single major gene (pse-c), which has been reported for some diseases (Kiyosawa, 1982; Parisi et al., 1993). ‘Champagne’ is therefore a valuable breeding resource for canker resistance.

Literature Cited

Abe, K., and K. Kobotuki. 1998. Polygenic inheritance of necrotic reaction to pear scab (Venturia nashicola Tanaka et Yamamoto) in Japanese pear (Pyrus pyrifolia Nakai) and Chinese pear (P. ussuriensis Maxim.). J. Jpn. Soc. Hort. Sci. 67:839–842.

Abe, K., K. Kobotuki, 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.

Brown, M.V., J.N. Moore, R.W. McNew, and P. Fenn. 1971. Many spores of Pseudomonas syringae pv. syringae: Evidence that one of them interacts with a bacterial elicitor. Theor. Appl. Genet. 81:133–138.

Kellerhals, M., A. Fouillet, and Y. Lespinasse. 1993. Effect of the scab inoculum and the susceptible parent on resistance to apple scab (Venturia inaequalis) in the progenies of crosses to the scab resistant cv ‘Floriana’. Agronomie 13:631–636.

Kiyosawa, S. 1982. Genetics and epidemiological modeling of breakdown of plant disease resistance. Annu. Rev. Phytopathol. 20:93–117.

Lai, M., W.O. McCartney, and C.W. Morin. 1971. Canker of loquat caused by Pseudomonas sp. Phytopathology 61:248–249.

Lamb, R.C., H.S. Aldwinckle, and D.E. Terry. 1985. ‘Freedom’, a disease-resistant apple. HortScience 20:774–775.

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.

Martin, G.B., S.H. Sharpee, and J. Janick. 1999. Loquat: Botany and horticulture. Hort. Rev. 23:233–276.
varietal resistance against loquat canker. Spec. Bull. Nagasaki Fruit Tree Expt. Sta. p. 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., I. Ichinose, and K. Asada. 1985. Analysis of resistant gene in loquat canker. I. Kyushu Agric. Res. 47:101.
Morton, J.F. 1987. Fruits of warm climates. Creative Resource Systems, Winterville, FL.
Mukoo, H. 1952. Studies on the causal bacteria of the loquat canker (1). Bull. Natl. Inst. Agr. Sci. C-1:1–190.
Nagato, J., O. Terai, T. Nakao, Y. Matsushita, N. Hiehata, K. Asada, A. Morita, M. Hashimoto, and Y. Sato. 1996. Characteristics in genetic resources of Eriobotrya spp. Bull. Nagasaki Fruit Tree Expt. Sta. 3:55–77.
Nakata, K. 1934. Crop disease figures [in Japanese]. Youkendo, Tokyo, Japan.
Nakazumi, H. and G. Hirai. 2004. Diallel analysis for resistance of melon (Cucumis melo) to fusarium wilt caused by Fusarium oxysporum Esp. melonis race 1,2y. Breeding Res. 6:65–70.
Nesumi, H. 2006. Loquat (biwa), p. 85–95. In: The Japanese Society for Horticultural Science (eds.). Horticulture in Japan 2006. Shoukadou Publication, Kyoto, Japan.
Olczak-Woltman, H., G. Bartoszewski, W. Mądry, and K. Niemirowiecz-Szczytt. 2009. Inheritance of resistance to angular leaf spot (Pseudomonas syringae pv. lachrymans) in cucumber and identification of molecular markers linked to resistance. Plant Pathol. 58:145–151.
Parisi, L., Y. Lespinasse, J. Guillaume, and J. Krüger. 1993. A new race of Venturia inaequalis virulent to apples with resistance due to the Vf gene. Phytopathology 83:533–537.
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.
Snedecor, G.W. and W.G. Cochran. 1967. Statistical methods. 6th Ed. The Iowa State Univ. Press, Ames, IA.
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. Bull. Nagasaki Fruit Tree Expt. Sta. 10:30–40.
Taylor, J.D., D.M. Teverson, and J.H.C. Davis. 1996. Sources of resistance to Pseudomonas syringae pv. phaseolicola races in Phaseolus vulgaris. Plant Pathol. 45:479–485.
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’. Bull. Nagasaki Fruit Tree Expt. Sta. 10:1–13.
Williams, E.B. and J. Kuc. 1969. Resistance in Malus to Venturia inaequalis. Annu. Rev. Phytopathol. 7:223–246.
Wimalajeewa, D.L.S., I.G. Pascoe, and D.L. Jones. 1978. Bacterial stem canker of loquat. Australas. Plant Pathol. 7:33.
Xu, L., Y. He, D. Zhang, J. Dai, and S. Wang. 2009. Identification and fine-mapping of a bacterial brown spot disease resistance gene in maize. Mol. Breed. 23:709–718.
Yaish, M.W.F., D. Sosa, F.J. Vences, and F. Vaquero. 2006. Genetic mapping of quantitative resistance to race 5 of Pseudomonas syringae pv. phaseolicola in common bean. Euphytica 152:397–404.
Yamada, M. 1993. Persimmon breeding in Japan. Jpn. Agr. Res. Q. 27:33–37.