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# Resistance Sources to *Xanthomonas fragariae* in Non-octoploid Strawberry Species

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***Abstract.*** **Forty-three accessions from 11 strawberry species were screened in the greenhouse for resistance to three strains of *Xanthomonas fragariae* Kennedy and King. Among the accessions tested, Pen-5 of *Fragaria pentaphylla* Losink expressed either no symptoms or a hypersensitive reaction, while accessions Pen-2 and Pen-4 developed either no symptoms or restricted water-soaked lesions. Two accessions of *F. moschata* Duch were characterized by reduced translucency at the inoculation site in the course of symptom development. These accessions, representing three resistance types, were classified as highly resistant, resistant, and moderately resistant, respectively, based on mean separation of disease severity ratings. The classifications proved to be consistent with the results from measurements of bacterial populations on inoculated leaves of those genotypes. The study suggests that species of *F. pentaphylla* and *F. moschata* harbour diversified sources of resistance. Resistant genotypes were not detected in *F. nilgerrensis* Schlect, *F. daltoniana* J. Gay, *F. nubicola* Lindl, *F. gracilis* Losinsk, *F. iinumae* Makino, *F. vesca* L., *F. viridis* Duch, or *F. orientalis* Losinsk.**

Bacterial angular leaf spot, caused by *Xanthomonas fragariae* Kennedy and King (1962a), is the most damaging bacterial disease of strawberries. Reported yield losses associated with this disease range from 4.8% to 7.4% in artificially inoculated fields (Roberts et al., 1997), to as high as 75% in a naturally infested field (Epstein, 1966). In the decades since its first documented discovery in Minnesota in 1949 (Kennedy and King, 1960), bacterial angular leaf spot has spread over many strawberry growing regions around the world (Maas et al., 2000). Concerns regarding dissemination of this pathogen were so high that European countries listed it as a quarantined pest (Smith et al., 1992). The yield losses caused by *X. fragariae* are largely due to leaf infection, although the calyx can also be infected to such an extent that its fruit becomes unmarketable (Maas et al., 1995). Chemical treatments can be effective in controlling the pathogen (Averre and Driver, 1994; Roberts et al., 1997), but this approach raises environmental and health concerns. Genetic resistance is considered to be an effective and achievable approach to manage this disease (Lewers et al., 2003).

Kennedy and King (1962b) tested 64 cultivars and clones from *Fragaria ×ananassa* and *F. vesca* L. and found that *F. ×ananassa* selection Minnesota 1716 and *F. vesca* L. 'Alpine' had the lowest disease severities. A genotype immune to *X. fragariae* was reported in *F. moschata* Duch (Hazel, 1981). Two other resistant genotypes were identified in the octoploid species *F. virginiana* and a hybrid (Maas et al., 2000). To date, there is little published information on the resistance sources concerning most other *Fragaria* species. The objective of this study was to screen non-octoploid *Fragaria* species for new sources of resistance to *X. fragariae*. To compare the level of resistance in different resistant types, we also analyzed bacterial population dynamics in genotypes showing typical reactions to the bacterial infection. The study was intended to generate important information for strawberry breeding programs involving synthetic octoploids, for which streamlined techniques are already available (Bors, 2000).

## Materials and Methods

*Plant materials.* A total of 43 accessions representing 11 strawberry species, namely *F. daltoniana*, *F. gracilis*, *F. iinnumae*, *F. nilgerensis*, *F. nubicola*, *F. pentaphylla*, *F. vesca*, *F. viridis*, *F. orientalis*, *F. moschata* and *F. ×ananassa*, were included in the study (Table 1). Strawberry plants were grown in plastic pots (8 × 8 cm) filled with Sunshine Mix No. 4 potting medium (Sun Gro Horticultural, Ltd., Canada), and kept in a greenhouse [22 °C day/15 °C night with a 16 h photoperiod (natural light supplemented with high-pressure sodium light)] for 2 to 3 months before use in experiments. Plants were watered as required and care was taken not to wet the leaves of those species susceptible to other leaf diseases. Fertilizer (20N–8.8P–16.6K) was applied weekly.

*Bacterial inoculum.* Three strains of *X. fragariae*, Xf-3, Xf-6, and Xf-1425 (courtesy of John S. Hartung, USDA, Beltsville, Md.) were used in resistance screening. To confirm pathogenicity upon receipt, the bacteria were used to inoculate a susceptible cultivar (*F. ×ananassa* 'Camarosa'). The bacteria were reisolated and propagated in 'Medium A' [0.8% (w/v) nutrient broth (Difco, Kansas City, Mo.), 0.2% (w/v) $Ca(NO_3)_2$, 0.001% (w/v) $FeSO_4 \cdot H_2O$, 0.001% (w/v) $MnSO_4$, 0.5% (w/v) casein hydrolysate and 0.1% (w/v) yeast extract (Hazel and Civerolo, 1980)] at 24 °C for 24 h before use in inoculation experiments. For preparation of inoculum, cultures were centrifuged at 2770 $g_n$ for 10 min, washed twice with sterile distilled water, and adjusted to a final concentration of $3.5 \times 10^8$ colony forming units (cfu)/mL ($OD_{595} = 0.1$).

*Inoculation and disease assessment.* Strawberry plants were inoculated using a syringe as described in Maas et al. (2000). Each leaflet of the two newly expanded trifoliate leaves was inoculated at three points, resulting in 18 inoculation sites per plant in all species except for *F. daltoniana* and *F. iinumae*, on which only six sites were inoculated per plant due to their small leaf size. Immediately after inoculation, plants were incubated for three days in transparent plastic bags in a shaded greenhouse (22 °C day/15 °C night with a 16 h photoperiod). They were subsequently moved onto a mist bed in another greenhouse, where mist was provided for periods of 45 s at 30 min intervals for 15 h every day. After 1 week on the mist bed, the plants were transferred back to the shaded greenhouse.

Disease severity was assessed 14 d postinoculation in preliminary screening, and 3, 8, 13, and 18 d postinoculation in verification screening. Symptoms were assessed according to a 0 to 5 scale modified from Maas et al. (2000), where 0 = no macroscopic symptoms, 1 = hypersensitive reaction, 2 = necrosis or lost translucency within the inoculation site, 3 = chlorosis or water-soaked lesion evident within the inoculated site, 4 = water-soaked lesion expanded beyond inoculation site, or development of secondary infection, with or without partial necrosis, and 5 = total and expanded necrosis of the inoculation site. A hypersensitive reaction was visually confirmed by the presence of necroses 24 h postinoculation.

*Resistance screening.* A factorial treatment (3 strains × 43 genotypes) in a randomized complete block design (RCBD) with two replicates of single-plant pots was used for the preliminary screening of 43 accessions against strains Xf-3, Xf-6, and Xf-1425 of *X. fragariae*. The preliminary screening was repeated twice, using the same genotypes and strains.

Following preliminary screening, eleven selected genotypes were subjected to an additional round of verification screening with bacterial strains Xf-6 and Xf-1425. In the

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verification screening, nine plants of each genotype were arranged in a complete randomized design.

*Bacterial population dynamics.* Bacterial population dynamics were studied on five selected genotypes inoculated with *X. fragariae* strain Xf-6. The genotypes selected showed a range of symptomatic reactions in the screening tests, and included: Pen-5 (no symptoms or a hypersensitive reaction), Pen-2 (no symptoms or restricted water-soaked lesions), Mcv-2 (lost translucency or restricted water-soaked lesions), Gra-2 (restricted necrosis 3 d after inoculation), and 'Camarosa' (expanded water-soaked lesions). To assess bacterial populations, an area of approximately 25 $mm^2$ around each of five randomly selected inoculation sites per genotype was excised with a sterile scalpel at 0, 4, 8, 12, and 16 d postinoculation. Harvested tissue was placed in a sterile 1.5 mL microcentrifuge tube, ground with a plastic pestle, and resuspended in a final volume of 1 mL sterile distilled water. The homogenate was serially diluted 10-fold in sterile distilled water, and 0.1 mL of each dilution was plated onto SPA medium (Hayward, 1960). The number of bacteria (cfu/$mm^2$) was calculated following incubation of the plates for four days at room temperature.

*Statistical analysis.* The average rating of all inoculation sites on a plant was taken as a data point in all screening tests. Normal score plotting indicated that the nontransformed data appeared more normally distributed than any transformed data from the preliminary or verification screening, and therefore the original data was used in analysis. As the analysis of variance (ANOVA) revealed no significant effect of blocks, strains, and strain × genotype interaction ($P > F = 0.64$), data on disease severity was pooled over strains for mean separation with least significant difference (LSD). However, due to a significant test × genotype interaction, mean disease severities are reported separately for the two repetitions of the preliminary screening (Table 1). The accessions were divided into five groups according to mean separation of disease severity ratings: highly resistant (HR), resistant (R), moderately resistant (MR), susceptible (S), or highly susceptible (HS) (grouping detail not shown).

In the study of bacterial population dynamics, data transformed by the natural logarithm appeared most normally distributed. In addition to individual analysis of the data collected at the various times after inoculation, the transformed data was also analyzed collectively using multivariate analysis, split-block analysis and orthogonal contrast with the model: $Y_0\ Y_4\ Y_8\ Y_{12}\ Y_{16}$ = genotype [using the repeat and polynomial options, where Y is the bacterial population measured at a particular time-point (i.e., 0, 4, 8, 12 or 16 d postinoculation)]. Data from bacterial population growth measurements on each genotype was also subjected to linear regression analysis. Statistical analyses were conducted with SAS 8.2 software (SAS Institute Inc., 1999), using the general linear model procedure (PROC GLM).

Table 1. Mean disease severity rating and reaction of *Fragaria* accessions to strains Xf-3, Xf-6 and Xf-1425 of *Xanthomonas fragariae* 14 d postinoculation.

| | Test 1 | | Test 2 | |
|---|---|---|---|---|
| Accession[z] | Rating | Reaction[y] | Rating | Reaction |
| *F. daltoniana* | | | | |
| Dal-3 $_{RBGE}$ | 3.08[x] | S | 3.83 | S |
| *F.gracilis* | | | | |
| Gra-2 $_{NCGR}$ | 2.13 | R | 2.0 | R |
| Gra-1 $_{NCGR}$ | 3.42 | HS | 3.47 | S |
| *F. iinumae* | | | | |
| Ii-3 $_{NCGR}$ | 3.58 | HS | 3.75 | HS |
| *F. nilgerensis* | | | | |
| Nil-6 $_{NCGR}$ | 3.25 | S | 2.82 | MR |
| Nil-4 $_{NCGR}$ | 3.42 | HS | 2.98 | S |
| Nil-1 $_{NCGR}$ | 3.25 | S | 3.15 | S |
| Nil-5 $_{NCGR}$ | 3.33 | HS | 3.47 | S |
| *F. nubicola* | | | | |
| Nub-6 $_{UGPH}$ | 2.43 | R | 2.18 | MR |
| Nub-1 $_{NCGR}$ | 2.58 | MR | 2.57 | MR |
| Nub-2 $_{NCGR}$ | 3.0 | MR | 3.05 | S |
| Nub-5 $_{UGPH}$ | 3.67 | HS | 4.05 | HS |
| *F. pentaphylla* | | | | |
| Pen-5 $_{NCGR}$ | 1.0 | HR | 0.83 | HR |
| Pen-2 $_{RBGE}$ | 2.05 | R | 1.7 | R |
| Pen-4 $_{UGPH}$ | 2.18 | R | 2.38 | MR |
| Pen-1 $_{RBGE}$ | 2.98 | MR | 2.58 | MR |
| Pen-3 $_{UGPH}$ | 2.92 | MR | 3.13 | S |
| *F. vesca* | | | | |
| Vw-20 $_{UGPH}$ | 2.97 | MR | 2.87 | MR |
| Vcv-13 $_{UGPH}$ | 3.18 | S | 2.93 | S |
| Vw-4 $_{UGPH}$ | 3.07 | S | 2.97 | S |
| Vcv-24 $_{UGPH}$ | 3.33 | HS | 3.02 | S |
| Vcv-21 $_{UGPH}$ | 3.17 | S | 3.15 | S |
| Vw-53 $_{UGPH}$ | 3.25 | S | 3.15 | S |
| Vw-76 $_{UGPH}$ | 3.33 | HS | 3.38 | S |
| Vcv-8 $_{UGPH}$ | 3.42 | HS | 3.40 | S |
| *F. viridis* | | | | |
| Vir-1 $_{NCGR}$ | 3.42 | HS | 3.07 | S |
| Vir-10 $_{UGPH}$ | 3.75 | HS | 3.25 | S |
| Vir-5 $_{RBGE}$ | 3.75 | HS | 3.27 | S |
| Vir-8 $_{UGPH}$ | 3.50 | HS | 3.67 | HS |
| *F. orientalis* | | | | |
| Orif-6 $_{UGPH}$ | 3.08 | S | 3.03 | S |
| Orim-1 $_{UGPH}$ | 3.33 | HS | 3.63 | HS |
| Orif-4 $_{UGPH}$ | 3.42 | HS | 3.67 | HS |
| Orim-6 $_{UGPH}$ | 3.50 | HS | 3.30 | S |
| *F. moschata* | | | | |
| Mw-1 $_{NCGR}$ | 2.12 | R | 1.52 | R |
| Mcv-2 $_{NCGR}$ | 2.22 | R | 1.73 | R |
| Mw-6 $_{UGPH}$ | 3.18 | S | 3.5 | S |
| Mw-7 $_{UGPH}$ | 3.33 | HS | 3.55 | HS |
| Mcv-1 $_{NCGR}$ | 3.42 | HS | 3.63 | HS |
| Mw-9 $_{UGPH}$ | 3.50 | HS | 4.0 | HS |
| *F. ×ananassa* | | | | |
| Camarosa | 3.08 | S | 2.68 | MR |
| Kent | 3.08 | S | 3.13 | S |
| Honeoye | 3.25 | S | 3.35 | S |
| Annapolis | 3.42 | HS | 3.55 | HS |
| LSD | 0.47 | $P \leq 0.05$ | 0.49 | $P \leq 0.05$ |

[z]Accessions of wild species are followed by subscripted abbreviations indicating sources: RBGE = Royal Botanical Garden Edinburgh, NCGR = National Clonal Germplasm Repository, UGPH = University of Guelph.

[y]The reactions were classified through mean separation by LSD at a significance of $P \leq 0.05$ (data not shown); HR = highly resistant, R = resistant, MR = moderately resistant, S = susceptible, HS = highly susceptible.

[x]Mean disease severity rating calculated from six plant data pooled over three bacterial strains, where each plant had 6 to 18 rated inoculation sites. Disease severity rating criteria are described in Materials and Methods.

## Results and Discussion

Of the 43 strawberry genotypes screened against *X. fragariae*, Pen-5 had the lowest disease severity rating, significantly different from that of all other genotypes, and was classified as highly resistant. Genotypes Gra-2, Pen-2, Mw-1, and Mcv-2 were classified as resistant in both repeats of the preliminary screening, while Nub-6 and Pen-4 were grouped as resistant in one test and moderately resistant in the other (Table 1). In the verification screening, early evaluation of disease severity did not differentiate well between resistant and susceptible genotypes. Therefore, the data from the 18th day postinoculation was used for mean separation analysis. The analysis indicated that Pen-5 was highly resistant, Pen-2 and Pen-4 were resistant, whereas Gra-2, Mw-1, Mcv-2, Nub-1, Nub-6, and Pen-1 were moderately resistant (Table 2).

Resistance to *X. fragariae* appeared sen-

sitive to environmental conditions in some accessions, and this was reflected by the significant test × genotype interaction ($P > F = 0.04$) in our preliminary screening. Such interaction occurred primarily on genotypes with moderate resistance, such as Nub-2 and Nub-6 (Table 1). In contrast, the highly resistant genotype Pen-5, as well as a number of resistant genotypes, such as Pen-2 and Gra-2, exhibited a consistent response to challenge by *X. fragariae* (Table 1). Nevertheless, due to the inconsistency in the reaction of some genotypes in the preliminary screening, we considered the results from the verification screening to be more accurate. Nine of eleven genotypes gave consistent reactions to the two strains used in the verification screening (Table 2), and their resistance classifications were also consistent with the results obtained in the bacterial population measurements (see below).

Multivariate and split-block analysis of *X. fragariae* colony forming units on five selected strawberry genotypes revealed a significant genotype effect on bacterial populations, while orthogonal contrast analysis also indicated a significant genotype effect on the slopes of population growth curves ($Pr > F = 0.00$ for all the statistics). These results are consistent with the fact that different genotypes showed varying levels of resistance to *X. fragariae* in preliminary and verification screening (Tables 1 and 2). Furthermore, regression analysis indicated that growth of *X. fragariae* populations was linear on the susceptible genotype 'Camarosa' (coefficient of determination = 0.92), but that it did not fit the linear model on the other genotypes tested (Fig. 1).

As would be expected, bacterial populations were generally found to be lower on genotypes classified as resistant or moderately resistant versus genotypes classified as susceptible (Fig. 1). The lowest bacterial populations were obtained from the highly resistant accession Pen-5 at all time-points beginning on the fourth day postinoculation (Fig. 1), although the numbers of colony forming units obtained from resistant (Pen-2) or moderately resistant (Mcv-2 and Gra-2) accessions were not significantly lower than those obtained from the susceptible genotype 'Camarosa' until the eighth day postinoculation (Fig. 1). However, from the eighth day onwards, bacterial populations were observed to be significantly lower in the resistant or moderately resistant accessions compared with 'Camarosa' (Fig. 1). These observations are reflected in the fact that multivariate and split-block analysis of *X. fragariae* colony forming units revealed a significant time effect on populations and a significant time × genotype interaction ($Pr > F = 0.00$), in addition to the significant genotype effect noted above.

Therefore, just as early evaluation of disease severity did not differentiate well between resistant and susceptible genotypes in the verification screening, early measurement of colony forming units also failed to accurately distinguish resistant from susceptible genotypes (Fig. 1). It appears that *X. fragariae* population dynamics are well-correlated with the resistance screening data, in terms of both the time-course and severity of disease development, and are an accurate reflection of the ability (or inability) of the bacterium to propagate in strawberry genotypes with differing levels of resistance.

Based on the progression and characteristics of symptoms on *Fragaria* species over the 18 d postinoculation period, we identified five types of symptomatic reactions among the accessions tested, which we termed: type I (no symptoms or a hypersensitive reaction, represented only by Pen-5), type II (no symptoms or appearance of restricted water-soaked lesions, observed in Pen-2 and Pen-4), type III (lost translucency or callus-like necrosis, observed in Mcv-1 and Mw-1), type IV (nonexpanding chlorosis turning into black necrosis 3 d postinoculation, observed in Gra-2, Nub-1, and Nub-6), and type V (expanding, translucent water-soaked lesions that might become necrotic, as observed in most susceptible genotypes). These reaction types differ from the categories described by Maas et al. (2000) in that they can accommodate the entire range of symptoms that may develop on a single genotype after inoculation. Furthermore, the assessment of symptoms using our scale is consistent with the results obtained from the

Table 2. Reaction of *Fragaria* genotypes to strains Xf-6 and Xf-1425 of *Xanthomonas fragariae* 18 d postinoculation.

| | Xf-6 | | Xf-1425 | |
|---|---|---|---|---|
| Genotype | Rating | Reaction[z] | Rating | Reaction |
| *F. pentaphylla* | | | | |
| Pen-5 | 0.7[y] | HR | 0.97 | HR |
| Pen-4 | 1.33 | R | 1.32 | R |
| Pen-2 | 1.43 | R | 1.74 | R |
| Pen-1 | 2.0 | MR | 2.46 | S |
| *F. moschata* | | | | |
| Mcv-2 | 1.93 | MR | 2.0 | MR |
| Mw-1 | 2.0 | MR | 1.94 | MR |
| *F. nubicola* | | | | |
| Nub-1 | 2.0 | MR | 1.92 | MR |
| Nub-6 | 1.92 | MR | 2.0 | MR |
| *F. gracilis* | | | | |
| Gra-2 | 1.97 | MR | 2.0 | MR |
| *F. ×ananassa* | | | | |
| Camarosa | 3.08 | S | 3.44 | HS |
| Annapolis | 3.56 | HS | 3.67 | HS |
| LSD | 0.47 | $P \leq 0.05$ | 0.58 | $P \leq 0.05$ |

[z]HR = highly resistant, R = resistant, MR = moderately resistant, S = susceptible, HS = highly susceptible.
[y]Mean disease severity rating of nine plants, each inoculated at 18 locations on two newly expanded trifoliate leaves. Rating criteria for each inoculation site are described in Materials and Methods.

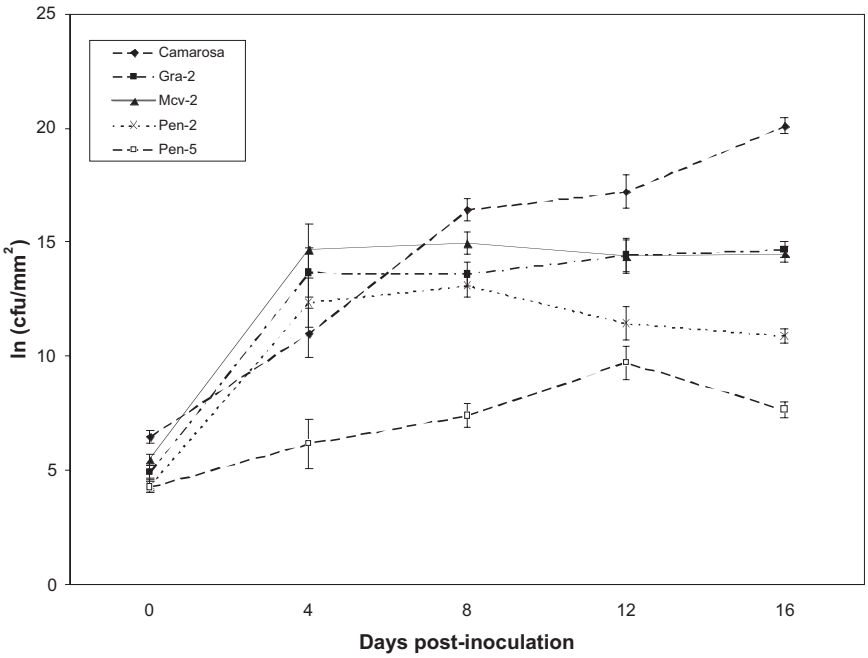


Fig.1. Colony-forming units of *Xanthomonas fragariae* strain Xf-6 on selected *Fragaria* genotypes at various times after inoculation. Colony forming units per square millimeter were calculated over five inoculated sites per genotype and transformed into the natural logarithm. 'Camarosa' is a susceptible cultivar of *F. ×ananassa*, Gra-2 is a moderately resistant accession of *F. gracilis*, Mcv-2 is a moderately resistant accession of *F. moschata*, and Pen-2 and Pen-5 are resistant and highly resistant accessions, respectively, of *F. pentaphylla*. Error bars represent the $LSD_{0.05}$ at each time-point after inoculation.

bacterial population measurements (Fig. 1).

The type IV reaction was referred to as normosensitive necrosis and regarded as a susceptible reaction by Smith and Mansfield (1981). Thus, it is debatable whether Gra-2, Nub-1 and Nub-6 are resistant. However, the type III reaction should be considered resistant, since the formation of a callus is probably associated with cell-wall modifications, a mechanism of resistance (Vidhyasekaran, 2002). In general, Pen-5 is a highly resistant genotype, Pen-2 and Pen-4 are resistant, and Mw-1 and Mcv-2 are recognized as moderately resistant.

Clearly, *F. pentaphylla* and *F. moschata* possess numerous sources of resistance. However, we did not find any immune genotypes in *F. moschata* as reported by Hazel (1981). Similarly, in contrast with the findings of Kennedy and King (1962b), no resistant accessions of *F. vesca* were identified. This may be related to the limited size of the collection that we tested, or is perhaps due to variation in the screening methods employed. In accession Pen-5, a lack of symptoms was often observed on older leaves, while a hypersensitive reaction always developed on younger leaves inoculated with a high concentration of *X. fragariae*. This suggests that this genotype may possess several resistance mechanisms: an antimicrobial substance(s) might contribute to the first line of defence, followed by a hypersensitive reaction when the first line of defence has failed. Perhaps older leaves possess more antimicrobial substances.

The various resistance reactions observed on different genotypes reinforced our hypothesis that non-octoploid wild species possess diversified sources of resistance against *X. fragariae*. In contrast, only a single type of resistance reaction has been identified to date in octoploid species, characterized by reduced translucency at the inoculation site (Maas et al. 2000). Thus, non-octoploid species may serve as an important resource in breeding for resistance to bacterial angular leaf spot, although incorporation of this resistance will involve interspecific crossing (Bors and Sullivan, 1997) and a long term breeding program. Such a long-term program can be justified by the development of multiresistant lines using these species.

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