Incidence and Severity of Crown and Root Rots on Four Apple Rootstocks Following Exposure to *Phytophthora* Species and Waterlogging

W.F. Wilcox

Department of Plant Pathology, Cornell University, New York State Agricultural Experiment Station, Geneva, NY 14456

Additional index words. collar rot, M.7, M.26, MM.111, 0.3, *Malus ×domestica*, *Phytophthora cactorum*, *Phytophthora cambivora*, *Phytophthora cryptogea*, *Phytophthora megasperma*

Abstract. Plants of four apple (*Malus ×domestica* Borkh.) rootstock clones, M.7, M.26, MM.111, and Ottawa (O.) 3, were grown in unamended potting medium or in the same medium infested with *Phytophthora cactorum* (Leb. & Cohn) Schroet., *P. cambivora* (Petri) Buisman, *P. cryptogea* Pethyb. & Laff., or *P. megasperma* Drechsler, causal agents of crown and root rots. Plants were flooded for either 0, 24, 48, or 72 h every 7 days for 4 months, then assessed for disease incidence and severity. Averaged across all pathogens and rootstocks, mean crown rot incidences were 2.5%, 6.3%, 19%, and 50% following weekly flooding periods of 0, 24, 48, and 72 h, respectively; when averaged across all rootstocks and flooding treatments, mean incidences of crown rot caused by *P. cryptogea*, *P. cactorum*, *P. cambivora*, and *P. megasperma* were 36%, 26%, 15%, and 8.8%, respectively; when averaged across all four pathogens, mean crown rot incidences after 72 h of flooding were 40%, 45%, 50%, and 75% for M.26, 0.3, M.7, and MM.111, respectively. In contrast, 72-h flooding periods in the absence of a pathogen were least detrimental to growth of MM.111 clones and most detrimental to shoot growth of M-26. Exceptions to general trends were reflected by statistical interactions among pathogens, rootstocks, and flooding durations, e.g., after 72-h floodings, 0.3 was the rootstock with the greatest amount of root rot caused by *P. cryptogea* but the least amount caused by *P. megasperma*. Differential disease susceptibility among rootstocks appeared greatest with respect to *P. cactorum* and least with respect to *P. cryptogea*.

Crown, collar, and root rots caused by various *Phytophthora* spp. are debilitating and often fatal diseases of apple trees, occurring in most production regions of the world (Jeffers and Wilcox, 1990). Although various factors have contributed to a declining importance of scion infections (collar rot) over the last generation, the widespread adoption of clonal size-controlling rootstocks during this same period has been accompanied by increased outbreaks of crown and root rots on the clonal stocks themselves (Jeffers and Wilcox, 1990; McIntosh, 1975).

Apple rootstocks vary widely in their susceptibility to *Phytophthora* crown and root rots, yet rankings of relative susceptibility to these diseases are usually subjective and often differ significantly among authorities. Whereas MM.104 and MM.106 are generally regarded as being among the most susceptible clones, some workers also have considered M.7, M.26, and/or MM.111 to be highly susceptible; others have considered one or more of this latter group to be only moderately susceptible, yet others have rated one or more as "never" encountering *Phytophthora* problems (Childers, 1983; McIntosh, 1975). Such inconsistency may result from unrecognized interactions among *Phytophthora* spp. and rootstock genotypes, from ratings derived primarily from empirical observations of disease frequencies in orchards associated with widely different horticultural practices, climates, and soil factors, and from the results of certain controlled tests that correlate poorly with rootstock performance under orchard conditions.

Root and crown rots caused by *P. cactorum*, *P. cambivora*, *P. cryptogea*, and *P. megasperma* are common on some clonal apple rootstocks in New York, particularly in soils that are chronically wet or subjected to periods of water logging (Jeffers and Aldwinckle,

1986; Merwin et al., 1992). This latter observation has led to some controversy concerning the relative importance of anoxia ("wet feet") vs. fungal parasitism on the decline and death of trees in such sites. The purpose of this experiment was to determine the main and interactive effects of various *Phytophthora* spp. and waterlogging regimes on the incidence and severity of crown and root rots on four apple rootstocks.

Materials and Methods

In a recent study (Jeffers and Aldwinckle, 1988), virtually all clonal rootstock samples obtained from 11 nurseries in North America and Europe were contaminated with *P. cactorum* or *P. cambivora*; therefore, the rootstock clones examined in the present experiment, M.7, M.26, MM.111, and Ottawa (O.) 3, were confined to those for which plants were obtainable from a source (AgriForest Technologies, Kelowna, B.C., Canada) employing micropropagation and subsequent plant production in a potting medium free of potentially contaminated field soil. After purchase, plants were grown in a greenhouse in individual pots containing ≈300 cm³ of potting mix (2 volumes fine vermiculite : 1 volume steam-pasteurized sandy loam) until their lower stems were well-lignified and shoots were ≈10 to 15 cm long. They then were transplanted into 1-liter plastic containers filled with the same potting mix that was either unamended or infested with inoculum of a single isolate of either *P. cactorum* (isolate no. NY 359), *P. cambivora* (NY 216), *P. cryptogea* (NY 353), or *P. megasperma* (NY 352) originally recovered from diseased apple trees in New York. Inoculum consisted of vermiculite that had been soaked with dilute vegetable juice broth and colonized by the test fungus, as described previously by Wilcox (1989), and was added at a rate of 30 cm³ per 1000 cm³ of potting medium.

Two weeks after transplanting, and at 7-day intervals thereafter, plants from each rootstock × *Phytophthora* sp. combination were

Received for publication 25 Mar. 1992. Accepted for publication 15 Aug. 1992. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked advertisement solely to indicate this fact.

flooded for either 24, 48, or 72 h by plugging the drainage hole at the bottom of each container and adding water until 5 to 10 mm of free water collected on the soil surface; a fourth group of plants from each combination was left unflooded. Plants were otherwise watered daily with unimpeded drainage and fertilized biweekly with half-strength Hoagland's solution. The experiment was conducted for 4 months in a greenhouse maintained at 18 to 24C with a 15-h photoperiod. The potting mix then was washed from each root system, crown rot incidence was determined, and disease severity was rated on the basis of the fresh weights of roots and shoots and a visual estimate of the percentage of the root system that was rotted. There were five replicate plants per treatment arranged in a completely randomized-block design.

To facilitate comparisons among rootstock clones of inherently different size and vigor, shoot and root fresh weights for individual plants in a rootstock x pathogen x flooding duration treatment were expressed and analyzed as a percentage of the mean weight of the five uninoculated control plants for the same rootstock x flooding duration combination. Similarly, to compare effects of periodic waterlogging events in the absence of a *Phytophthora* sp., root and shoot weights of individual uninoculated plants in each flooding treatment were expressed as a percentage of the mean weight of the five unflooded control plants for the same rootstock. Analysis of

variance (ANOVA) was performed on arcsin-transformed values of all root rot and fresh weight percentage data.

Results

Crown rot incidence was highly variable, depending on rootstock, pathogen, and flooding duration (Table 1). For instance, averaged across all pathogens and rootstocks, mean disease incidences were 2.5%, 6.3%, 19%, and 50% following weekly flooding periods of 0, 24, 48, and 72 h, respectively. When averaged across all rootstocks and flooding treatments, mean incidences of crown rot caused by *P. cryptogea*, *P. cactorum*, *P. cambivora*, and *P. megasperma* were 36%, 26%, 15%, and 8.8%, respectively, and when averaged across all four pathogens, mean crown rot incidences in the most disease-conducive (72 h) flooding treatment were 40%, 45%, 50%, and 75% for M.26, O.3, M.7, and MM.111, respectively. Apparent differences in susceptibility among rootstocks were greatest with respect to *P. cactorum* (20% incidence for M.26 vs. 100% incidence for MM.111 with 72 h of flooding) and least with respect to *P. cryptogea* (80% to 100% incidence for all rootstocks in the 72-h flooding treatment) (Table 1). No crown rot developed on plants grown in uninfested potting medium.

Table 1. Incidence of crown rot and severity of root rot caused by four *Phytophthora* spp. on four apple rootstocks subjected to various flooding treatments.

Pathogen and flooding duration (h) ^y	Rootstock					Root rot (%) ^z				
	Crown rot incidence (%) ^z									
	M.7	M.26	MM.111	O.3	$\bar{X}$	M.7	M.26	MM.111	O.3	$\bar{X}$
<i>P. cactorum</i>										
0	40	0	0	0	10	43	4	5	5	14
24	20	20	20	0	15	32	12	25	6	19
48	20	0	40	20	20	39	9	47	31	32
72	80	20	100	40	60	84	30	90	54	65
$\bar{X}$	40	10	40	15	26	50	14	42	24	32
<i>P. cambivora</i>										
0	0	0	0	0	0	8	4	8	5	6
24	0	40	0	0	10	5	44	12	22	21
48	0	20	20	0	10	32	44	32	27	34
72	20	20	60	0	25	36	30	44	48	40
$\bar{X}$	5	20	20	0	11	20	31	24	25	25
<i>P. cryptogea</i>										
0	0	0	0	0	0	12	6	6	4	7
24	0	0	0	0	0	23	9	23	21	19
48	40	20	60	40	40	64	30	78	70	61
72	80	80	80	100	85	94	87	86	98	91
$\bar{X}$	30	25	35	35	31	48	33	48	48	45
<i>P. megasperma</i>										
0	0	0	0	0	0	9	6	7	5	7
24	0	0	0	0	0	12	9	5	5	8
48	0	0	20	0	5	10	10	30	8	15
72	20	40	60	0	30	60	42	72	34	52
$\bar{X}$	5	10	20	0	9	23	17	29	13	20
None (control)										
0	0	0	0	0	0	8	2	2	2	4
24	0	0	0	0	0	7	5	4	4	5
48	0	0	0	0	0	6	4	3	3	4
72	0	0	0	0	0	13	8	5	11	9
$\bar{X}$	0	0	0	0	0	9	5	4	5	6

^zValues represent the means from five replicate plants per treatment.

^yIndicated flooding durations imposed every 7 days throughout the 4-month duration of the experiment.

Table 2. Relative shoot and root weights of four apple rootstock subjected to various flooding treatments in the presence or absence of four *Phytophthora* species.

Pathogen and flooding duration (h) ^y	Rootstock									
	Shoot fresh wt (% control) ^z					Root fresh wt (% control) ^z				
	M.7	M.26	MM.111	O.3	$\bar{X}$	M.7	M.26	MM.111	O.3	$\bar{X}$
<i>P. cactorum</i>										
0	25	80	100	106	78	58	113	110	125	102
24	20	68	62	61	53	36	100	94	74	76
48	45	78	41	46	52	63	80	83	55	70
72	16	94	23	54	47	59	104	50	71	71
$\bar{X}$	27	80	56	67	58	54	99	84	81	80
<i>P. cambivora</i>										
0	102	91	89	82	91	117	100	96	80	98
24	65	48	55	43	53	84	78	71	59	73
48	46	55	59	35	49	74	48	89	44	64
72	64	102	50	49	66	67	79	68	65	48
$\bar{X}$	69	74	63	52	81	85	76	81	62	76
<i>P. cryptogea</i>										
0	100	71	102	100	93	118	99	98	104	105
24	79	92	86	97	89	103	122	91	76	98
48	40	65	34	34	43	82	73	51	48	63
72	19	69	18	22	32	48	74	31	39	48
$\bar{X}$	60	74	60	63	64	88	92	68	67	79
<i>P. megasperma</i>										
0	84	100	109	82	94	115	104	111	87	104
24	109	109	95	100	103	116	121	96	109	111
48	106	96	70	82	88	108	92	82	88	92
72	61	91	25	77	63	73	95	55	92	78
$\bar{X}$	90	99	75	85	87	103	103	86	94	96
None (control)										
0	---	---	---	---	---	---	---	---	---	---
24	73	72	103	83	83	94	88	92	76	87
48	61	60	90	86	74	82	115	95	86	94
72	39	31	81	53	51	65	64	93	58	70
$\bar{X}$	58	54	91	74	69	80	88	93	73	84

^zValues represent the means from five replicate plants per treatment. Shoot and root weights of individual inoculated plants were expressed as a percentage of the mean value of the five uninoculated controls for the same rootstock × flooding duration combination; those of uninoculated plants were expressed as a percentage of the mean value of the five unflooded controls for each rootstock.

^yIndicated flooding durations imposed every 7 days throughout the 4-month duration of the experiment.

Estimated root rot percentages and the relative shoot and root weights for plants in individual treatments varied widely (Tables 1 and 2). ANOVA for all three measures of disease severity showed a highly significant ($P < 0.001$) contrast between infested and uninfested substrate (Table 3). The main effects of pathogen species, rootstock, and flooding duration were also highly significant (Table 3). The data in Tables 1 and 2 illustrate the highly significant linear component of the flooding duration effect and the significant to highly significant pathogen × flooding duration interactions revealed by the ANOVA for each measure of disease severity (Table 3). For instance, when averaged across all rootstocks *P. cryptogea* caused 7.0%, 19%, 60%, and 91% root rot after 0, 24, 48, and 72 h of flooding, respectively, whereas *P. megasperma* caused 6.8%, 7.8%, 14%, and 52% root rot after the same respective flooding treatments. The highly significant pathogen × rootstock interaction for root rot percentages (Table 3) is also illustrated in Table 1, e.g., after repeated 72-h floodings, O.3 was the rootstock suffering the most root rot caused by *P. cryptogea* (98%), whereas it was the rootstock least affected by *P. megasperma* (34% root rot). Root rot was only 2.0% to 13% among uninoculated controls, regardless of rootstock or flooding duration.

The depressions in shoot and root weights relative to control treatments generally were correlated with estimated root rot percentages for the infested but not for the uninfested treatments. Differences among treatments often were more pronounced for shoot than for root weights (Table 2), as indicated by the respectively lower F-statistic probability for some sources of variation (Table 3). Generally, the imposition of flooding treatments in the presence of a *Phytophthora* sp. was most deleterious to the final shoot weights of M.7 and MM.111 plants and least deleterious to those of M.26. In contrast, weekly 72-h flooding treatments in the absence of a pathogen reduced shoot weights of MM.111 plants by only 19% relative to unflooded controls, but reduced those of M.26 plants by 69% (Table 2). Such data are reflected by the highly significant infest × rootstock × flood time interaction (Table 3).

Discussion

Although the main effects of *Phytophthora* sp. (or absence thereof), rootstock clone, and flooding duration were highly pronounced, the interactions among these factors vividly illustrate the complications in rating rootstocks for general susceptibilities to

Table 3. F-statistic probability from ANOVA for three measures of disease severity in an experiment examining the effect of four *Phytophthora* spp. (or lack thereof) and four weekly flooding treatments on four apple rootstock.

Source of variation ²	Measure of disease severity		
	Root rot (%) ^y	Shoot wt (%) ^{y*}	Root wt (%) ^{y*}
Infest	<0.001	<0.001	<0.001
Infest × pathogen	<0.001	<0.001	0.002
Infest × rootstock	0.003	<0.001	<0.001
Infest × flood time	<0.001	<0.001	<0.001
Linear	<0.001	<0.001	<0.001
Quadratic	0.002	0.188	0.550
Deviations	0.761	0.585	0.034
Infest × pathogen × rootstock	<0.001	0.092	0.021
Infest × pathogen × flood time	<0.001	<0.001	0.030
Linear	<0.001	0.064	0.098
Quadratic	0.008	<0.001	0.016
Deviations	0.211	0.049	0.581
Infest × rootstock × flood time	0.468	<0.001	0.202
Linear	0.073	<0.001	0.133
Quadratic	0.852	0.874	0.160
Deviations	0.736	0.805	0.712

²Infest = the contrast between infested and noninfested treatments; infest × pathogen = the variation between pathogens within the infested treatments; infest × flood time = the variation between flooding treatments, separately for infested and noninfested treatments; infest × pathogen × flood time and infest × pathogen × rootstock = the variation between pathogens and flooding treatments or rootstocks, respectively, within the infested treatments; infest × rootstock × flood time = the interaction between rootstocks and flooding treatments, separately for infested and noninfested treatments.

^yAnalysis conducted using arcsin-transformed values.

^{*}Shoot and root weights of individual inoculated plants were expressed as a percentage of the mean value of the five uninoculated controls for the same rootstock × flooding duration combination; those of uninoculated plants were expressed as a percentage of the mean value of the five unflooded controls for each rootstock

Phytophthora crown and root rots or suitabilities for wet soil conditions. Such interactions also may account for some of the inconsistencies in previous ratings noted above. For instance, Childers (1983) rated MM.111 and M.26 as “moderately resistant” and “susceptible” to root rot, respectively. However, in the present study, MM. 111 was generally the more susceptible of the two to crown and root rots caused by *P. cactorum*, *P. cryptogea*, and *P. megasperma*, whereas it was the markedly more tolerant of “wet feet” conditions in the absence of a pathogen. Similarly, although Rom and Brown (1979) found that growth suppression and mortality of ‘Red Delicious’ scions after 10 to 15 days of flooding treatments was far greater on MM.111 than on M.26 and attributed these differences to relative susceptibilities of the rootstock to anoxia, it is very possible that the rootstock were contaminated with *P. cactorum* when the experiment was initiated (Jeffers and Aldwinckle, 1988). If this were true, their data would support rather than contradict the results obtained in the present study. Furthermore, whereas *P. cryptogea* caused a 100% incidence of crown rot on 0.3 plants subjected to 72 h of flooding, 0.3 was the only rootstock on which *P. megasperma* caused no crown rot. Such examples collectively emphasize the importance of precisely identifying the cause of tree decline in wet soils when attempting to assess rootstock susceptibilities to such general symptoms as poor vigor or decay of root and crown tissues.

In controlled tests, the relative susceptibilities of apple rootstock to diseases caused by *Phytophthora* spp. generally have been evaluated on the basis of reactions following inoculation of fungal mycelium into wounded stems or excised twigs, sometimes with

misleading results. Using such techniques, which they acknowledged “do not necessarily reflect (a rootstock’s) liability to infection in the field,” Sewell and Wilson (1959) determined MM. 106 and MM.104 to have “exceptionally high” and “high” levels of resistance, respectively, to *P. cactorum*, conclusions that were subsequently contradicted by orchard experience. In contrast, Barritt et al. (1990) used a related technique to compare rootstock reactions to *P. cactorum* and confirmed that MM. 106 is relatively susceptible, that M.9 is relatively resistant (Cummins and Aldwinckle, 1982; Jeffers and Wilcox, 1990), and supported the present indications that M.26 is relatively resistant. However, their data also suggested a comparable degree of susceptibility for MM.106 and domestic seedling, a rootstock that is generally regarded as among the most resistant in common usage (Jeffers and Wilcox, 1990; McIntosh, 1975). Whereas the limitations of the techniques employed in the present experiment are acknowledged, they may provide a more accurate measure of relative disease susceptibility than do stem or twig inoculation tests by more closely mimicking natural conditions under which Phytophthora crown and root rots develop.

Although extensive death of root and crown tissues and attendant fruit tree losses in waterlogged soils have sometimes been attributed strictly to the physiological effects of anoxia (Rem and Brown, 1979; Rowe and Beardsell, 1973), the present study clearly demonstrates that pathogenesis by *Phytophthora* spp. can produce such symptoms after periods of waterlogging insufficient to do so when these pathogens are not present. Flooding periods of the durations tested optimize the production and dispersal of infective

zoospores of the *Phytophthora* spp. examined and may also increase host susceptibility to infection or colonization by these pathogens (Browne and Mircetich, 1988; Duniway, 1976; Wilcox and Mircetich, 1985a, 1985 b). However, the number and duration of flooding episodes necessary for the development of disease under field conditions is unknown. Browne and Mircetich (1988) recently reported that *P. cactorum* and *P. cambivora* caused significantly more damage on small 'Delicious' apple seedlings subjected to biweekly 4-h flooding periods than these same pathogens caused on the four rootstock subjected to weekly 24-h flooding periods in the present experiment; reasons for these different results are not known. Conversely, apple trees commonly survive waterlogged periods of several days or more under orchard conditions, even in soils known to be contaminated with *Phytophthora* spp. (personal observation). It is likely that in addition to genetic and edaphic factors, the ultimate development of *Phytophthora* root and crown rots on apple trees is influenced by qualitative and quantitative aspects of inoculum availability, seasonal fluctuations in disease susceptibility (Jeffers and Aldwinckle, 1986), and an undetermined number of additional physiological factors that influence an individual rootstock's susceptibility to initial attack and subsequent colonization by these pathogens.

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