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Crown Gall Resistance in Accessions of 20 *Prunus* Species

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***Abstract*. Crown gall is an important disease of many fruit and nut crops, but little is known about sources of resistance. We screened germplasm from *Prunus armeniaca* L., *P. angustifolia* Marsh., *P. argentia* L., *P. avium* L., *P. besseyi* Bailey, *P. bokhariensis* Schneid., *P. brigantica* L., *P. cerasifera* Ehrh., *P. cerasus* L., *P. dulcis* (Mill.) D.A. Webb, *P. fruiticosa* Pall., *P. hortulana* Bailey, *P. insititia* L., *P. japonica* Thunb., *P. mahaleb* L., *P. persica* (L.) Batsch, *P. serotina* Ehrh., *P. simonii* Carr., *P. sogdiana* L., and *P. webbii* (Spach) Vieh. When either main stems or lateral branches of seedlings were inoculated with strains K12 and C58 of *Agrobacterium tumefaciens* (Smith and Townsend) Conn., the incidence of resistance was less than 10% except in some accessions of *P. mahaleb* L. where up to 30% of the plants were resistant. Some resistant plants were identified in other species, with *P. insititia* L. being the most promising. Symptoms based on presence and size of galls should be allowed to develop for up to 90 days after inoculation to reduce the likelihood of misclassifying plants as resistant when they are slightly susceptible.**

Crown gall disease incited by *A. tumefaciens* is an important problem for nursery and field production of many stone fruit and nut crops (Kennedy and Alcorn, 1980). Soil fumigation is effective as a means of control, but because of increasing regulation, continued use of chemicals will probably be limited. Biological agents such as strain K84 of *A. radiobacter* var. *tumefaciens* provide some protection against the disease (Pierronnet and Escalettes, 1991; Ryder and Jones, 1991), and crown gall-resistant rootstocks would be an attractive complement.

Germplasm assessment is the first step towards determining the feasibility of breeding for resistance and developing a strategy for selecting plants that combine crown gall resistance with other important traits (e.g., resistance to other diseases, size control, etc.). Because evaluation of *Prunus* germplasm for crown gall reaction has been limited, little is known about the occurrence of resistance (DeCleene and DeLey, 1976; Smith, 1925). Recently, Peirronnet and Salesses (1996) found varying reactions to *A. tumefaciens* among several species of plum. No resistance was found, and only a few accessions of *P. insititia*, *P. domestica* L., *P. besseyi* Bailey, and some interspecific hybrids were less susceptible, but they concluded that *P. domestica* might be useful in breeding for low susceptibility. There has been occasional mention of plants that are resistant, e.g., 'Rubira' peach [*Prunus persica* (L.) Batsch] (see Layne, 1987), but the conditions surrounding those observations were not specified.

In addition to limited information about sources of crown gall resistance, little is known about the pattern of inheritance in crop plants. In *Vitis*, Sule et al. (1994) reported differential sensitivity to *Agrobacterium* strains and some resistance, and Stover et al. (1997a) found different levels of susceptibility but no immunity among species and interspecific hybrids. Segregation analyses have shown phenotypic differences in, e.g., soybean [*Glycine max* (L.) Merr.] (Owens and Cress, 1985), rose (*Rosa* sp.) (Boelema, 1969), chrysanthemum (*Dendranthema ×grandiflora* Kitam.), and raspberry (*Rubus ideas* L.) (Miller et al., 1975; Zurowski et al., 1985), and have demonstrated that resistance is heritable and expressed quantitatively in, e.g., pea (*Pisum sativum* L.) (Robbs et al., 1991), soybean (Bailey et al., 1994; Mauro et al., 1995), and grape (*Vitis* sp.) (Szegedi and Kozma, 1984), but no specific resistance genes were identified. Nam et al. (1997) found differences in susceptibility among *Arabidopsis thaliana* (L.) ecotypes and segregation at a single locus in one hybrid population, with resistance being recessive.

Little is known about the mechanisms of crown gall resistance. Beneddra et al. (1996) reported that genotypic differences in reactions among aspen (*Populus* sp.) cultivars were related to differences in sensitivity to cytokinin, and Nam et al. (1997) found that one partially resistant *A. thaliana* ecotype showed impaired transformation and integration of T-DNA into the host genome.

Among dicots, *A. tumefaciens* has a wide host range. Differences in virulence exist among pathogenic strains in, e.g., strawberry (*Fragaria vesca* L.) (Uratsu et al., 1991), and in most cases there is some specificity between host genotype and pathogen strain [e.g., chrysanthemum (Bush and Pueppke, 1991), pea (Robbs et al., 1991), and soybean (Bailey et al., 1994; Byrne et al., 1987)]. Thus, when screening for resistance, the pathogen strain and conditions surrounding inoculation and disease development should be considered, as well as the host plant genotype.

Crown gall often occurs on plants wounded during transplanting and cultivation. However, when bacteria enter the potential host through natural openings and incidental wounds, disease expression may vary even among susceptible plants. To ensure inoculation and enhance uniform disease development for efficient screening, artificial wounding [i.e., inoculation of the cut surface of cuttings (Peirronnet and Salesses, 1996), inoculation of stem incisions, etc.] may be used. Susceptibility can be judged by the occurrence of galls, rate of gall growth, and gall size. Our objectives were to optimize procedures for a disease screen, then to screen seedlings of a range of *Prunus* accessions for reaction to *A. tumefaciens* and identify sources of resistance to the pathogen.

Materials and Methods

Plant materials. To begin a multiyear study, accessions of *Prunus* sp. were chosen in 1994 as sources of seedling populations, primarily because of their current or potential use as rootstocks. In some cases there was a prior indication of possible resistance or tolerance to crown gall. Seeds were collected from source trees in the germplasm collection at the Univ. of California, Davis (UCD), and some were received from other sources, including David Byrne, Texas A&M Univ., College Station, and the IR-2 Program, Pullman, Wash. After cold stratification under moist conditions for a time sufficient for each species, endocarps were cracked, the seed coats removed, and the embryos placed on the surface of soil contained in plastic cones. The soil surface was kept moist with intermittent misting until after germination, when the plants were moved to a greenhouse with supplemental light.

Bacterial inoculum. Four wild-type strains of *A. tumefaciens* (A208, C58, K12, and ACH5) were used for resistance studies, and a strain of C58 selected for kanamycin resistance (C58Km1) to study the mobility of the bacteria in inoculated branches.

Bacterial cultures were prepared as follows: 100 µL of bacterial culture, stored at –80 °C in 15% glycerol, were placed in a test tube containing 15 mL of the growth medium. The LB medium (10 g tryptone, 5 g·L^{-1} yeast extract, pH 7.1) was used for the wild type strains K12 and C58. The growth medium 523

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(Kado et al., 1972), supplemented with 50 mg·L^{-1} kanamycin sulfate, was used for the growth of C58Km1. The cultures were placed on a rotary shaker (100 rpm) at 25 °C for 16 h. Inoculum had a bacterial density, as measured by absorbance at 420 nm, of ≈10^9 cells/mL.

Seedling inoculation. Seedlings 2 to 12 cm tall were wounded at three sites on the main stem by removing a piece of tissue ≈1 cm long from the stem surface into the cambial area with a scalpel. One drop (≈20 µL) of overnight culture of *A. tumefaciens* was placed on each wound site, which was then wrapped with Parafilm to prevent drying. Various inoculant concentrations were applied to susceptible *P. mahaleb* seedlings to determine an optimum concentration for symptom development. Thereafter, the optimum concentration was used for screening of all *Prunus* accessories. Individual plants were examined and wound response was rated at specified time intervals after inoculation. Frequency of tumor occurrence at each wound site, tumor size, and rate of tumor emergence and growth were used to provide an estimate of disease reaction as follows: RO = no galls formed; R1 = slow formation of a few small galls; MS = medium galls at one or two inoculation sites; S = medium to large galls at three sites; VS = rapid formation of large galls at all three sites. *Kalanchoe daigremontiana* (L.) plants were inoculated as positive controls to assure oncogenicity of the strains used for inoculation.

Mobility of bacteria in inoculated branches. Stems of 4-month-old seedlings of 'Lovell' peach and a susceptible *P. mahaleb* accession were cut back to induce growth of lateral branches. A cut 1 cm long was made near the middle of each branch, then a drop of overnight culture of the armed *A. tumefaciens* strain C58Km1 was placed on the cut. The wounded area was wrapped with Parafilm to prevent drying. Noninoculated branches were used as controls.

Branches were harvested at monthly intervals and 1-cm-long cross-sectional segments were cut aseptically from the basal and apical ends toward the inoculation site. Presence of gall formation at the wound site was noted to indicate positive infection. The stem segments were placed in sterile test tubes containing 3 mL of 523 medium and 250 mg·L^{-1} of the antifungal agent cycloheximide. Tubes were incubated at room temperature with constant shaking (100 rpm) for up to 5 d. Once bacterial growth was observed (i.e., the medium became turbid), 750 µL of that medium was mixed with 250 µL sterile 60% glycerol and placed in a sterile microfuge tube. The microfuge tubes were then stored at –80 °C. To determine whether strain C58Km1 was present, the microfuge tubes were removed from the freezer and thawed. 100 µL of the thawed culture were removed from each tube and added to sterile culture tubes containing 3 mL of 523 medium, to which had been added 250 mg·L^{-1} cyclohexamide and 50 mg·L^{-1} kanamycin sulfate. Tubes were incubated at room temperature with constant shaking (100 rpm) for up to 5 d. The tubes were evaluated for the presence of the antibiotic-resistant strain of *A. tumefaciens* by the presence or absence of turbidity in the growth medium. An additional test for 3-ketolactose production (Schuerman, 1996) was used to confirm the identity of isolated kanamycin-resistant bacteria. A positive reaction indicated that the bacterium was C58Km1, since this ability is a specific indicator of *Agrobacterium* biovar 1 strains and C58 is a strong producer of 3-ketoglycosides (Klekner et al., 1989).

Results and Discussion

Symptom development. Galls developed at each inoculation site on susceptible apricot [*P. armeniaca* (L.)] and almond [*P. dulcis* (Mill.) D.A. Webb] (data not shown) seedlings by 30 d after inoculation with four virulent strains. Because large galls developed rapidly and consistently from inoculation with K12 and C58 (Fig. 1), these strains were used thereafter to screen for crown gall reaction. An inoculant concentration of 10^9 cells/mL and a 1:10 dilution of the C58 strain produced uniformly large galls on susceptible *P. mahaleb* seedlings. With dilutions of 1:100 and 1:1000, especially at short intervals after inoculation, galls were smaller, and susceptible plants that would otherwise receive ratings of VS, S, and MS were sometimes rated R1, increasing the possibility of misclassification of susceptible seedlings. For screening studies an inoculant concentration of ≈10^9 cells/mL was used.

Lateral branches of susceptible peach and *P. mahaleb* plants that were inoculated with strain C58Km1 formed galls at the infection site, and bacteria were recovered from branch cross-sections in both apical and basipetal directions from the site. Three months after inoculation, bacteria were detected in peach branches up to 2 cm, and in *P. mahaleb*, up to 5 cm from the infection site. After 4 months bacteria were present up to 10 cm in each direction in *P. mahaleb* branches.

Resistance to strains K12 and C58. In the initial screening of seedlings inoculated with strain K12, no plants were rated RO among seedling populations from 52 accessions of *P. dulcis* and 21 accessions of *P. armeniaca* (Table 1). From among 600 seedlings of 22 *P. persica* accessions, only eight seedlings rated RO were recovered, four of which were from 'Rubira'. Although no RO seedlings were found in *P. dulcis* and *P. armeniaca*, and only a few *P. persica* rated RO, there were differences among families for levels of susceptibility based on the ratio of R1:S plants, ranging from populations with no R1 plants to others with about one-half of the plants with an R1 rating. The frequency of RO seedlings was low in other *Prunus* sp., except in some accessions of *P. insititia*, *P. cerasus*, and *P. sogdiana* and *P. mahaleb*.

We were especially interested in *P. mahaleb*, in which there were a substantial number of RO-rated seedlings, since one objective of our rootstock breeding program is to develop genetically-improved *P. mahaleb* seedling rootstocks for sweet cherry (*P. avium* L.) cultivars. We inoculated seedlings from open-pollination of the *P. mahaleb* clones that are important rootstock sources maintained in the IR2 collection and of which we have clones at UCD. When the same seedlings were rated at 30 and 90 d after inoculation, galls were larger and more frequent, there were fewer seedlings rated RO, and there was a shift in all populations toward greater frequencies of plants judged to be susceptible after 90 d compared with 30 d (Fig. 2). After 90 d, there were three groups of seedlings based on the distributions of plants in the five reaction classes. One group (Fig. 2A) included two populations, each with about 30% RO plants. Another group (Fig. 2B) included nine populations, each with about 10% RO seedlings, and a third group (Fig. 2C) had two populations each with no RO seedlings.

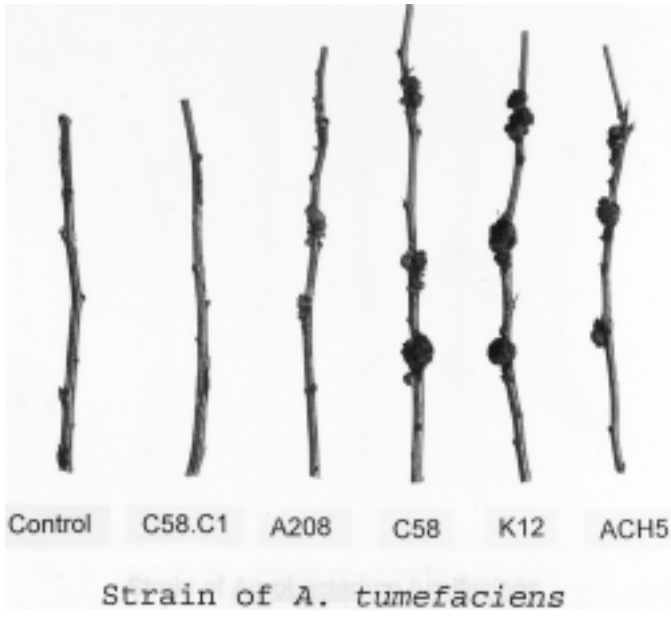

Fig. 1. Crown gall disease reaction on 1-year-old seedlings of apricot cv. Blenheim, inoculated with a nonvirulent (C58.C1) and four virulent strains (A208, C58, K12 and ACH5) of *A. tumefaciens*.

Table 1. Crown gall reaction of open-pollinated seedlings of accessions of *Prunus* sp. after inoculation on the main stem with *A. tumefaciens* strain K12.

		No. plants			
			Crown gall reaction[z]		
Species	Accessions(s)/cultivars	Total	RO	R1	S
P. dulcis	4[y]	49	0	26	23
	13[x]	178	0	56	122
	15[w]	232	0	32	200
	20[v]	292	0	0	292
P. armeniaca	7[u]	339	0	11	328
	14[t]	226	0	0	226
P. persica	4[s]	174	8	18	148
	7[r]	247	0	23	224
	11[q]	179	0	0	179
P. angustifolia	336-1	12	4	0	8
P. argentia	No. 0195	5	0	0	5
P. avium	143-1	1	1	0	0
	148-2	2	0	0	2
	293-2	2	0	0	2
	Bing	11	0	1	10
P. besseyi	Seedling	77	0	6	71
	Seedling	24	0	3	21
	Seedling	35	1	5	29
P. bokhariensis	No. 0853	13	0	0	13
P. brigantica	W.E.O.	23	0	0	23
P. cerasifera	No. 0434	12	0	0	12
	No. 0718	13	0	0	13
P. cerasus	Shubinka	1	1	0	0
	9853	29	6	4	19
	Kansas sweet	23	1	0	22
P. fruiticosa	Seedling	7	0	0	7
P. hortulana	W.E.O.	23	7	3	13
P. insititia	No . 0362				
	Mirabele Precoce	12	6	3	3
	655-2	24	14	2	8
	GM 61 (1994)	32	1	3	28
	Queen Ann plum	17	0	4	10
	Langley plum	14	0	4	10
	Kirkes plum	13	4	2	7
P. japonica	Weeping Santa Rosa	4	1	0	3
P. mahaleb	163-1	97	11	7	79
	11-4	91	7	5	79
	9-4	43	1	4	38
	295-3	51	2	5	44
	PI 163091	28	0	3	25
	PI 193688	28	1	0	27
	PI 193693	28	1	1	26
	PI 193699	21	0	3	18
	NY 34	15	1	6	8
P. serotina	Capuli	11	0	0	11
	wild	27	2	3	22
P. simonii	apricot plum	4	0	0	4
P. sogdiana	Seedling	31	0	12	19
	Seedling	24	4	17	3
P. webbii	F8 15-33	27	0	0	27

[z]Plants evaluated ≈50 d after inoculation. RO = no galls formed at any site; R1 = slow formation of a few small galls usually at a single site; S = medium to large galls form quickly at one or more inoculation sites.
[y]Cultivar names: Merced, Monarch, Donna, Morely.
[x]Cultivar/accession names: Planada, 1-69, Wood Colony, Aldridge, Vallenta, Monterey, Sano, Plateau, Yogut, 25-75, 13-1, 1-87, Chips.
[w]Ripon, Mission, Yosemite, Butte, LeGrand, NePlus Ultra, Peerless, Sonora, 24-5z, 1-46, Fritz, Solano, Kapareil/PA, Jenette, NonPareil.
[v]Vesta, All-In-One, Tardy Nonpareil, Jordanola, Mono, Livingston, Tokyo, Grace, Padre, Thompson, Ruby, NePlus, Sauret, Rosetta, Price, Carmel, Jeffries, Dottie Won, Sauret 2, Pearl.
[u]Blenheim, NJA 32, PA7005-2, PA7005-6, Patterson, Tilton, 10.1-29.
[t]K106-2, K102-93, K210-35, K247-86, Mariani 9, Moorpark, NJA 41, PAK 1425.10, Red Sweet Sport, Stark Sweetheart, Wanatchee, Westley, 10.1-63, 16.23-6.
[s]Flordaguard seedling-1, Lovell, PI55776, Rubira.
[r]Flordaguard seedlings-2, -3, -4, Nemared, Okinawa, Petite, Boone Co.
[q]Halford, Indian Cling, PI 106062, Rutgers Red Leaf, Saharanpur 1, Siberian C, Nemaguard, Bailey, Ferris St. 916-1, Harrow Blood, Tennessee Natural.

In 1995, we also screened populations of seedlings from several nonselected plants that had resulted from open pollination of *P. mahaleb* clones 9-4, 11-4, 163-1 and 295-3. Those populations also produced three groups of seedlings based on the proportion of RO plants 90 d after inoculation (Table 2).

Sometimes plants rated RO developed small galls rather slowly and were difficult to distinguish from R1 phenotypes. Therefore, the proportion of RO plants in each population is probably an overestimation of resistance. Although no definitive conclusions can be made without using seedlings from controlled pollinations, resistance appears to be recessive to susceptibility in the *P. mahaleb* populations.

Because some putative resistant (RO) plants showed slower symptom development, we reinoculated with strains K12 and C58, lateral branches on plants that had been rated resistant to strain K12. Some plants gave slightly different responses to K12 on the lateral branches compared with their ratings as seedlings, and some that were resistant to K12 were not always resistant to strain C58 (Table 3). In 1996, seedlings from clonal sources and from nonselected seedling parents were inoculated with strain C58. Results were similar to inoculations with strain K12, in that most seedlings were susceptible and a few with RO ratings were recovered (Table 4). Resistance, or at least the level of susceptibility, appears to be somewhat strain-dependent. We have not yet determined clearly whether any seedlings are resistant (RO) to both strains, but a few appear to be. Subsequently, we now reinoculate plants tested against either K12 or C58 with both strains to verify the level of initial resistance and to test for multiple resistance.

Despite the economic cost of crown gall and the attractiveness of having rootstocks with genetic resistance, few sources of resistance have been reported in *Prunus* sp. Some *A. tumefaciens* strains that were virulent on susceptible seedlings were selected and used for *in vivo* assays where either the main stem or lateral branches were inoculated after wounding. While either strain K12 or C58 was suitable for assessing resistance, plants did not necessarily react similarly to both strains, and tests with each strain are required to detect plants resistant to both.

Large galls had developed on highly susceptible plants by 30 d after inoculation. Other plants showed slower gall development, resulting in a resistant rating at 30 d, but by 90 d after inoculation, small galls sometimes had formed. Thus, some plants that are slightly susceptible may be erroneously classified as resistant unless disease symptoms are allowed to develop for at least 90 d and the plants are reinoculated for confirmation. To reduce the likelihood of misclassification, RO plants should be reinoculated with the original strain and other virulent strains if multiple strain resistance is desired.

The frequency of resistance to strain K12 was quite low, especially in apricot, almond, and peach. However, some seedling populations of *P. mahaleb* were identified with up to 30% RO seedlings. Some of these plants have been retained for seed production and their progeny will be tested against strains K12 and C58. Based on the limited number of accessions tested, *P. insititia* may also be a useful source of resistant plants.

We have used inoculation methods that facilitate symptom development for screening large populations of seedlings, since our ob-

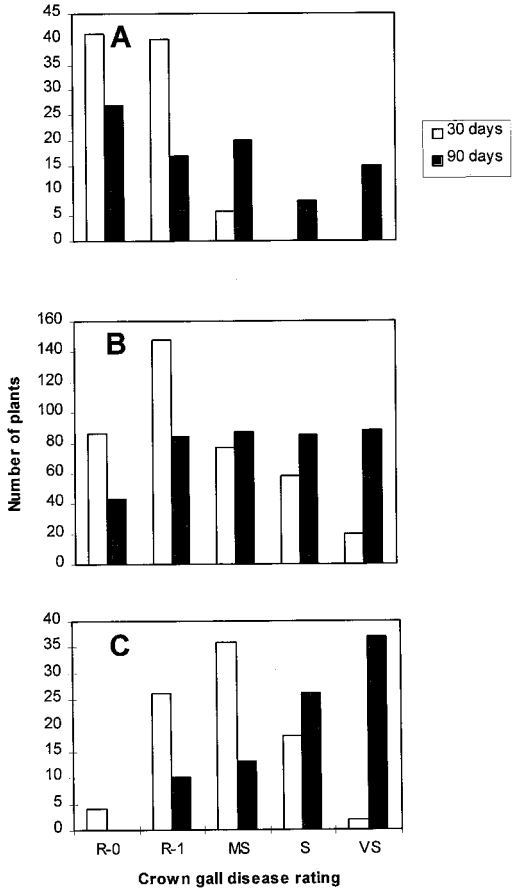

Fig. 2. Crown gall disease ratings of seedlings from open pollination at U.C. Davis, of clonal trees of *P. mahaleb* accessions held in the IR2 collection at Pullman, Wash. Seedlings were inoculated with strain K12 of *A. tumefaciens* and ratings made at 30 and 90 d after inoculation. Disease ratings were: RO = no galls formed; R1 = slow formation of a few small galls; MS = medium galls at one or two inoculation sites; S = medium to large galls at all three sites; VS = rapid formation of large galls at all three sites. (**A**) Populations from clones 8-4 (PI 181721) and 289-1 (PI 194098); (**B**) populations from clones 9-4, 10-4, 11-4 138-2 (PI 193702), 155-1, 294-3, 297-2, 295-3, and Dwarf mahaleb; (**C**) populations from clones 154-2 and 460-1 (PI 194217).

Table 2. Crown gall reaction of seedlings in populations resulting from open pollination of U.C. Davis *P. mahaleb* selections after inoculation on the main stems with *A. tumefaciens* strain K12.

	No. plants		
		Crown gall reaction[z]	
Accession	Total	RO	(R1 + MS + S + VS)
(9-4)-S1-OP1	47	10	37
(9-4)-S1-OP1	48	19	29
(11-4)-S1-OP1	31	12	19
(11-4)-S1-OP1	18	6	12
(11-4)-S1-OP1	22	6	16
Total	*166*	*53*	*113*
(9-4)-S1-OP1	34	4	30
(11-4)-S1-OP1	25	2	23
(11-4)-S1-OP1	32	4	28
(11-4)-S1-OP1	21	2	19
(11-4)-S1-OP1	41	5	36
(11-4)-S1-OP1	32	6	26
(11-4)-S1-OP1	32	3	29
(11-4)-S1-OP1	31	5	26
(11-4)-S1-OP1	27	3	24
(163-1)-OP1-OP1	49	7	42
(295-3)-S1-OP1	42	3	39
(295-3)-S1-OP1	46	8	38
Total	*412*	*52*	*360*
(11-4)-S1-OP1	3	0	3
(163-1)-OP1-OP1	25	0	25
Total	*28*	*0*	*28*

[z]Seedlings inoculated on main stem and reaction evaluated ≈90 d after inoculation. RO = no galls formed; R1 = slow formation of a few small galls; MS = medium to large galls at one or two sites; S = medium to large galls at all three sites; VS = rapid formation of large galls at all three sites.

jective is to produce improved seedling rootstocks that combine several desirable traits. In contrast with findings in *Vitis* (Stover et al., 1997b), we detected bacterial movement in both directions from the inoculation site on lateral branches. When lateral branches are used to screen for resistance and to validate prior ratings of selected plants, the inoculation site should be far enough away from the main stem for symptom development to continue for at least 2 to 3 months. Then, if branches are cut near the main stem, disease-free plants should be available for further experimentation and seed production.

These screening methods are not necessarily representative of conditions encountered in the nursery or production field, where infection often occurs in the "crown" area of the plant. The severity of wounding and the high concentration of inoculum that we used experimentally provides a more severe challenge than plants are likely to encounter, and we feel that the levels of resistance that were identified will be sufficient to be of practical importance.

The resistant plants from these accessions will be useful not only as potential new rootstocks, but also for determining the basis of genetic resistance. In the *P. mahaleb* populations, resistance appeared to be recessive, as was found in *A. thaliana* (Nam et al., 1997), and was controlled by several genes, but because these populations came from open-pollination of mother trees this conclusion is tentative.

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Table 3. Crown gall reaction[z] of seedlings of three *Prunus* species inoculated on the main stems with *A. tumefaciens* strain K12 followed by re-inoculation of four lateral branches with strain K12 and three with strain C58.

	A . tumefaciens strain							
		K12				C58		
	K12	Branch no.				Branch no.		
Accession	Main stem rating	1	2	3	4	1	2	3
		P. mahaleb						
(163-1)-OP1	R1	R1	MS	RO		MS	MS	MS
(295-3)-S1	R1	RO	R1			RO		
(11-4)-S1	RO	RO	R1			RO	MS	RO
(163-1)-OP1	RO	MS	MS	RO	RO		R1	R1
(163-1)-OP1	RO	RO	RO	R1		R1	RO	
(163-1)-OP1	RO	R1	RO	R1		R1	MS	MS
(163-1)-OP1	RO	RO	RO	R1		R1	R1	R1
		P. cerasus						
(9853)-OP1	RO	RO	RO	RO	RO		MS	MS
(9853)-OP1	R1	MS	MS			MS		
Shubinka-OP1	RO	RO				RO		
		P. avium						
Bing-OP1	RO	RO						
(148-2)-OP1	R1	R1	MS			R1		

[z]Inoculation reaction: RO = no gall formation at inoculation site; R1 = slow formation of small galls; MS = small to medium galls; S = medium to large galls; VS = early and rapid formation of large galls.

Table 4. Crown gall reaction of seedlings in populations resulting from open pollination of U.C. Davis *P. mahaleb* selections after inoculation on the main stems with *A. tumefaciens* strain C58.

	No. plants		
		Crown gall reaction[z]	
Accession	Total	RO	(R1 + MS + S+ VS)
Seedling Sources			
(9-4)-S1-OP1	28	5	23
(9-4)-S1-OP1	31	8	23
(9-4)-S1-OP1	71	11	60
Total	*130*	*24*	*106*
(9-4)-S1-OP1	87	1	86
(9-4)-S1-OP1	53	1	52
(9-4)-S1-OP1	77	0	77
(9-4)-S1-OP1	90	0	90
(11-4)-S1-OP1	19	0	19
(11-4)-S1-OP1	43	0	43
(11-4)-S1-OP1	32	0	32
(9-4)-S1-OP1	66	0	66
(9-4)-S1-OP1	63	0	63
Total	*530*	*2*	*528*
Clonal Sources			
(138-2)-OP1	19	5	14
(159-5)-OP1	69	3	66
(PI 193688)-OP1	50	0	50
(141-1)-OP1	20	0	20
(PI 194099)-OP1	102	0	102
(PI 193699)-OP1	48	0	48
(7-5)-OP1	7	0	7
(155-1)-OP1	17	0	17
(8-4)-OP1	54	0	54

[z]Seedlings inoculated on main stem and reaction evaluated ≈90 d after inoculation. RO = no galls formed; R1 = slow formation of a few small galls; MS = medium to large galls at one or two inoculation sites; S = medium to large galls at all three sites; VS = rapid formation resulting in large galls at all three sites.

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