Relative Resistance of Thirteen Apple Rootstocks to Three Species of *Phytophthora*

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Accepted for publication 8 January 1993.

ABSTRACT

Browne, G. T., and Mircetich, S. M. 1993. Relative resistance of thirteen apple rootstocks to three species of *Phytophthora*. Phytopathology 83:744-749.

Thirteen apple rootstocks (Antonovka [Ant.] 313, Budagovsky [Bud.] 490, Bud.118, Bud.9, M.4, MM.111 EMLA, MM.106 EMLA, M.7 EMLA, M.26 EMLA, M.9 EMLA, Mark, Polish [P.] 18, and a domestic seedling [*Malus domestica*]) were evaluated for resistance to root and crown rots caused by *Phytophthora cactorum*, *P. cambivora*, and *P. cryptogea* in artificially infested soil and for resistance to canker development caused by *P. cactorum* and *P. cambivora* in excised and intact stems. In soil infested with *P. cactorum*, M.9 EMLA, Mark, Bud.118, and Bud.9 were highly resistant (mean crown circumference girdled 2–11%); MM.106 EMLA, Ant.313, and the domestic seedling were highly susceptible (mean crown circumference girdled 74–96%); and the remaining rootstocks were intermediate. With *P. cambivora*, Mark and Bud.118 were highly resistant (mean root rot 9%); Bud.9, M.7 EMLA, and P.18 were intermediate, and the other rootstocks were moderately to highly susceptible (mean root rot 47–98%). With *P. cryptogea*, most rootstocks were relatively resistant (mean root rot 1–10%), except M.4, MM.111 EMLA, Ant.313, and P.18 (mean root rot 18–42%). After stem inoculations with *P. cactorum*, mean canker lengths in excised and intact rootstock stems were correlated positively with mean crown rot lengths in corresponding apple rootstocks grown in infested soil ($r = 0.59$–0.79, $P = 0.05$–0.004). With *P. cambivora*, however, mean canker lengths from stem assays of resistance did not correlate significantly with mean crown rot lengths from infested soil assays of resistance ($P = 0.93$–0.11). Relative resistance to *Phytophthora* spp. in apple rootstocks can vary by *Phytophthora* sp. and by method of evaluation.

Phytophthora root and crown rots of apple are among the most serious soilborne diseases of the crop (16). The diseases occur worldwide and often result in the death of affected trees. Historically, the symptoms were attributed primarily to *Phytophthora cactorum* (Lebert & Cohn) Schröt., but recently, several *Phytophthora* spp. have been implicated in the diseases (16). Exposure of commercial apple trees to the pathogens may be common because of infestation of orchard soils and nursery stock with *Phytophthora* spp. prior to orchard establishment (7,15,20), introduction of fungi by contaminated irrigation water (21), and dissemination of infested soil by interorchard traffic (20). When the exposed trees are subjected to periods of frequent or prolonged water saturation in soil, incidence and severity of Phytophthora root and crown rots in apple can increase greatly (6).

Of the various approaches for control of the diseases, one of the most environmentally and economically appealing is the use of apple rootstocks that are desirable horticulturally and that are genetically resistant to *Phytophthora* spp. (12,19,20). Based on several reports, some species of *Malus* and some clonally propagated apple rootstocks show high levels of resistance to *P. cactorum* (10–12).

Despite progress in the development and use of apple rootstocks that are resistant to Phytophthora root and crown rots, the approach has been subject to complications. For example, assessments of resistance to the diseases based on field observations often contradict assessments of resistance to *P. cactorum* made under controlled conditions in laboratory or greenhouse studies (19). Furthermore, field observations of resistance of rootstocks sometimes disagree when they originate in different apple-production regions (19,20). This lack of consensus in assessments of resistance has been attributed to variation in the procedures used to evaluate resistance (16), as well as to geographical differences in the edaphic environments and distributions of *Phytophthora* spp. where the rootstocks are evaluated (20). Finally, assessments of resistance made under greenhouse and laboratory conditions have been limited almost exclusively to evaluations with *P. cactorum*, despite the fact that several *Phytophthora* spp. are now implicated in the diseases (16,20).

This study was undertaken to investigate the relative resistance of 13 apple rootstocks to Phytophthora root and crown rots under controlled conditions. Experiments were designed to compare the relative resistance of the rootstocks not only to *P. cactorum* but also to *P. cambivora* (Petri) Buisman and *P. cryptogea* Pethybr. & Lafferty. With *P. cactorum* and *P. cambivora*, parallel evaluations of resistance in apple rootstocks were conducted with three different procedures that utilized infested soil, excised stems, and intact stems, so the degree of correlation among the three assessments of resistance could be tested. A portion of this work was reported previously (8).

MATERIALS AND METHODS

Plant materials. Twelve different clonal rootstocks for apple were obtained as dormant "liners" (Treco Inc., Woodburn, OR). The rootstocks, 4–8 mm in stem diameter, were planted during April in 3-L pots with U.C. soil mix (2), trimmed to a height of 30 cm above the soil line, and grown in a lathhouse. The plants were fertilized at 6-mo intervals with 17-6-10 (N-P-K) slow-release fertilizer with minor elements (Sierra Chemical Co., Milpitas, CA) and were watered as needed. Once established, the rootstocks served either as material for direct evaluations of resistance to *Phytophthora* spp. in stem-inoculation experiments or as sources of softwood cuttings that were propagated for evaluations of resistance in artificially infested soil.

The cuttings were subjected to mist-propagation techniques (13) to provide small plants of the rootstocks that were free of soilborne pathogens. Shoot tips of the rootstocks were cut from the distal 15 cm of current season's growth and subdivided into individual cuttings that consisted of three to four nodes each. The apical two to three nodes of each cutting retained the attached leaves, but cuts were made near the basal node to remove the attached leaf and define the lower boundary of the cutting just below the node. The basal 0.5–1 cm of each cutting was dipped for 1 s in an aqueous solution of 2,500 ppm of indole-3-butyric acid dissolved in 50% ethanol. The basal 1–4 cm of the treated cuttings was inserted into a mixture (1:1, v/v) of moistened horticultural vermiculite and perlite maintained at 20–25 C under intermittent

mist until the cuttings rooted. Slow-release fertilizer (17-6-10 [N-P-K] plus minor elements) was added at a rate of 5 ml/L of rooting medium to aid in establishment of the cuttings after roots developed. When the cuttings had developed a sufficient root system, they were transplanted into 175-ml pots with U.C. soil mix and maintained under a reduced frequency of misting for several weeks. Once acclimated to the reduced frequency of mist, the rooted cuttings were moved out of the intermittent mist and into the greenhouse environment, where they were fertilized weekly with 11-7-26 (N-P-K) liquid nutrient solution (National Research and Chemical, Gardena, CA) and watered daily. Although the cuttings generated ample root systems in the greenhouse, the axillary buds of the plants failed to grow. To completely break the dormancy of the buds, the plants were placed in cold storage (5 C) in the dark for 3 mo. The chilled cuttings were returned to the greenhouse, where they grew vigorously. The plants were fertilized every 5–7 days with the liquid nutrient solution and were watered as needed.

In addition to the clonally propagated rootstocks, the seed-propagated domestic seedling rootstock (*Malus domestica* Borkh.) was included in the evaluations of rootstock resistance to *Phytophthora* spp. Seeds obtained commercially (Schumacher Co., Sandwich, MA) were stratified to break dormancy, as described previously (6). Once stratified, the seeds were planted in 175-ml pots while the clonally propagated cuttings were rooted under mist. The seedlings were subjected to the same treatments as the clonally propagated cuttings after the rooted cuttings were removed from mist (i.e., the greenhouse period of acclimation and dormant chilling).

Production of inocula. Inocula were produced by two methods. For experiments that utilized artificially infested soil, inocula of single isolates of *P. cactorum*, *P. cambivora*, and *P. cryptogea* were grown on a vermiculite-based medium, as described previously (6). For evaluations of rootstock resistance after direct inoculation of apple rootstock stems, the same isolates of *P. cactorum* and *P. cambivora* used to artificially infest soil were grown in petri-dish cultures of V8 agar (200 ml of V8 juice, 2 g of $CaCO_3$, 17 g of agar, and 800 ml of distilled water per liter).

Evaluations of resistance to *Phytophthora* spp. in soil. The evaluations of apple rootstock resistance in infested soil were initiated 2.5 mo after the cuttings and seedlings were removed from the cold-storage treatment. Inoculum and rootstock treatments were assigned randomly in a split-plot design (17). The rootstock plants were treated as subplots within main plots of inoculum treatments, and the main plots were randomized in complete blocks. In preparation for the transplanting, the actively growing rootstocks were trimmed so approximately three nodes of current season's growth remained. The rootstocks (with soil on the roots) were transplanted into 1-L pots containing U.C. soil mix that was either noninfested (sterile vermiculite-based medium added as a control) or artificially infested with the vermiculite-based inocula of *P. cactorum*, *P. cambivora*, or *P. cryptogea*. Using methods previously described (6), the inocula and sterilized vermiculite-based medium were added to their respective treatments at a rate of 45 ml/L of final soil volume.

Ten days after transplanting and once every 2 wk thereafter, the soil in each plant's pot was flooded for 48 h to stimulate production and release of zoospores by the *Phytophthora* sp. in the soil (6). To facilitate flooding, the pots were placed in bowls slightly larger than the pots. Water was added to maintain the water level at 0.5–1 cm above the surface of the soil for 48 h. The flooding was discontinued as the pots were removed from the bowls and allowed to drain. Between the episodes of flooding, the soil in each pot was watered one to two times a day as needed and was allowed to drain freely. During the experiments, soil temperature ranged from 17 to 30 C. Three months after transplanting, resistance was assessed in each plant's root system according to these measurements: percent crown girdling with rot (based on visual estimates of the lateral extent of lesions around the root crown circumference); crown rot length (based on measurements of the vertical length of crown rot lesions); and percent root rot (based on visual estimates of the percentage of roots with rot that extended into the stele). Rotted roots exhibited reddish-brown decay that was visible externally. To verify that the externally visible decay extended into the stele, cortex tissue was scraped away from several individual, discolored roots of each plant to check for reddish-brown decay in the stele tissue.

The complete experiment was repeated once, and results were similar between experiments (i.e., there was no significant statistical interaction between experiment and rootstock; $P = 0.32$, 0.66, and 0.33 for percent crown girdling, length of crown rot, and percent root rot variables, respectively). Some of the rootstocks also had been evaluated for resistance to *P. cactorum*, *P. cambivora*, and *P. cryptogea* in three previous experiments in which they performed similarly (G. T. Browne and S. M. Mircetich, *unpublished data*). The results from the two complete experiments were combined for presentation. The means for each combination of rootstock and *Phytophthora* sp. were based on five to 10 replicate plants. Prior to the final analyses of variance and separation of means, transformations were applied to the data when necessary to stabilize the variances around treatment means (4). The means were compared with the aid of 95% confidence intervals. The means and confidence limits were back-transformed (17) before presentation in results.

Evaluation of resistance to *Phytophthora* spp. in stems. The liners of clonal apple rootstocks that had been planted, grown, and overwintered in the lathhouse during the previous year were moved to the greenhouse for evaluations of rootstock resistance by two methods of direct inoculation. In the first method, which was similar to procedures reported previously (3,14), 20-cm sections of stem tissue were removed from basal, median, and apical regions of the stem of each rootstock for subsequent inoculation. From near the middle of each excised stem piece, a 5-mm-diameter disk of bark was removed with a cork borer to expose the cambium tissue. The exposed cambium face was inoculated with a 5-mm-diameter mycelial disk of *P. cactorum* or *P. cambivora* from the margins of actively growing cultures on V8 agar. Controls were inoculated with sterile V8-agar disks. The inoculated wounds were wrapped firmly with electrical tape (Super 33+, 3M Co., Hutchinson, MN) to prevent drying, and each stem section was identified according to plant and position of origin to facilitate subsequent analysis of variance. The inoculated excised stems were incubated for 7 days in a dark chamber at 20–26 C and 100% relative humidity.

At the same time that the excised stem pieces were inoculated, similar inoculations were made in intact stems. This method of direct inoculation followed the same procedures as those utilized in excised stem inoculations, except the stems were left intact on the rootstocks. As with inoculations of excised stems, the inoculated wounds of the basal, median, and apical regions of the stem tissue were covered with electrical tape. The inoculated plants were arranged in a completely randomized design in the greenhouse, where they were incubated for 1 mo after inoculation. During the incubation period, the rootstocks were watered as needed one to two times a day, and air temperatures near the points of inoculation ranged from 17 to 28 C. For both intact and excised stems, three to four plants (nine to 12 stem segments, respectively) were inoculated in each experiment for each treatment combination of rootstock and *Phytophthora* sp.

At the end of the incubation periods for intact and excised stems, the length of necrotic cankers was measured in each inoculated section of stem. The surface of the stem bark was cut to locate the margins of necrotic, reddish-brown, and healthy, greenish-white, tissue. Isolation from some of the stems confirmed that *P. cactorum* or *P. cambivora* had colonized the discolored tissue at the margins of the stem cankers.

The experiments on resistance of intact and excised apple rootstock stems to development of cankers were repeated once. There was significant rootstock by experiment interaction for both intact and excised stem inoculations ($P = 0.005$–0.07); therefore, means are shown for each experiment. Analyses of variance were applied separately to the data from intact and excised stems, and the data from individual stem pieces were treated as repeated measures within the experimental units of the individual plants.

RESULTS

Evaluations of resistance to *Phytophthora* spp. in soil. The control plants grown in noninfested soil developed no crown rot and negligible root rot (data not shown; 1–4% root rot), but analysis of variance of the data from the rootstocks grown in infested soil revealed a significant interaction between *Phytophthora* sp. and rootstock ($P = 0.0001$ for percent crown girdling, crown rot length, and percent root rot). Therefore, final analyses of variance and separation of rootstock means were applied after

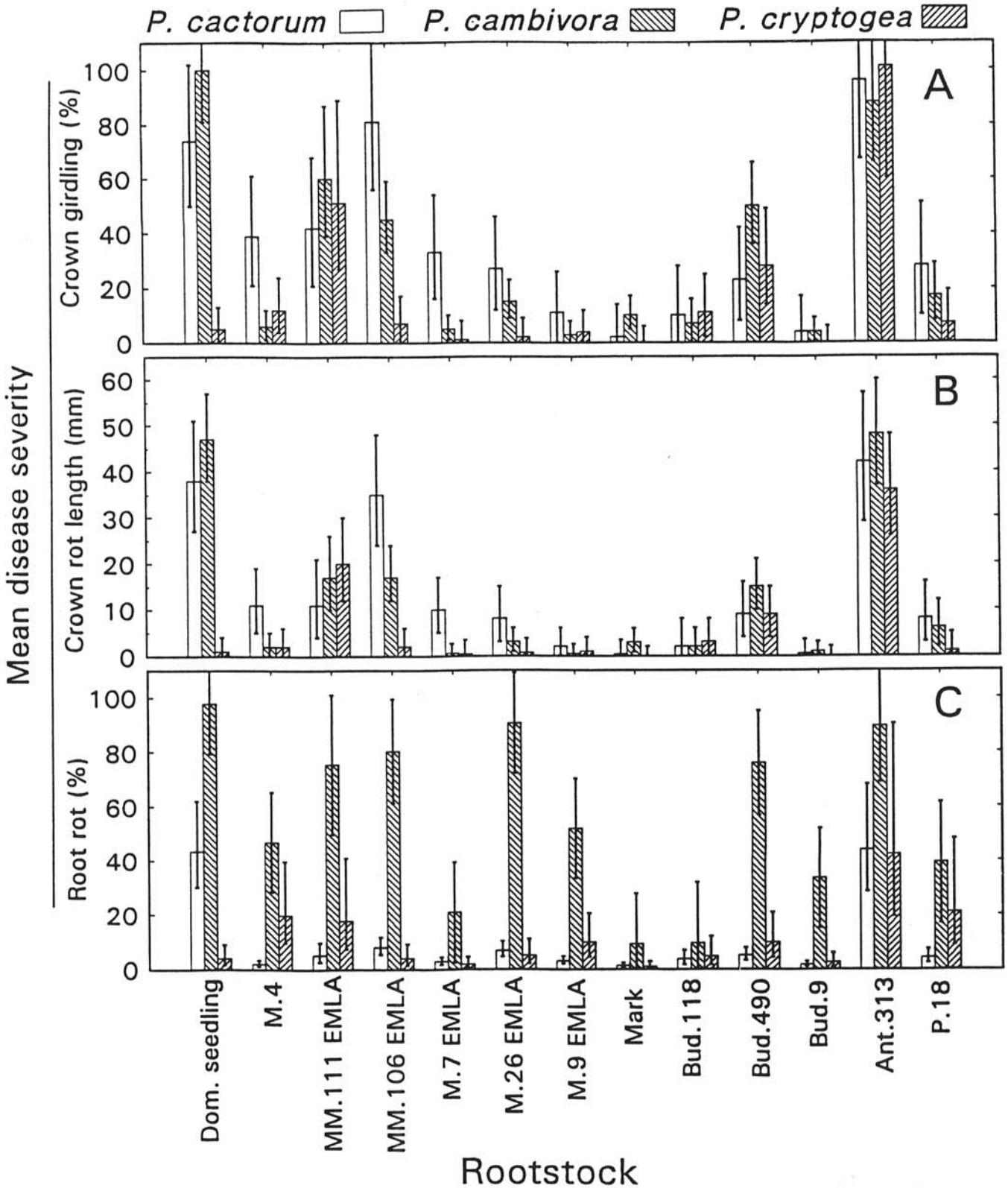

Fig. 1. Relative resistance of 13 apple rootstocks to crown and root rots caused by *Phytophthora cactorum*, *P. cambivora*, and *P. cryptogea*. Vegetative cuttings and seedlings were grown for 3 mo in noninfested soil (controls) or soil artificially infested with one of the three *Phytophthora* spp. At the end of experiments, resistance was assessed according to **A,** percent crown girdling with rot (visual estimates of lateral extent of crown lesions around root crown circumference); **B,** crown rot length (measurements of vertical length of crown rot lesions); and **C,** percent root rot (visual estimates of percent roots with reddish-brown decay extending into the stele). No crown rot and negligible root rot (means 1–4%) developed in controls (data not shown). Means = five to 10 replicate plants. For each measurement of disease severity, statistical interaction between *Phytophthora* sp. and rootstock was significant, $P = 0.0001$. Vertical bars delimit 95% confidence intervals.

exclusion of the data from the controls and within the treatments of *Phytophthora* sp. The transformations applied to stabilize the variance around treatment means included $Y = \log_{10}(y + 1)$ for percent root rot data in treatments with *P. cactorum* and *P. cryptogea*, $Y=(y+0.125)^{0.5}$, $Y=(y+0.125)^{0.25}$, and $Y=\log_{10}(y+0.125)$ for data on percent crown girdled in treatments with *P. cactorum*, *P. cambivora*, and *P. cryptogea*, respectively, and $Y = (y + 1)^{0.5}$ for data on length of crown lesions in all three soil-infestation treatments (in which Y and y denote the transformed and nontransformed data values, respectively). No transformation was applied to the root rot data from inoculation with *P. cambivora*.

In soil artificially infested with *P. cactorum*, the domestic seedling, MM.106 EMLA, and Ant.313 developed severe crown rot (mean crown girdled 74–96%; mean length of crown rot 35–42 mm; Fig. 1A and B). Comparatively, M.9 EMLA, Mark, Bud.118, and Bud.9 sustained relatively little crown rot (mean crown girdled 2–11%; mean length of crown rot 1–3 mm; Fig. 1A and B). M.4, MM.111 EMLA, M.7 EMLA, M.26 EMLA, Bud.490, and P.18 developed intermediate levels of crown rot in soil infested with *P. cactorum* (Fig. 1A and B). *P. cactorum* caused moderate levels of root rot in the domestic seedling and Ant.313 (means 43–44%; Fig. 1C) but very little root rot in the other rootstocks.

The relative resistance of the rootstocks to crown and root rots caused by *P. cactorum* did not always extend to *P. cambivora* and *P. cryptogea*. For example, M.4, MM.111 EMLA, MM.106 EMLA, M.26 EMLA, M.9 EMLA, Bud.9, and Bud.490, which sustained little root rot with *P. cactorum*, developed moderate to severe levels of root rot in soil infested with *P. cambivora* (means 33–90%; Fig. 1C). In addition, MM.111 EMLA and Bud.490, of intermediate susceptibility to crown rot caused by *P. cactorum*, were significantly more susceptible than were most of the other rootstocks to crown rot in soil infested with *P. cryptogea* ($P = 0.05$; Fig. 1A and B). Conversely, the domestic seedling and MM.106 EMLA, both highly susceptible to crown rot caused by *P. cactorum*, developed only low levels of crown and root rot in soil infested with *P. cryptogea* (Fig. 1A–C).

Only Bud.118 and Mark were highly resistant to root and crown rot caused by all three species of *Phytophthora* used in the evaluations. Ant.313 and P.18 were highly susceptible and intermediate in resistance to root and crown rots caused by the three *Phytophthora* spp., respectively (Fig. 1A–C).

Evaluations of resistance to *Phytophthora* spp. in stems. As with evaluations of resistance of apple rootstocks in infested soil, stem inoculations revealed significant interaction between the effects of *Phytophthora* sp. and rootstock ($P = 0.003$ and 0.016 for excised and intact stem inoculations, respectively). Means are presented by experiment for each combination of rootstock, *Phytophthora* sp., and stem-inoculation method (Fig. 2A–D). The intact and excised stems that served as controls when inoculated with sterile V8 agar developed no cankers.

In both experiments, excised stems inoculated with *P. cactorum* or *P. cambivora* developed longer mean canker lengths than did the intact stems (Fig.2 A–D). Most rootstocks exhibited similar responses in the first and second experiments; the rootstock means for experiment one were often within one standard-error unit of the comparable mean in the second experiment. However, the response of some of the rootstocks differed by a factor of approxi-

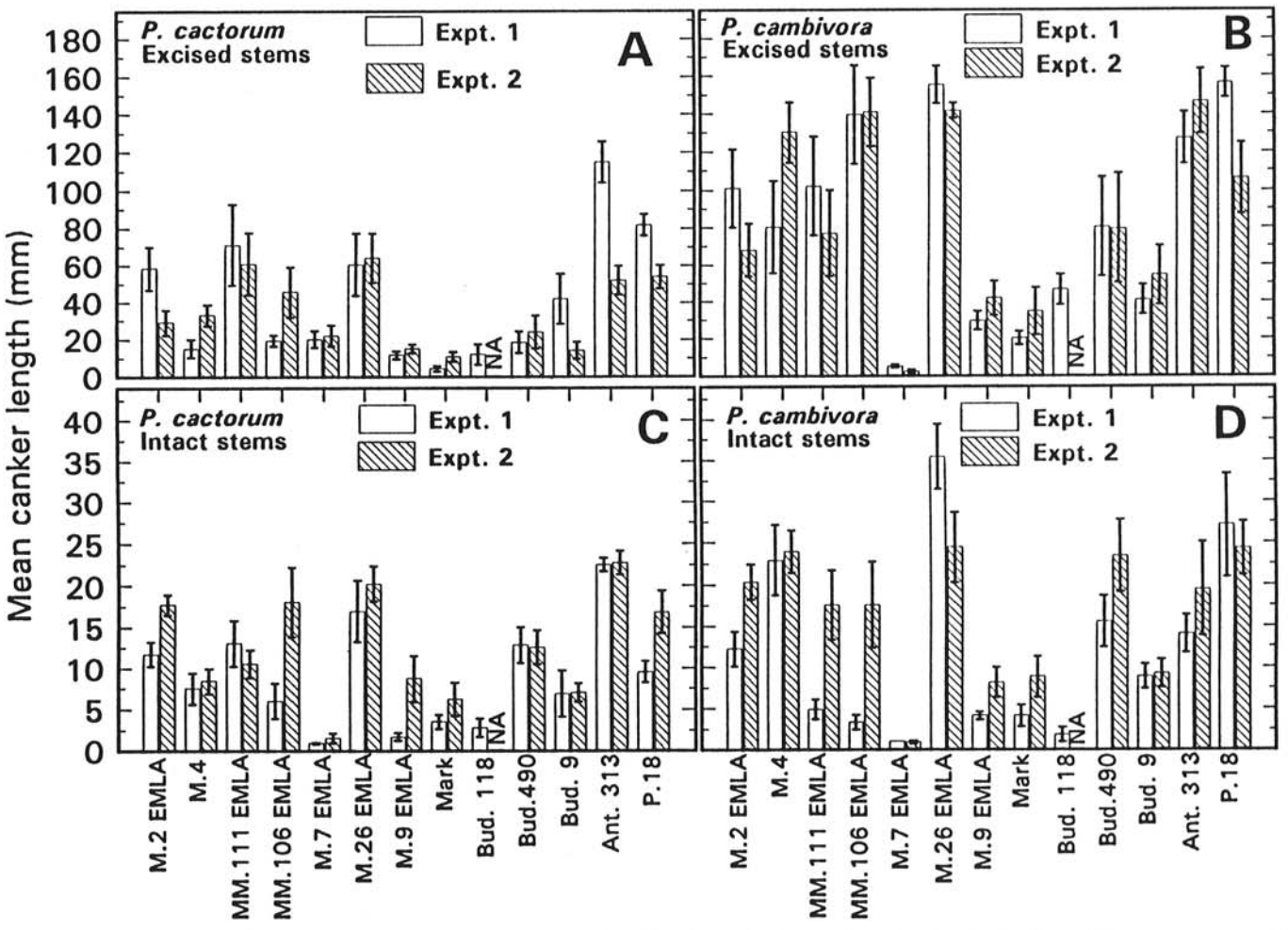

Fig. 2. Relative resistance of 13 apple rootstocks to development of cankers in excised stems inoculated with **A,** *Phytophthora cactorum* or **B,** *P. cambivora* and intact stems inoculated with **C,** *P. cactorum* or **D,** *P. cambivora*. Length of cankers measured after 7 days of incubation for excised stems and after 4 wk of incubation for intact stems. Interaction between *Phytophthora* sp. and rootstock was statistically significant for both excised and intact stem inoculations, $P = 0.003$ and 0.016, respectively. Vertical bars indicate +/− standard error of means.

mately two or more between the experiments (i.e., excised Ant.313 and intact MM.106 EMLA inoculated with *P. cactorum*, intact MM.111 EMLA and MM.106 EMLA inoculated with *P. cambivora*; Fig. 2A, C, and D).

After both intact and excised stem inoculations with *P. cactorum* and *P. cambivora*, Ant.313, M.26 EMLA, and P.18 developed relatively long mean canker lengths compared to mean canker lengths in M.7 EMLA, M.9 EMLA, Mark, and Bud.118. Most of the other rootstocks developed intermediate canker lengths, but in some cases, the response varied considerably between experiments, species of *Phytophthora*, and method of stem inoculation (Fig.2A–D).

For the 12 rootstocks evaluated in both stem and soil assays of resistance, correlation was tested between rootstock means for canker length in the stem assays and corresponding rootstock means for crown rot length in the infested soil assays. The sets of means from experiments one and two of stem-inoculation assays were tested separately because of experiment by treatment interaction, but means from the infested soil assays were left combined over experiments. After stem inoculations with *P. cactorum*, mean canker lengths in excised and intact rootstock stems were correlated positively with mean crown rot lengths in corresponding apple rootstocks grown in infested soil ($r = 0.59$–0.79, $P = 0.05$–0.004). However, with *P. cambivora*, mean canker lengths from stem assays of resistance did not correlate significantly with mean crown rot lengths from infested soil assays of resistance ($P = 0.93$–0.11).

DISCUSSION

The results of our evaluations of rootstock resistance with infested soil revealed that expressions of resistance to *P. cactorum* in apple rootstocks do not consistently extend to *P. cambivora* and *P. cryptogea*. In some rootstocks, high levels of susceptibility to *P. cactorum* were accompanied by relatively high resistance to *P. cryptogea* (e.g., domestic seedling and MM.106 EMLA). Conversely, in other rootstocks, comparatively high levels of resistance to *P. cactorum* were associated with high relative susceptibility to root and/or crown rot caused by *P. cambivora* (e.g., M.4, MM. 111 EMLA, M.26 EMLA, M.9 EMLA, Bud.490, and Bud.9).

The fact that relative resistance of different apple rootstocks to root and crown rots varied with species of *Phytophthora* may explain some of the controversy that surrounds assessments of resistance to Phytophthora root and crown rots in apple rootstocks. Controlled assessments of resistance in apple to Phytophthora root and crown rots have historically been limited to evaluations with *P. cactorum*, but it is now known that in some production regions several *Phytophthora* spp. in addition to *P. cactorum* are associated with the diseases (16). Furthermore, the *Phytophthora* spp. associated with root and crown rots of apple in California exhibit regional differences in prevalence within the state (5). Our results suggest that some of the inconsistency in ratings of apple rootstock resistance may result from involvement of different species of *Phytophthora* that elicit unique responses of resistance and susceptibility in different areas in which ratings are made.

The relatively low to lacking correlation between resistance detected with stem-inoculation procedures and resistance detected with infested soil raises questions of which type of assay is most reliable and why. We did not attempt to evaluate the relative merits of the assays based on their relationships to published field observations of resistance to Phytophthora crown rot because these reports can be inconsistent and often do not document the species of *Phytophthora* involved. In addition, some of the rootstocks evaluated here have not been used widely in commercial production, and field observations on their resistance to crown rot are limited. Nevertheless, based on our observations and isolations from apple trees with Phytophthora root and crown rots in California, field expressions of resistance in MM.111 EMLA, MM.106 EMLA, M.26 EMLA, and M.7 EMLA to *Phytophthora* spp. in the state are more accurately reflected by our results from infested soil assays than by the results of the stem assays.

In our study, the results of the stem assays of resistance were less repeatable over successive experiments than were the results of the soil assays. A possible explanation for this is that the relatively short period of interaction between host and pathogen in the stem- and shoot-inoculation procedures (1–4 wk) may inherently provide more variable results than does the infested soil procedure in which cycles of infection are stimulated repeatedly during biweekly intervals of flooding over a 3-mo period; the rate at which *Phytophthora* spp. colonize stems and shoots of apple rootstocks can vary greatly over monthly intervals (9,14,20).

Another limitation of shoot- and stem-inoculation procedures compared to evaluations of resistance in infested soil may arise from the lack of a natural infection process in the direct inoculations of stem bark with mycelial disks (14). Furthermore, the detachment of stem or shoot sections from growing plants may change active resistance responses to colonization by the pathogen; this was not investigated.

In the present study, the domestic seedling, when transplanted at 10 mo into soil infested with *P. cryptogea*, was highly resistant to root and crown rot. This resistance to *P. cryptogea* was consistent in several years' experiments and with several different lots of rootstock seed. In contrast, in a different series of experiments in which seedlings from the same lots of the domestic seedling were transplanted at 5–7 wk into soil infested with the same isolate of *P. cryptogea* as that used in the present study, the rootstock developed severe root and crown rot (5). A possible explanation for the discrepancy between the two series of experiments is that the rootstock becomes more resistant to *P. cryptogea* with age.

The use of single isolates of *Phytophthora* spp. to artificially infest soil and to inoculate intact and excised stems affords comparison of results between the three procedures but also limits the scope of conclusions based on the relative resistance of the rootstocks involved. Because there are reports of cultivar specificity among isolates of *P. cactorum* (1), it is possible that the relative resistance detected in this study with one isolate of *P. cactorum* is not representative of the relative resistance of these rootstocks to other isolates or mixtures of *P. cactorum*. Nevertheless, the degree of host specificity that exists among most *Phytophthora* spp. that affect deciduous fruit and nut trees appears to be rather limited (7,18,20,22,23).

The results of this study highlight the importance of the particular procedures and *Phytophthora* spp. used to evaluate resistance of apple rootstocks to Phytophthora root and crown rots. The fact that resistance to the disease in apple can vary with species of *Phytophthora* justifies the inclusion of other species of *Phytophthora*, in addition to *P. cactorum*, in evaluations of resistance to root and crown rots. The inability of stem-inoculation procedures to consistently and adequately reflect the resistance of some apple rootstocks to *Phytophthora* spp. in infested soil suggests that stem assays of resistance should not be used as reliable indicators of resistance to the disease.

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