Resistance of Geneva and Other Apple Rootstocks to *Erwinia amylovora*

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ABSTRACT

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When vigorously growing shoots of 49 different apple rootstocks grown in a greenhouse were inoculated with different strains of *Erwinia amylovora,* Budagovsky 9 (B.9), Ottawa 3, Malling 9, and Malling 26 were the most fire blight susceptible rootstocks and Geneva 11, Geneva 65, Geneva 16, Geneva 30, Pillnitzer Au51-11, Malling 7, and several breeding selections were the most resistant. Significant strain–rootstock interactions were observed in the amount of fire blight that resulted from inoculation. Field-grown fruiting 'Royal Gala' trees on Geneva 16 and Geneva 30 rootstocks were highly resistant to rootstock infection (no tree mortality) when trees sustained severe blossom infection with *E. amylovora*, compared with Malling 9 and Malling 26 rootstock clones, which were highly susceptible to infection (36 to 100% tree mortality). In contrast to potted own-rooted B.9 plants inoculated in a greenhouse, B.9 rootstocks of orchard trees appeared resistant to rootstock infection (0% tree mortality). Orchard trees on Geneva 11 were moderately resistant to rootstock infection (25% tree mortality). There was general agreement in the evaluation of resistance under orchard conditions when rootstock resistance was evaluated in relation to controlled blossom inoculation or to natural blossom infection.

Additional keywords: disease resistance, disease susceptibility, *Malus*

Fire blight, caused by *Erwinia amylovora* (Burrill) Winslow et al., is a destructive disease of apple that kills blossoms, shoots, and woody plant organs (23). Recently, fire blight of apple rootstocks has become a serious economic problem in high-density orchard systems (11). Over the past 50 years, most apple-growing regions have adopted the use of high-density orchard systems that depend upon dwarfing rootstocks to control tree size. The most commonly used dwarfing rootstocks, Malling (M.) 9 and M.26, are highly susceptible to *E. amylovora* and infection usually kills trees by girdling the rootstock. Several avenues of rootstock infection have been demonstrated, including infection of rootstock suckers (vegetative shoots developing from the rootstock), internal spread of bacteria from infections in the scion, or direct infection of the rootstocks through discontinuities in the bark caused by growth or various injuries (12). Currently, there are no effective cultural practices or chemical treatments available to control the rootstock phase of fire blight in high-density orchard systems.

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The objective of the Geneva apple rootstock-breeding program has been to develop pomologically excellent rootstocks with resistance to abiotic and biotic stresses, including fire blight. The program was begun by J. N. Cummins, Department of Horticultural Sciences, Cornell University (Geneva, NY) in 1968. H. S. Aldwinckle, Department of Plant Pathology, Cornell University, joined the program in 1970. It became a joint program for the United States Department of Agriculture-Agricultural Research Service (USDA-ARS) and Cornell in 1998. Based upon inoculations with strain *E. amylovora* Ea273, *Malus* × *robusta* cv. Robusta 5 was identified as highly resistant to fire blight and was widely used as a parent in the Geneva breeding program (7). Repeated direct inoculation of actively growing shoot tips with *E. amylovora* strain Ea273 was used to identify resistant progeny of controlled crosses (8). Robusta 5 later was found to be differentially susceptible to infection by *E. amylovora* strain E4001a (also referred to as Ea266; 14,17,19). When rootstock selections were inoculated with strain E4001a or with a mixture of strains including E4001a, several rootstocks previously identified as resistant to strain Ea273 became severely infected and were discarded from the program (15,16). Recently four apple rootstocks, Geneva (G.) 65, G.11, G.30, and G.16, were released for commercial sales (4). Several other selections are in the final stages of evaluation.

Although the Geneva rootstocks are known to be resistant to direct shoot inoculation with *E. amylovora* strains Ea273 or E4001a, it was not known if these apple rootstocks are resistant to natural infection by *E. amylovora* under orchard conditions or if they would be resistant to direct shoot inoculation with other highly aggressive strains of *E. amylovora*. The objectives of this study were to (i) compare the resistance of the Geneva rootstocks with that of other apple rootstocks when inoculated with the differentially virulent strain E4001a and other highly aggressive *E. amylovora* strains and (ii) evaluate the resistance of the Geneva rootstocks and advanced selections of the breeding program as rootstocks of grafted trees grown under orchard conditions.

MATERIALS AND METHODS

Bacterial strains and inoculum. *E. amylovora* strains used in this study are listed in Table 1. Inoculum consisted of 18-h-old shake cultures grown in Kado 523 broth (9) at 28°C. Inoculum concentration was estimated by absorbance at 620 nm using a standard curve and adjusted to the desired concentration by dilution with sterile 0.05 M potassium phosphate buffer, pH 6.5. Inoculum was maintained on ice and was used for plant inoculation within 2 h of dilution.

Direct inoculation of ungrafted rootstock plants in greenhouse. The parentage of the apple rootstocks used in this study and the size of the tree they produce relative to the Malling series of rootstocks are described in Table 2 (13). Rootstocks were evaluated in the greenhouse for their resistance to fire blight by direct inoculation of vigorous shoots with one to four strains of *E. amylovora* (Tables 3 and 4). Stoolbed-propagated liners (rooted, hardwood shoot cuttings) obtained from various suppliers were potted in cylindrical pots (5 by 20 cm) containing a peat and vermiculite soil mix, and trained to a single shoot. Vigorously growing shoots at least 15 cm in length were selected for inoculation. Due to a limited supply of many of the rootstocks, not all rootstocks were inoculated with all four strains. If less than 20 shoots were available for inoculations, a minimum of five shoots were inoculated with each individual strain. The priority of strain selection for shoot inoculation was first Ea273, then E2002a, then E4001a, and finally E2017p.

Shoots were inoculated on 16 June 2000 by transversally bisecting the two youngest actively growing leaves with scissors dipped in a suspension of a single strain of *E. amylovora* (1×10^9 CFU ml^{-1}). Current season's shoot length and the length of the necrotic lesion were measured on 5 July 2000. The necrotic lesion length was expressed as a percentage of the current season's shoot length and used as the measure of host plant resistance. Individual plants were the unit of replication. GLM (SAS Institute Inc., Cary, NC) of the proportion of the shoot length necrotic was used to analyze treatment effects. Because the analysis indicated a significant rootstock by strain interaction, differences in rootstock resistance were analyzed for each strain using a Waller-Duncan *k*-ratio *t* test.

Evaluation of rootstock resistance under orchard conditions following inoculation. Rootstocks of grafted fruiting trees were evaluated for their resistance to *E. amylovora* when grown in orchards subjected to an induced blossom blight epiphytotic (Table 5). Rootstock liners were planted in a nursery (spring 1995), bud chip grafted with the 'Royal Gala' scion (summer 1995), grown in the nursery for a second season, dug (fall 1996), graded, and stored. In spring 1997, an orchard was established at the Research North Farm of the New York State Agricultural Experiment Station (Geneva, NY) in a randomized block design that was blocked based upon trunk diameter measured immediately above the graft union on stored trees. Trees were grown under recommended commercial orchard practices, trained to a vertical axe (18), and provided with post support.

Trees at the Research North Farm all bloomed heavily in 1999 and open blossoms were spray inoculated with *E. amylovora* strain E4001a using a backpack sprayer. Trees were inoculated twice (12 and 17 May 1999) to compensate for rootstock effects on the time of bloom and rootstock effects on the number of blossoms on 1-year-old wood, which tends to bloom later than spur blossoms. The inoculum concentration for the first inoculation was 1.0×10^7 CFU/ml, but was reduced for the second inoculation to 1.4×10^6 CFU/ml due to the forecast of warmer weather conditions more favorable for blossom blight development.

Evaluation of rootstock resistance under orchard conditions following natural infection. Rootstocks of grafted fruiting trees also were evaluated for their resistance to *E. amylovora* after the occurrence of a natural blossom blight epiphytotic (Table 5). An orchard was established at Ray Smith Farm, Geneva, NY, as described above. Trees at the Ray Smith Farm bloomed heavily in 2000, and blossoms were heavily infected in May 2000 due to natural infection. Development of rootstock blight was recorded based upon the presence of bacterial ooze on rootstocks or typical fire blight necrosis of rootstock tissue with evidence of either tree death or premature leaf coloration in fall.

Differences among quantitative traits of the rootstocks (percent blossom clusters infected on scion) were analyzed using a generalized linear model and Waller-Duncan *k*-ratio *t* test. Differences among nominal traits (presence or absence of rootstock blight symptoms) were analyzed using Ryan's (20) significance test for multiple comparison of proportions. Due to the nonparametric nature of the data and the limited size of the orchard trials, a type I error rate of $P = 0.2$ was selected when testing the null hypothesis.

RESULTS

Direct inoculation of ungrafted rootstock plants in greenhouse. Budagovsky (B.) 9, Ottawa 3, M.9, and M.26 were the most fire blight susceptible rootstocks when vigorously growing shoots of ungrafted, own-rooted rootstock liners were inoculated with different strains of *E. amylovora* in the greenhouse (Table 3). B.9 had the greatest mean disease rating over all four strains and developed the greatest amount of fire blight among the rootstocks inoculated with strains Ea273, E4001a, and E2002a. G.11, G.65, G.16, G.30, Pillnitzer (Pi) Au51-11, M.7, and several advanced selections from the Geneva breeding program (CG) were the most resistant rootstocks when challenged by direct inoculation in the greenhouse. The Vineland rootstocks, Mark, Malling Merton (MM.) 106, M.27, Pi-Au56-83, Pi-Au51-4, some CG selections, Marubakaido, and other Japanese material were intermediate in their reaction to direct inoculation with *E. amylovora*.

Overall, strain E2002a caused the greatest amount of disease among the four strains used in the greenhouse inoculations (Table 3). Strain E4001a, which is differentially virulent to *Malus* × *robusta* Robusta 5 (15), caused a greater amount of disease on the resistant rootstocks than did either strain Ea273 or E2017p; however, it tended to cause less disease on susceptible rootstocks so that its overall mean virulence was similar to that of strains Ea273 and E2017p.

GLM analysis of the proportion of the shoot length that was necrotic indicated significant effects of rootstock and strain, and a significant rootstock–strain interaction on the amount of fire blight resulting from direct inoculation in the greenhouse (Table 4). Specific rootstock–strain interactions also were evident from changes in the resistance ranking of specific rootstocks when they were inoculated with different strains (Table 3). For example, when MM.106 EMLA (virus-tested clone developed at the East Malling and Long Ashton Research Stations, UK) was inoculated with either strain E4001a or strain E2002a, it was evaluated as relatively resistant and not significantly different from Marubakaido. However, when inoculated with either Ea273 or E2017p, MM.106 EMLA was evaluated as highly susceptible and not significantly different from B.9. Conversely, when Robusta 5 progeny CG.3007, CG.6879, and CG.6253 were inoculated with strain E4001a, they were ranked significantly more susceptible compared with other rootstocks than when they were inoculated with strain Ea273. However, there was no consistent pattern in the reaction of the Robusta 5 progeny to inoculation with strain E4001a. For example, CG.5087 and CG.4202 were ranked

Table 1. Strains of *Erwinia amylovora* used in this study

Strain	Origin: Location	Origin: Host	Isolator	Characteristics	References
E2002a[y]	Ontario	*Malus* × *domestica* 'Jonathan'	W. G. Bonn	Highly aggressive strain	14,17,19
E2017p	Ontario	*Pyrus communis* 'Clapp's Favorite'	W. G. Bonn	Reported to be virulent to Geneva 16	3,19
E4001a[z]	Ontario	*Malus* × *domestica* 'R.I. Greening'	W. G. Bonn	Differentially virulent to *Malus* × *robusta* 'Robusta 5'	14,15,17
Ea273	New York	*Malus* × *domestica* 'R.I. Greening'	S. V. Beer	Standard NY strain previously used for evaluation of cultivar resistance	1,14,21

[y] Also referred to as Ea265 (14,17).
[z] Also referred to as Ea266 (14,15,17).

more resistant when inoculated with E4001a than when inoculated with Ea273. Like MM.106 EMLA, Supporter 4 was evaluated as highly susceptible when inoculated with the less aggressive strain Ea273, yet intermediate in its resistance when inoculated with the highly aggressive strain E2002a.

Evaluation of rootstock resistance under orchard conditions following inoculation. Based on blossom, leaf, and fruit characteristics, it was apparent that M.9 had not been grafted with Royal Gala but with 'McIntosh' or a cultivar closely resembling McIntosh. Blossom inoculation in May 1999 of orchard-grown Royal Gala trees (Research North Farm) on 3 Geneva rootstocks, 16 advanced Geneva selections (CG), and 7 other rootstocks with *E. amylovora* strain E4001a resulted in 5 to 23% of the blossom clusters infected. There was a significant effect of rootstock on the amount of blossom blight (Table 5).

Severe fire blight resulted from initial blossom infections with several lesions extending into 2-year-old wood on all trees. Several trees had lesions that extended into 3-year-old wood and the tree trunk; however, no visible scion infections extended to within 30 cm of the rootstock. Rootstock suckers of several trees developed symptoms typical of fire blight shoot infections; however, there were no significant differences among the rootstocks in the incidence of sucker infection (Table 5). Ooze typical of *E. amylovora* infection was first observed on rootstocks in the second week of June 1999. By 15 June 1999, 67 and 58% of the M.26 EMLA and M.9 trees, respectively, had ooze on the rootstock; however, only M.26 EMLA showed a significantly greater (P = 0.2) number of trees with oozing rootstocks (Table 5). For trees grafted on G.11, 17% exhibited oozing rootstocks by 15 June 1999. For some rootstocks, such as Poland (P.) 14, CG.5012, and CG.103, the number of trees with oozing rootstocks continued to increase into July. By 8 July 1999, necrosis typical of fire blight had developed on most of the rootstocks that had previously shown ooze and on some rootstocks on which ooze had not been detected. Again, only M.26 EMLA showed a significantly greater number of trees with necrosis compared with other rootstocks. Trees on CG.4003 and CG.60, and some trees on CG.5012, had signs of ooze on the rootstock but did not subsequently develop necrosis typical of fire blight. Several rootstocks, including G.16, G.30, MM.111, B.9, CG.3041, and CG.5179, had no evidence of fire blight infection on 8 July 1999 (Table 5).

By 9 September 1999, the symptoms of rootstock blight were apparent not only in rootstock tissue but also in tree scions that had either symptoms of tree death or premature leaf coloration (Table 5). At this date, green-colored leaves characterized healthy trees with

Table 2. Parentage of the apple rootstocks used in study and the size of the tree they produce relative to Malling (M.) and Malling Merton (MM.) rootstocks

Rootstock[w]	Parentage	Tree size
B.9	M.8 × Red Standard[x]	M.9
B.491	Unknown	M.27 to M.9
CG.2	*Malus halliana* × B.491	M.9 to M.26
CG.8	Unknown	Unknown
CG.9	M.9 × Sissipuk	M.26
CG.26	M.7 × MM.106	M.26
CG.48	MM.111 × Alnarp 2	M.27 to M.9
CG.60	Novole × Poland 16	Unknown
CG.67	Robusta 5 × M.9[y]	M.26
CG.103	M.9 × Robusta 5	MM.111
CG.132	Robusta 5 × M.9	M.7
CG.134	CG.24 × Robusta 5	MM.111
CG.602	M.27 × Robusta 5	M.26
CG.756	Robusta 5 × M.9	MM.106
CG.3007	Ottawa 3 × Robusta 5	M.9
CG.3029	Dolgo Crab × M.9	M.9
CG.3041	M.27 (M.13 × M.9) X Robusta 5	M.9
CG.4003	(Antonovka Kamienaja × Ottawa 3) × Robusta 5	M.26
CG.4013	Ottawa 3 × Novole	M.26
CG.4202	M.27 × Robusta 5	M.26
CG.4213	Ottawa 3 × Robusta 5	M.26
CG.4214	Ottawa 3 × Robusta 5	M.26
CG.4247	Ottawa 3 × Robusta 5	M.26
CG.4814	Ottawa 3 × Robusta 5	M.7
CG.5008	(Novole × Ottawa 3) × M.9	M.26 to M.7
CG.5012	Ottawa 3 × Robusta 5	M.26 to M.7
CG.5046	Novole × B.146 (unknown)	M.26 to M.7
CG.5087	Ottawa 3 × Robusta 5	M.26 to M.7
CG.5156	Robusta 5 × M.9	M.26 to M.7
CG.5179	Ottawa 3 × Robusta 5	M.26 to M.7
CG.5757	Ottawa 3 × Robusta 5	M.26 to M.7
CG.5890	Ottawa 3 × Robusta 5	M.26 to M.7
CG.5935	Ottawa 3 × Robusta 5	M.26 to M.7
CG.6143	M.27 × Robusta 5	M.7
CG.6210	Ottawa 3 × Robusta 5	M.7
CG.6253	Ottawa 3 × Robusta 5	M.7
CG.6589	Novole × B.9	M.7
CG.6723	Ottawa 5 × M.9	M.7
CG.6737	Robusta 5 × M.9	M.7
CG.6874	Ottawa 3 × Robusta 5	M.7
CG.6879	Robusta 5 × M.9	M.7
CG.6969	Ottawa 3 × Robusta 5	M.7
CG.7707	Robusta 5 × M.9	MM.106
CG.8228	Robusta 5 × M.9	MM.111
Geneva 11	M.26 × Robusta 5	M.26
Geneva 16	Ottawa 3 × *Malus floribunda*	M.9
Geneva 30	Robusta 5 × M.9	M.26 to M.7
Geneva 65	M.27 × Beauty Crab	M.27
J.3	Unknown	Unknown
JM.2	Unknown	Unknown
JM.4	*M. prunifolia* 'Seishi' × M.9	M.9
JM.10	*M. prunifolia* 'Seishi' × M.9	M.9
J-TE-B	Unknown	M.7
J-TE-C	Unknown	M.7
J-TE-D	Unknown	MM.106
M.7	Unknown[x]	M.7
M.9	Unknown[x]	M.9
M.26	M.16 × M.9[x]	M.26
M.27 EMLA	M.13 × M.9[x]	M.27
MM.106	Northern Spy × M.1[x]	MM.106
MM.111 EMLA	Northern Spy × Merton Immune 793 (Northern Spy × M.2)[x]	MM.111
Mark	M.9 open pollinated	M.27 to M.9
Marubakaido	Selection of *M. prunifolia*	Seedling
Naga	Selection of *M. prunifolia*	Seedling
Novole	Selection of *M. prunifolia*	Seedling

(*continued on next page*)

[w] B. = Budagovsky; CG. = Cornell Geneva, advanced selection of Geneva apple rootstock breeding program; JM. = Japan, Morioka; J-TE = Jablon Technobuzice, Czech Republic; Pi = advanced selection of Pillnitzer.

[x] M.7, M.8, M.9, M.11, M.13, M.16, M.1, M.2, M.4 = English selection from a group of French genotypes known collectively as 'Jaune de Metz' in the late 1800s.

[y] Robusta 5 is a selection of *Malus* × *robusta.*

[z] Pollen parent believed to be M.9.

Table 2. (*continued from preceding page*)

Rootstock[w]	Parentage	Tree size
Ottawa 3	Robin (hardy crab) × M.9	M.26
Pi-Au56-83	M.11 open pollinated[x]	M.9
Pi-Au51-11	M.4 open pollinated	M.26
Pi-Au51-4	M.4 open pollinated	M.26
Poland 14	M.9 open pollinated	M.26
Supporter 4	M.4 × M.9[x]	M.26 to M.7
Vineland 1	Kerr (Dolgo × Haralson) open pollinated[z]	M.26 to M.7
Vineland 2	Kerr (Dolgo × Haralson) open pollinated	M.26
Vineland 4	Kerr (Dolgo × Haralson) open pollinated	MM.106
Vineland 7	Kerr (Dolgo × Haralson) open pollinated	M.7

no evidence of rootstock blight, whereas many trees with fire blight-infected rootstocks had bronze-colored leaves. By September 1999, both M.26 EMLA and M.9 showed a significantly greater number of trees with rootstock blight symptoms than many other rootstocks, including MM.111, B.9, G.16, and G.30. Most trees that exhibited symptoms of rootstock infection in September 1999 died the following season, either failing to break dormancy in the spring or initially producing leaves that were small, often

Table 3. Severity of fire blight symptoms on 49 apple rootstocks inoculated with strains of *Erwinia amylovora* in greenhouse trial[y]

	Strain of *Erwinia amylovora*									
	Ea273		E2002a		E4001a		E2017p		Cultivar mean	
Rootstock[z]	N	% SLB	N	% SLB	N	% SLB	N	% SLB	N	% SLB
Budagovsky 9	10	93.3 a	10	97.5 a	7	73.9 a	9	82.8 ab	36	88.1
Ottawa 3	7	84.4 ab	6	89.2 abc	…	…	…	…	13	86.6
M.9 EMLA	6	91.0 a	6	95.6 ab	6	72.7 a	…	…	18	86.4
M.26 EMLA	6	83.4 ab	6	74.4 bcdefg	…	…	…	…	12	78.9
J-TE-D	5	76.9 abc	…	…	…	…	…	…	5	76.9
Budagovsky 491	6	75.8 abcd	…	…	…	…	…	…	6	75.8
Supporter 4	7	80.3 abc	7	57.1 efghijkl	…	…	…	…	14	68.7
MM.106 EMLA	5	84.5 ab	5	62.9 defghij	5	35.3 cdefghijkl	5	91.0 a	20	68.4
M.27 EMLA	7	68.2 bcde	…	…	…	…	…	…	7	68.2
JM.10	8	55.0 defg	7	92.6 ab	7	28.9 fghijlkm	7	88.9 a	29	65.9
Pi-Au56-83	7	58.5 cdefg	8	77.2 abcdef	7	58.0 abcde	…	…	22	65.1
Pi-Au51-4	5	48.4 efgh	5	78.5 abcde	…	…	…	…	10	63.5
CG.3007	6	37.8 fghij	5	92.0 abc	5	61.6 abcd	…	…	16	62.2
CG.6879	6	30.5 hijkl	6	92.7 ab	…	…	…	…	12	61.6
J-TE-C	5	50.2 efgh	6	69.6 cdefgh	5	62.8 abc	…	…	16	61.4
Mark	8	37.6 ghij	7	59.1 efghijk	7	56.4 abcdef	7	80.6 ab	29	57.7
J.3	…	…	6	53.3 ghijklmn	…	…	…	…	6	53.3
Vineland 2	6	39.1 fghij	6	54.6 ghijklmn	6	54.2 abcdefg	5	66.8 b	23	53.1
CG.5087	6	59.6 cdef	6	62.3 defghij	5	33.3 defghijklm	…	…	17	52.8
JM.2	8	51.3 efgh	…	…	…	…	…	…	8	51.3
JM.4	7	46.2 fghi	6	63.1 defghij	6	43.9 cdefghij			19	50.8
CG.6253	5	23.0 jklmn	4	83.0 abcd					9	49.6
J-TE-B	6	47.5 efgh	5	64.4 defghi	5	34.8 cdefghijkl			16	48.8
Vineland 7	6	47.6 efgh	…	…	…	…	…	…	…	…
Vineland 1	5	32.1 hijk	5	55.2 fghijklm	…	…	…	…	10	43.7
CG.6210	7	38.3 fghij	…	…	…	…	…	…	7	38.3
CG.4013	7	14.9 klmno	8	51.3 hijklmno	7	46.7 abcdefghi	8	36.1 c	30	37.7
Marubakaido	9	13.8 klmno	10	62.5 defghij	10	45.3 bcdefghi	9	24.9 cd	38	37.5
Vineland 4	7	24.5 ijklm	7	36.7 klmnopqr	6	48.6 abcdefgh	6	38.1 c	26	36.5
Naga	6	7.1 mno	6	50.1 hijklmno	6	44.3 cdefghij	…	…	18	33.8
CG.5046	5	0.0 o	5	49.9 hijklmno	5	38.7 cdefghij	…	…	15	29.5
CG.4202	7	31.1 hijk	7	43.6 ijklmnop	7	21.0 hijklm	7	18.7 de	28	28.6
M.7 EMLA	6	12.0 klmno	6	42.4 ijklmnopq	6	45.1 bcdefghij	6	11.0 de	24	27.6
CG.5890	8	6.0 mno	9	47.4 hijklmnop	8	36.4 cdefghij	8	16.9 de	33	27.3
CG.5179	5	0.0 o	5	46.6 ijklmnop	5	33.5 defghijklm	…	…	15	26.7
CG.5935	7	5.8 mno	7	56.2 efghijkl	6	30.1 efghijklm	6	5.9 ef	26	25.0
CG.7707	6	9.1 lmno	6	32.6 nopqr	6	26.8 ghijklm	…	…	18	22.9
Geneva 30	8	0.7 o	8	44.8 ijklmnop	7	39.2 cdefghij	7	5.0 ef	30	22.4
CG.4003	9	0.0 o	8	41.0 jklmnopq	9	39.5 cdefghijk	8	4.8 ef	34	21.2
CG.5757	5	0.0 o	5	49.4 hijklmno	5	13.9 klm	…	…	15	21.1
CG.6969	7	1.0 o	7	37.3 klmnopqr	5	26.6 ghijklm	…	…	19	21.1
Geneva 16	9	1.1 no	8	45.8 ijklmnop	8	18.4 ijklm	8	9.5 def	33	18.2
Pi-Au51-11	6	6.1 mno	5	30.7 opqr	…	…	…	…	11	17.3
CG.6589	8	0.0 o	8	34.9 lmnopqr	7	16.7 jklm	…	…	23	17.2
CG.6874	6	10.4 klmno	5	25.1 pqr	…	…	…	…	11	17.1
Geneva 65	8	0.0 o	7	32.9 mnopqr	7	25.8 ghijklm	7	7.1 ef	29	15.9
CG.4814	7	0.0 o	6	21.0 pqr	6	7.5 lm	…	…	19	9.0
CG.3041	4	0.0 o	5	17.2 r	5	5.2 m	…	…	14	8.0
Geneva 11	7	1.7 no	7	14.9 r	7	12.8 klm	7	0.0 f	28	7.4
Strain mean	317	33.4	277	56.4	209	37.7	120	33.6	923	41.2

[y] N = number of plants inoculated and % SLB = mean percent of the current season's shoot length that became necrotic after inoculation. Means within a column followed by the same letter did not differ significantly at $P = 0.05$ according to a Waller and Duncan's *k*-ratio *t* test.

[z] M. = Malling; MM. = Malling Merton; JM. = Japan, Morioka; J-TE = Jablon Technobuzice, Czech Republic; Pi = advanced selection of Pillnitzer; CG. = Cornell Geneva, advanced selection of Geneva apple rootstock breeding program; EMLA = virus-tested clones developed at the East Malling and Long Ashton Research Stations, UK.

chlorotic, and failing to continue growth. Notable exceptions were one tree of CG.3041 and one tree of CG.5179, which had typical fire blight necrosis on 80 and 100%, respectively, of the rootstock circumference in September 1999, but grew normally during the 2000 growing season. One tree on MM.111 was dead on 18 May 2000, but there were no symptoms typical of fire blight associated with the rootstock and it was presumed to have died from other causes. Although the block was not pruned during the 1999–2000 winter, only light blossom infection occurred in the 2000 season. Additional trees on M.26, M.9, CG.5012, CG.5179, CG.602, and CG.6737 continued to develop symptoms of fire blight rootstock infection during the 2000 season (Table 5).

Evaluation of rootstock resistance under orchard conditions following natural infection. During the 2000 growing season, an epiphytotic of rootstock blight resulting from natural blossom infection occurred in another trial of Geneva rootstocks planted in a commercial orchard at Geneva, NY (Ray Smith Farm). All Gala trees within the block sustained blossom infection and most trees had over 50% of the blossom clusters infected. Blocks of Jonagold, Spartan, and Cortland trees on M.9 rootstock adjacent to the trial sustained 60 to 80% incidence of rootstock blight. Generally, the incidence of rootstock blight resulting from natural blossom infection in the scion was in close agreement with the results obtained following spray inoculation during bloom (Table 5). Differences between natural and spray blossom inoculation trials included a higher incidence of rootstock infection in the natural blossom infection block in MM.111 and P. 14, and a lower incidence in M.9, CG.5012, and CG.5179. As in the spray-inoculated blocks, trees on M.9 were not grafted with Royal Gala. Of 24 trees on G.30 in the natural infection block, 1 had symptoms of rootstock blight on 14 October 2000. As in the spray-inoculation block, in the natural-infection block no tree on B.9 showed evidence of rootstock infection and 23% of trees on G.11 had evidence of rootstock blight (Table 5).

DISCUSSION

When shoots of rootstock cultivars were inoculated with different strains of *E. amylovora*, significant strain–rootstock interactions were observed in the amount of fire blight that resulted from inoculation. Those interactions were clearly differential and could not be explained by the greater aggressiveness of strain E2002a because some rootstocks (e.g., MM.106, Supporter 4) were evaluated as significantly more susceptible when inoculated with the less aggressive strain Ea273 than when inoculated with the highly aggressive strain E2002a (Table 3). Previous research had determined that strain E4001a is differentially virulent to specific resistant cultivars, such as ‘Quinte’, ‘Novole’, and Robusta 5 (14,15). Unfortunately, liners of Quinte, Novole, and Robusta 5 were not available for inclusion in these tests. Consistent with previous reports, strain E2002a was clearly more aggressive than either strain Ea273 or E4001a (14,17). The virulence pattern of E2017p was more similar to that of Ea273 than that of E4001a.

G.11, G.30, G.16, G.65, and most CG selections were resistant to all four strains used for inoculation in a nondifferential manner, even though many, including G.11 and G.30, are progeny of Robusta 5, which is known to be differentially susceptible to strain E4001a. These rootstocks were selected or evaluated with a pooled mixture of different strains, and their resistance to individual strains indicates that pooled strains of *E. amylovora* can be used successfully to select for resistance to several strains of differing virulence (16). Resistance effective against strains of different virulence patterns (or races) should be more durable than that selected against a single strain.

Although there were dramatic differences among the rootstocks in the development of rootstock blight symptoms under orchard conditions, there was relatively little statistical separation of rootstock resistance in orchard trials due to the nonparametric nature of the data and financial constraints that limited the size of the field plantings. Because of these limitations, a relatively high error rate probability of 0.2 was selected for comparison of rootstock resistance in the orchard trial. Differences in the amount of blossom cluster infection that resulted from blossom inoculation of the Royal Gala scion on different rootstocks could not be explained by any obvious biological factor such as amount of bloom, time of bloom, tree size, or susceptibility of the rootstock. Aldwinckle et al. (2) previously have reported an effect of rootstock clone on the susceptibility of scion shoots to direct inoculation with *E. amylovora*.

CG.3041 (ready for commercial release), G.16, and G.30 all had very high levels of resistance to *E. amylovora* in both greenhouse and orchard trials. Considering the high level of resistance of G.11 against all strains of *E. amylovora* in the greenhouse trial, it developed more disease than expected in both orchard trials (approximately 25% of the trees diseased). However, compared with disease development in M.9 and M.26 clones (70 to 100% tree death in the blossom inoculated trial), the level of resistance in G.11 should be commercially useful under conditions of lower disease pressure.

B.9 was evaluated as the most susceptible rootstock when vegetative shoots of rootstock liners were inoculated in the greenhouse (Table 3) but, surprisingly, it did not develop any rootstock blight in either orchard trial (Table 5). Visual comparison of leaf, flower, and fruit morphology between B.9 trees grown in the USDA-ARS Plant Genetic Resources Unit germ plasm collection (Geneva, NY) and a B.9 rootstock sucker that flowered and developed fruit in 2000 in the Experiment Station trial provided no indication that the material in our trial was not authentic B.9. In addition, trees grown on B.9 in our trials appeared consistent with expected tree size, yield, and general appearance for trees grown on B.9. However, it is still possible that there may be different genotypes labeled as B.9 in commercial and research stoolbeds. A high level of orchard resistance has been reported for trees grown on B.9 rootstock in Ohio, where rootstock blight resulted in losses of up to 67% of the trees on M.26 rootstock but none of the trees on B.9 were lost due to fire blight (5,6). Mortality of trees on B.9 rootstock has been reported in the NC-140 trials; however, the cause of tree death usually was not reported and it is possible that these trees may have died from other causes (10).

The varying response of B.9 and G.11 as grafted orchard trees compared with ungrafted liners in the greenhouse may be due to altered susceptibility of the rootstocks when challenged by a different avenue of infection, such as systemic movement of internal bacteria (12) or by changes in rootstock physiology when the rootstock was grafted under scions and grown as fruiting trees (22). The high severity of fire blight observed in an infected rootstock sucker of G.11 in the orchard compared with the low disease severity in an infected B.9 sucker (Table 5) suggests the latter possibility (that growth under orchard conditions may alter susceptibility) because rootstock sucker infection should

Table 4. Generalized linear model analysis of severity of fire blight symptoms on 49 apple rootstocks inoculated with strains of *Erwinia amylovora* in greenhouse trial

Source of variation	Degrees of freedom	Sums of square	F^z
Model	138	68.580	10.65**
Error	784	36.909	…
Corrected total	922	105.489	…
Type III error			
Rootstock	47	47.086	21.28**
Strain	3	9.300	65.85**
Rootstock × strain	88	11.803	2.85**

z ** Denotes statistical significance, $P = 0.01$.

Table 5. Fire blight symptoms observed on scions ('Royal Gala') and rootstocks grown under orchard conditions[n]

	Inoculated trial[o]											
		1999							2000		Natural[p]	
		Blossom	Rootstock suckers		Ooze[q]		Blight[r]		Dead[s]	Blight[r]		Blight[r]
Rootstock	N	cluster[t]	Tree[u]	Shoot[v]	6/15	7/8	7/8	9/9	5/18	9/14	N	10/14/00
M.26 EMLA	12	12 defgh	17 a	100	67 a	58 a	75 a	92 a	92 a	100 a	14	93 a
M.26 VF	10	13 cdef	30 a	100	30 ab	20 a	30 ab	60 abc	60 abc	70 abc	14	57 ab
M.26 C	…	…	…	…	…	…	…	…	…	…	13	69 ab
M.9 VF ('McIntosh')[w]	12	11 defgh	17 a	93	58 ab	58 a	58 ab	83 ab	83 ab	100 a	11	36 ab
M.7	…	…	…	…	…	…	…	…	…	…	13	31 ab
MM.106	…	…	…	…	…	…	…	…	…	…	14	43 ab
MM.111 EMLA	12	11 efgh	0 a	0	0 b	0 a	0 b	0 c	8 c	0 c[x]	13	15 ab
Marubakiado	12	23 a	17 a	75	0 b	8 a	0 b	0 c	0 c	0 c	14	0 b
Budagovsky 9	12	18 bc	8 a	5	0 b	0 a	0 b	0 c	0 c	0 c	14	0 b
Poland 14	7	13 cdef	14 a	83	0 b	29 a	0 b	29 abc	29 abc	29 c	11	73 ab
Geneva 11	12	15 bcde	8 a	100	17 ab	17 a	17 b	25 bc	25 bc	25 c	13	23 ab
Geneva 16	6	16 bcd	17 a	75	0 b	0 a	0 b	0 c	0 c	0 c	19	0 b
Geneva 30	18	10 efgh	11 a	9	0 b	6 a	0 b	0 c	0 c	0 c	24	4 b
Novole	…	…	…	…	…	…	…	…	…	…	5	0 b
CG.3007	…	…	…	…	…	…	…	…	…	…	12	0 b
CG.3041	12	15 bcde	0 a	0	0 b	0 a	0 b	8 c	0 c	0 c[y]	13	0 b
CG.4003	12	7 hi	8 a	67	8 b	0 a	0 b	0 c	0 c	0 c	13	8 b
CG.4202	12	7 ghi	8 a	36	0 b	0 a	0 b	8 c	0 c	0 c[y]	27	7 b
CG.4213	…	…	…	…	…	…	…	…	…	…	6	0 b
CG.4214	6	9 fghi	0 a	0	0 b	0 a	0 b	0 c	0 c	0 c	13	0 b
CG.4247	11	12 defgh	0 a	0	0 b	0 a	0 b	0 c	0 c	0 c	12	0 b
CG.4814	…	…	…	…	…	…	…	…	…	…	12	0 b
CG.5012	9	12 defgh	33 a	76	0 b	33 a	0 b	11 c	11 c	44 abc	13	0 b
CG.5046	…	…	…	…	…	…	…	…	…	…	13	15 ab
CG.5179	12	12 defgh	0 a	0	0 b	0 a	0 b	8 c	8 c	17 c	11	0 b
CG.5757	12	12 defg	17 a	85	0 b	0 a	0 b	0 c	0 c	8 c	13	0 b
CG.6143	…	…	…	…	…	…	…	…	…	…	12	42 ab
CG.6210	…	…	…	…	…	…	…	…	…	…	14	7 b
CG.6253	…	…	…	…	…	…	…	…	…	…	9	0 b
CG.2 (dis)[z]	…	…	…	…	…	…	…	…	…	…	7	0 b
CG.8 (dis)	…	…	…	…	…	…	…	…	…	…	14	0 b
CG.9 (dis)	…	…	…	…	…	…	…	…	…	…	13	38 ab
CG.26 (dis)	12	13 cdef	0 a	5	0 b	0 a	8 b	8 c	8 c	8 c	13	0 b
CG.48 (dis)	…	…	…	…	…	…	…	…	…	…	9	33 ab
CG.60 (dis)	9	5 i	0 a	0	0 b	11 a	0 b	0 c	0 c	0 c	13	15 ab
CG.67 (dis)	…	…	…	…	…	…	…	…	…	…	13	0 b
CG.103 (dis)	12	12 defgh	8 a	80	8 b	50 a	25 ab	58 abc	58 abc	58 abc	12	33 ab
CG.132 (dis)	…	…	…	…	…	…	…	…	…	…	12	8 b
CG.134 (dis)	11	12 defgh	9 a	100	0 b	9 a	0 b	9 c	9 c	9 c	10	0 b
CG.602 (dis)	12	9 fghi	8 a	100	8 b	8 a	8 b	8 c	8 c	33 bc	12	33 ab
CG.756 (dis)	…	…	…	…	…	…	…	…	…	…	12	8 b
CG.3029 (dis)	…	…	…	…	…	…	…	…	…	…	6	0 b
CG.5008 (dis)	12	15 bcde	8 a	81	0 b	0 a	0 b	0 c	0 c	0 c	…	…
CG.5156 (dis)	…	…	…	…	…	…	…	…	…	…	10	0 b
CG.6723 (dis)	12	19 a	0 a	0	0 b	0 a	0 b	0 c	0 c	0 c	11	0 b
CG.6737 (dis)	6	11 efgh	0 a	0	0 b	0 a	0 b	0 c	0 c	17 c	14	0 b
CG.8228 (dis)	…	…	…	…	…	…	…	…	…	…	9	0 b

[n] Fire blight of the rootstock was characterized by the presence of bacterial ooze on rootstock during the growing season and/or typical fire blight necrosis (black in color) with evidence of either tree death or premature leaf coloration in fall. N = number of trees in trial; … = rootstock not included in inoculation trial; CG = Cornell Geneva, advanced selection of apple rootstock breeding program of the USDA-ARS and Cornell University; EMLA = virus-tested clones developed at the East Malling and Long Ashton Research Stations, UK; VF = virus-free clone; C = clone grown at Cornell for several years.

[o] Trees were inoculated by spraying blossoms with *Erwinia amylovora* strain E4001a on 12 May 99 and 17 May 99.

[p] Fire blight rootstock infection resulting in commercial orchard after natural blossom blight epidemic that occurred May 2000.

[q] Percent trees with ooze present on rootstock. Values followed by the same letter did not differ significantly at $P = 0.2$ as determined by Ryan's significance test for multiple comparison of proportions.

[r] Rootstock blight; percent trees with symptoms of rootstock infection (blackish necrosis of rootstock usually accompanied by evidence of previous ooze, weak scion growth and/or premature leaf coloration in fall). Values followed by the same letter did not differ significantly at $P = 0.2$ as determined by Ryan's significance test for multiple comparison of proportions.

[s] Percent dead or dying trees (failed to leaf out in the spring or initial leaves were small, yellowed and failed to continue growth). Values followed by the same letter did not differ significantly at $P = 0.2$ as determined by Ryan's significance test for multiple comparison of proportions.

[t] Percent blossom clusters with fire blight infection on 27 May 99. Values followed by the same letter did not differ significantly at $P = 0.05$ as determined by a Waller-Duncan *k*-ratio *t* test.

[u] Percent trees with fire blight infected rootstock suckers observed on 15 June 99 or 8 July 99. Values followed by the same letter did not differ significantly at $P = 0.2$ as determined by Ryan's significance test for multiple comparison of proportions.

[v] Shoot length blighted; percent rootstock sucker's current season's shoot length necrotic (mean of suckers with fire blight symptoms on 8 July 99).

[w] Trees on M.9 rootstock were grafted with 'McIntosh' rather than 'Royal Gala'.

[x] Dead tree showed no symptoms of fire blight rootstock infection and was presumed to have died from other causes.

[y] Trees previously exhibiting symptoms of fire blight infection recovered and showed normal rootstock appearance and tree growth.

[z] Selection discarded (dis) from breeding program.

be similar to direct inoculation in the greenhouse. However, rootstock sucker infection occurred on only one tree each of B.9 and G.11 in the orchard trial; therefore, no conclusion can be reached.

It also is possible that other unknown environmental factors are responsible for the differences observed between greenhouse and orchard tests. Cline et al. (3) have reported that when vegetative shoots of M.7, B.9, and G.16 liners grown in a nursery were directly inoculated with strain E2017p, all three rootstocks were evaluated as moderately resistant, with approximately 40 to 50% of their shoot length becoming blighted. In the current study, B.9 was evaluated as highly susceptible, and M.7 and G.16 were evaluated as resistant when vegetative shoots of rootstock liners were directly inoculated in the greenhouse (Tables 3 and 4); however, the resistance of all three rootstocks appeared similar in orchard trials (Table 5).

There was general agreement in the evaluation of rootstock resistance in the controlled blossom inoculation trial and when rootstock infection resulted from natural blossom infection. High disease pressure in the natural infection block was indicated by the relatively high incidence of rootstock infection observed in M.7, MM.106, and MM.111 (Table 5) which are generally considered resistant or moderately resistant to fire blight (23). The lower-than-expected incidence of rootstock infection for M.9 in the natural infection block could have been due to a lower incidence of blossom infection in the earlier blooming McIntosh-type scion than in the Royal Gala trees, but accurate assessment of the incidence of blossom blight in individual trees was not made in this block. The virulence characteristics of the *E. amylovora* strain or strains that caused infection in the natural infection block are not known.

Compared with traditional plantings of large trees, high-density apple plantings on dwarfing rootstocks have many economic benefits, including higher yields, quicker return on investment, more efficient utilization of pesticide and labor inputs, and improved fruit quality. However, the increased planting costs of high-density plantings combined with the extreme fire blight susceptibility of M.9 and M.26 rootstocks has resulted in devastating financial losses for apple growers in some areas of the United States. We have calculated that, when the cost of tree replacement, lost investment in tree maintenance, and reduced yields over several years are considered, a 10% incidence of rootstock blight in a 4-year-old high-density planting can result in losses up to $3,500 per acre (11). New apple rootstocks that combined desirable pomological characteristics with resistance to infection by *E. amylovora* have the potential to provide practical control for the rootstock phase of fire blight.

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