Susceptibility of Fraser, Canaan, and Nordmann Fir to Root Rot Incited by *Phytophthora cactorum* and *Phytophthora drechsleri*

Benjamin K. Hoover^{1,3} and R.M. Bates²

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SUMMARY. The susceptibility of fraser fir (*Abies fraseri*), canaan fir (*A. balsamea* var. *phanerolepis*), and nordmann fir (*A. nordmanniana*) to phytophthora root rot (PRR) incited by *Phytophthora cactorum* or *P. drechsleri* was assessed in two experiments in central Pennsylvania. In an 8-week greenhouse study, seedlings and transplants growing in soilless substrate were inoculated with *Phytophthora* in flooded and non-flooded settings. In an 8-week outdoor study conducted in raised planting boxes filled with soil, transplants were inoculated with *Phytophthora* species in well-drained and poorly drained soil. Based on foliar disease ratings, mortality rates, and dry shoot and root weights, differences in susceptibility to *P. cactorum* and *P. drechsleri* existed between these true fir (*Abies*) species. Fraser fir was very susceptible to *P. cactorum* and *P. drechsleri*. Canaan fir had strong resistance to *P. cactorum* and *P. drechsleri* in well-drained settings but was susceptible in poorly drained settings. Nordmann fir had very strong resistance to *P. cactorum* and *P. drechsleri* in both well-drained and poorly drained settings.

Fraser fir was the most valuable cut Christmas tree species in the United States in 2009, accounting for \$89.1 million in sales for producers (U.S. Department of Agriculture, 2009). In the past two decades, demand for fraser fir has increased and consumers now consider it a premium product (Chastagner and Benson, 2000; Tompkins, 2000; Williams, 2002). This demand has resulted in production of fraser fir in sites ill-suited to the species, including poorly drained soils (Johnson, 2009; Owen, 2005). The limiting factor in fraser fir Christmas tree production on poorly drained sites is PRR, which may be incited by several *Phytophthora* species (Benson et al., 1976; Kuhlman

and Hendrix, 1963; Quesada-Ocampo et al., 2009; Shew and Benson, 1981). Fraser fir specimens with PRR symptoms sent to the Pennsylvania Department of Agriculture Plant Diagnostic Laboratory between 1986 and 2011 most frequently contained *P. cactorum*, *P. cryptogea*, or *P. drechsleri* (T. Olson, personal communication).

Fraser fir is considered very susceptible to PRR, with minor differences in susceptibility occurring between seed sources (Frampton and Benson, 2004). Canaan fir is closely related to fraser fir and has been reported to survive in soils conducive to PRR (Brown, 2000; Potter et al., 2010). Greenhouse and shadehouse testing of multiple seed sources of canaan fir two-year-old and three-year-old seedlings growing in soilless substrate in North Carolina found susceptibility to *P. cinnamomi* in all seed sources, although some variation in degree of susceptibility occurred (Benson et al., 1998b).

Studies conducted in North Carolina indicate variation in resistance to *P. cinnamomi* exists between true fir species as containerized seedlings in soilless substrate, with the greatest tolerance or resistance to *P. cinnamomi* being observed in momi fir (*A. firma*) and turkish fir [*A. nordmanniana* ssp. *equi-trojani* (syn. *A. bornmuelleriana*)] (Benson et al., 1998a; Hinesley et al., 2000). In the Benson et al. (1998a) study, nordmann fir had less severe foliar symptoms than fraser fir but was still determined to be very susceptible to *P. cinnamomi*.

Despite having considerable resistance to *P. cinnamomi*, momi fir has little potential as a cut Christmas tree crop because of its morphological features and susceptibility to spring frost damage (Hibbert-Frey et al., 2010; Hinesley and Frampton, 2002). Turkish fir is a better candidate as a cut Christmas tree crop and is considered either a natural hybrid between greek fir (*A. cephalonica*) and nordmann fir or a subspecies of nordmann fir (Farjon, 2010; Liu, 1971). The close relationship between turkish fir and nordmann fir suggests that nordmann fir might possess *Phytophthora* resistance genes. Nordmann fir is more readily available in the U.S. conifer industry than turkish fir and additional testing on its resistance to PRR-inciting *Phytophthora* is warranted.

This study involved testing fraser fir, canaan fir, and nordmann fir for resistance to PRR incited by *P. cactorum* or *P. drechsleri*. Inoculation tests were done in a 2009 greenhouse experiment with seedlings and transplants growing in soilless substrate and in a 2010 outdoor experiment in planting boxes containing transplants growing in soil, with a flooding treatment included to create conditions favorable for PRR.

Materials and methods

In Summer 2009, a greenhouse experiment was conducted in University

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¹Graduate Research Assistant, Department of Plant Science (previously Department of Horticulture), The Pennsylvania State University, 310 Tyson Building, University Park, PA 16802

²Associate Professor of Horticulture, Department of Plant Science (previously Department of Horticulture), The Pennsylvania State University, 303 Tyson Building, University Park, PA 16802

³Corresponding author. E-mail: benjamin.k.hoover@gmail.com.

Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
0.3048	ft	m	3.2808
2.54	inch(es)	cm	0.3937
16.3871	inch ³	cm ³	0.0610
0.0254	mil	mm	39.3701
28.3495	oz	g	0.0353
1	ppm	mg·L ⁻¹	1
(°F - 32) ÷ 1.8	°F	°C	(°C × 1.8) + 32

Park, PA (lat. 40°80'N, long. 77°86'W). On 5 May 2009, firs purchased from a commercial grower were planted in pots (656 cm³ volume, D40 Deepots; Stuewe & Sons, Tangent, OR) with a pine bark-based soilless substrate (NX-6; Frey Brothers, Quarryville, PA). The fraser (Roan Mountain provenance) and canaan fir were one-year-old seedlings in plugs, the nordmann fir were (Bakuriani provenance) two-year-old seedlings in plugs and (Bakhmaro provenance) 3- to 6-inch-tall bare-root transplants. Before potting, roots were washed to remove all existing substrate. The root systems of the fraser, canaan, and Bakuriani provenance nordmann fir seedlings were very similar in size. The Bakhmaro provenance nordmann fir transplants had larger root systems than the other seedlings. Potted plants were placed on racks (D20C Deepots, Stuewe & Sons). Each rack contained eight pots, with 5-cm spacing between pot edges. The racks were placed on two benches in a greenhouse. Until the conclusion of the experiment, the firs were fertilized every other week with a 280 mg·L⁻¹ nitrogen (N) solution (21N-3.1P-5.8K; Scotts, Marysville, OH). Watering was provided by hand as needed. Air temperature in the greenhouse was recorded with a sensor and data logger (HOBO Pendant; Onset, Cape Cod, MA) suspended 1 m above one of the benches during the experiment.

Isolates of *P. cactorum* [Phytophthora Database ID: PD_00551 (Kang, 2012a)] and *P. drechsleri* [PD_00640 (Kang, 2012b)] from dead fraser fir seedlings were obtained from the Pennsylvania Department of Agriculture Plant Diagnostic Laboratory. Inoculum was cultured on long grain rice (*Oryza sativa*) following the methods described by Hoover (2012). Firs were inoculated on 30 May 2009 with 0.5 g of rice sprinkled on the media surface of each pot. The *Phytophthora* negative control consisted of noninfested rice that had been autoclaved. The factors in addition to fir species were *Phytophthora* (absent, *P. cactorum*, or *P. drechsleri*) and flooding (absent or 24 h/week), for a total of 24 treatment combinations. Each treatment combination had 20 replicates, resulting in 480 plants in the experiment. Treatments were assigned randomly. Flooding treatments began on 1 June 2009. Each pot to be flooded was

wrapped in plastic and then watered until ≈2 cm of standing water covered the substrate surface. Weekly foliar disease ratings, adapted from top ratings used by Hinesley et al. (2000), were recorded. The ratings were as follows: 1 = healthy, 2 = slightly chlorotic, 3 = severely necrotic, and 4 = dead. The first data collection occurred on 30 May 2009, and the experiment ran for 8 weeks. Weekly plant mortality was recorded with dead plants recorded as 1 and live plants 0 to provide a proportion of mortality. At the conclusion of the experiment, shoots and roots were oven dried at 150 °F for 1 week, then weighed. Before drying, roots were plated on semiselective media to isolate *Phytophthora* using the methods described by Hoover (2012). Morphological identification of the isolated *Phytophthora* was done under a microscope using the key of Gallegly and Hong (2008).

An outdoor planting box experiment was conducted during Summer 2010 at the Russell E. Larson Agriculture Research Center at Rock Springs in Pennsylvania Furnace, PA (lat. 40°42'N, long. 77°56'W). On 25 May 2010, fir transplants purchased from a commercial grower were planted in 32 boxes 36 inches by 33 inches by 11.25 inches (volume 13,365 inches³) with Hagerstown silt loam, which contained enough subsoil to be classified as a clay loam. The fraser fir (Roan Mountain provenance) were bare root plug+1 + 1 transplants (plug plus one year in a transplant bed plus one year in another transplant bed), the canaan fir were bare root plug+1.5 (plug plus 1.5 years in a transplant bed) transplants, and the nordmann fir (Apsheronsk provenance) were bare root plug+1 + 1 transplants. The transplants were very uniform in size within and between species. Ten plants of each species were randomly assigned to three rows in each box, with 3-inch spacing within rows and 8-inch spacing between rows. Flooded treatment boxes were lined with a double layer of 6-mil clear plastic. The soil was kept above field capacity and at or very near saturation at all times during the experiment. When the water level exceeded 2 cm above the soil surface, a siphon was used to drain off excess. Two spray stakes in each box provided ≈2 cm of water daily for non-flooded boxes.

The rate of water supplied to flooded boxes was reduced after the soil reached saturation to reduce the amount of standing water above the soil surface.

The experimental design was a randomized complete block with four blocks. Each box received one combination of the following factors: *P. cactorum* (absent, present), *P. drechsleri* (absent, present), and flooding (absent, present). *Phytophthora* inoculum was produced using the same method as mentioned earlier in the greenhouse study and applied on 7 June 2010. The *P. cactorum* and *P. drechsleri* absent treatments consisted of noninfested autoclaved rice. Each plant received 0.5 g of rice from one of the *P. cactorum* and one of the *P. drechsleri* treatments sprinkled on the soil surface within a 2-cm radius of the stem.

Weekly foliar disease ratings were recorded. The scale was adjusted from the four point scale used in 2009 to a 5-point scale based on percentage of foliar necrosis: 1 = healthy (no necrosis), 2 = mild symptoms (1% to 33% necrosis), 3 = moderate symptoms (34% to 67% necrosis), 4 = severe symptoms (68% to 99% necrosis), 5 = dead (100% necrosis). The experiment ran for 8 weeks, with the final rating recorded on 2 Aug. 2010. Weekly plant mortality was recorded as a proportion of each fir species in each box that had died. A weather station at the Russell E. Larson Agriculture Research Center provided air temperature and precipitation data during the experiment. At the conclusion of the experiment, *Phytophthora* isolations from root samples were conducted using the plating techniques mentioned earlier.

Data from foliar disease ratings at the conclusion of the 2009 experiment were analyzed with a Model I (fixed factor) analysis of variance (ANOVA) using PROC GLM in SAS (version 9.3; SAS Institute, Cary, NC). The 2010 foliar disease ratings data from the conclusion of the experiment were analyzed with a MODEL III (mixed-model) ANOVA using PROC MIXED with blocks treated as a random factor. Residual plots were generated to confirm that the assumptions of ANOVA were met. Residuals of the response variable were normally distributed, and the variances of the response variable were equal. Multiple

comparisons were conducted with PROC GLIMMIX using an adjusted Tukey's Studentized range test with slice statements. Mortality data were analyzed with a repeated measures statement in PROC GLIMMIX with an autoregressive covariance structure; multiple comparisons were done with an adjusted Tukey's Studentized range test. Dry weight of shoots and roots from the 2009 experiment were separated by true fir species and analyzed with PROC GLM, followed by multiple comparisons in PROC GLIMMIX with an adjusted Tukey's Studentized range test. The significance level (α) used to reject null hypotheses for all statistical tests was set at 0.05.

Results and discussion

Interactions between factors in the 2009 experiment preclude the discussion and analysis of main effects (Table 1). Fraser fir had a higher foliar disease rating than canaan fir and nordmann fir when exposed to *P. cactorum* in both non-flooded and

flooded conditions (Table 2). Fraser fir also had higher foliar disease ratings than canaan fir and nordmann fir when exposed to either *Phytophthora* species in non-flooded conditions (Table 2). When flooding was added to the *P. drechsleri* treatment, fraser fir and canaan fir had the same foliar disease rating, which was higher than that of nordmann fir (Table 2). When flooded, all fraser fir had the same high foliar disease rating regardless of *Phytophthora* treatment (Table 2). Canaan fir had the same low foliar disease rating in all non-flooded *Phytophthora* treatments (Table 2). Flooding with exposure to *P. cactorum* or *P. drechsleri* resulted in increased foliar disease ratings in canaan fir compared with the non-flooded *P. cactorum* and *P. drechsleri* treatments (Table 2). Nordmann fir remained healthy regardless of flooding or *Phytophthora* treatments (Table 2).

Plant mortality began to show differences between fir species in week 4 of the 2009 experiment [Fig. 1

($P \leq 0.05$)]. Differences between true fir species in the mortality data were very similar to the foliar disease ratings. In the flooded *P. cactorum* treatment and in the flooded *P. drechsleri* treatment, a gradient of mortality existed from week 6 to the end of the experiment, with fraser fir having the highest mortality rate, canaan fir having a lower rate, and nordmann fir having the lowest mortality rate [Fig. 1 ($P \leq 0.05$)].

Dry root weight of fraser fir was reduced when flooding or *Phytophthora* treatments were present ($P < 0.0001$), with the lowest weights in the *P. cactorum* treatment with or without flooding and the flooded *P. drechsleri* treatment (Fig. 2). Both canaan fir and nordmann fir of Bakuriani provenance had the lowest root weights in the flooded *Phytophthora* treatments (Fig. 2). Dry shoot data followed a similar pattern, though no differences between treatments existed for nordmann fir (Fig. 2). More differences in root and shoot dry weights between treatments may have been observed if the duration of the experiment was extended.

Fraser fir inoculated with *Phytophthora* had severely diseased roots at the conclusion of the 2009 experiment. Canaan fir inoculated with *Phytophthora* had little root disease in non-flooded treatments but moderate to severe disease in flooded treatments. Nordmann fir inoculated with *Phytophthora* had little root disease in non-flooded or flooded treatments. Both *P. cactorum* and *P. drechsleri* were recovered from inoculated fraser fir and canaan fir roots. No *Phytophthora* were isolated from plated nordmann fir roots.

In the 2009 greenhouse experiment, fraser fir was highly susceptible to *P. cactorum* and *P. drechsleri* based on foliar disease ratings and dry tissue weights. Canaan fir showed resistance to *P. cactorum* and *P. drechsleri* in non-flooded conditions, though in flooded conditions some susceptibility occurred. Nordmann fir was very resistant to *P. cactorum* and *P. drechsleri*. The differences between nordmann fir provenances observed in foliar disease ratings and root dry weights after exposure to flooded *Phytophthora* treatments may be a reflection of differences in sizing or preconditioning since the Bakuriani plants were seedlings and the Bakhmaro

Table 1. Analysis of variance for foliar disease ratings^z of true fir transplants exposed to *Phytophthora* species and flooding treatments, 2009.

Effect	df	F	P
True fir ^y	3	141.44	<0.0001
Flooding ^x	1	70.76	<0.0001
<i>Phytophthora</i> ^w	2	28.72	<0.0001
True fir × flooding	3	20.08	<0.0001
True fir × <i>Phytophthora</i>	6	9.05	<0.0001
Flooding × <i>Phytophthora</i>	2	1.48	0.2289
True fir × flooding × <i>Phytophthora</i>	6	5.53	<0.0001

^z1 = healthy, 2 = slightly chlorotic, 3 = severely necrotic, 4 = dead.

^yFraser fir, canaan fir, nordmann fir.

^xFlooding levels: absent, present (24 h/week).

^w*Phytophthora* levels: absent (0.5-g noninfested rice), *P. cactorum* (0.5-g infested rice), *P. drechsleri* (0.5-g infested rice); 1 g = 0.0353 oz.

Table 2. True fir foliar disease rating least squares (LS) means at the conclusion of the experiment after exposure to *Phytophthora* species and flooding treatments, 2009.

		Foliar disease ratings ^z (LS means)			
	<i>Phytophthora</i> treatment	Fraser fir	Canaan fir	Nordmann fir (Bakhmaro)	Nordmann fir (Bakuriani)
Non-flooded	Control	1.0 a ^y A ^x	1.1 a A	1.0 a A	1.0 a A
	<i>P. cactorum</i>	3.5 c B	1.2 a A	1.3 a A	1.2 a A
	<i>P. drechsleri</i>	2.6 b B	1.0 a A	1.0 a A	1.0 a A
Flooded ^w	Control	3.1 bc B	1.6 ab A	1.0 a A	1.1 a A
	<i>P. cactorum</i>	4.0 c C	2.3 bc B	1.3 a A	1.5 a AB
	<i>P. drechsleri</i>	3.6 c B	2.9 c B	1.0 a A	1.0 a A

^z1 = healthy, 2 = slightly chlorotic, 3 = severely necrotic, 4 = dead.

^yLS means within a column with the same lowercase letter are not different according to an adjusted Tukey's Studentized range test at $P \leq 0.05$.

^xLS means within a row with the same uppercase letter are not different according to an adjusted Tukey's Studentized range test at $P \leq 0.05$.

^wFlooding treatment: 2 h/week.

Fig. 1. True fir mortality over time in transplants exposed to *Phytophthora* treatments and flooding, 2009. Flooding treatment = weekly 24 h periods of saturation. Weekly mortality least squares means of fir species under each treatment with the same letter are not different according to an adjusted Tukey's Studentized range test ($P \leq 0.05$).

Fig. 2. True fir shoot and root dry weight least squares (LS) means in grams at the conclusion of the experiment after exposure to *Phytophthora cactorum*, *P. drechsleri*, and flooding treatments. LS mean totals in each fir species with the same letter are not different according to an adjusted Tukey's Studentized range test ($P \leq 0.05$); 1 g = 0.0353 oz.

plants were transplants. The difference in plant age and size between the nordmann fir (two-year-old seedlings or 3- to 6-inch transplants) and the fraser fir and canaan fir (one-year-old seedlings) may have been a complicating factor in the experiment.

In the 2010 experiment, differences in foliar disease ratings were

found between treatments (Table 3). Canaan fir and nordmann fir had the same foliar disease rating regardless of flooding, whereas fraser fir had a higher disease rating when flooded than when not flooded ($P < 0.0001$). Fraser fir and canaan fir had higher foliar disease ratings when exposed to *P. cactorum* than when not exposed

to *P. cactorum*, whereas nordmann fir had the same foliar disease ratings regardless of exposure to *P. cactorum* ($P = 0.0154$). Fraser fir had higher foliar disease ratings when exposed to *P. drechsleri* than when not exposed to *P. drechsleri*, whereas canaan fir and nordmann fir had the same foliar disease ratings regardless of exposure to *P. drechsleri* ($P = 0.0039$).

Fraser fir had higher disease ratings than canaan fir and nordmann fir when exposed to either *P. cactorum* or *P. drechsleri* in non-flooded conditions (Table 4). In the flooded *P. cactorum* treatment, fraser fir and canaan fir had higher disease ratings than nordmann fir (Table 4). Differences within fir species were observed for fraser fir and canaan fir, whereas nordmann fir had no differences. Fraser fir had the lowest foliar disease rating in the non-flooded treatment with no *Phytophthora*, and all flooded treatments were the same with higher foliar disease ratings (Table 4). Canaan fir showed a split based on flooding treatment. All non-flooded treatments were the same, while all the flooded treatments were the same and had higher foliar disease ratings than the non-flooded treatments (Table 4).

Mortality rates of canaan fir and nordmann fir were the same in all non-flooded *Phytophthora* treatments, whereas fraser fir had higher mortality

Table 3. Analysis of variance for foliar disease ratings^z of true fir transplants exposed to *Phytophthora* species and flooding treatments, 2010.

Effect	df	F	P
True fir ^y	2	330.49	<0.0001
Flooding ^x	1	345.56	<0.0001
<i>P. cactorum</i> ^w	1	28.09	<0.0001
<i>P. drechsleri</i> ^w	1	15.85	0.0002
<i>P. cactorum</i> × <i>P. drechsleri</i>	1	2.59	0.1123
True fir × flooding	2	41.92	<0.0001
True fir × <i>P. cactorum</i>	2	4.44	0.0154
True fir × <i>P. drechsleri</i>	2	6.01	0.0039
Flooding × <i>P. cactorum</i>	1	12.67	0.0007
Flooding × <i>P. drechsleri</i>	1	5.02	0.0282
True fir × flooding × <i>P. cactorum</i>	2	4.26	0.0180
True fir × flooding × <i>P. drechsleri</i>	2	3.87	0.0254
True fir × <i>P. cactorum</i> × <i>P. drechsleri</i>	2	1.96	0.1493
True fir × flooding × <i>P. cactorum</i> × <i>P. drechsleri</i>	3	1.27	0.2914

^z1 = healthy (no necrosis), 2 = mild symptoms (1% to 33% necrosis), 3 = moderate symptoms (34% to 67% necrosis), 4 = severe symptoms (68% to 99% necrosis), 5 = dead (100% necrosis).

^yFraser fir, canaan fir, nordmann fir.

^xFlooding levels: absent, present (soil continually near saturation).

^w*P. cactorum* and *P. drechsleri* treatments: present (0.5-g infested rice) and absent (0.5-g noninfested rice); 1 g = 0.0353 oz.

Table 4. True fir foliar disease rating least squares (LS) means at the conclusion of the experiment after exposure to *Phytophthora* species and flooding treatments, 2010.

<i>Phytophthora</i> treatment		Foliar disease ratings ^z (LS means)		
		Fraser	Canaan	Nordmann
Non-flooded	Control	1.6 a ^y A ^x	1.2 a A	1.1 a A
	<i>P. cactorum</i>	3.3 b B	2.0 a A	1.2 a A
	<i>P. drechsleri</i>	3.3 b B	1.5 a A	1.2 a A
	Both	4.1 bc B	2.1 a A	1.5 a A
Flooded ^w	Control	4.7 cd C	3.3 b B	1.8 a A
	<i>P. cactorum</i>	4.8 cd B	4.1 b B	1.7 a A
	<i>P. drechsleri</i>	5.0 d C	4.0 b B	1.7 a A
	Both	5.0 d C	3.9 b B	1.7 a A

^zFoliar disease ratings scale: 1 = healthy (no necrosis), 2 = mild symptoms (1% to 33% necrosis), 3 = moderate symptoms (34% to 67% necrosis), 4 = severe symptoms (68% to 99% necrosis), 5 = dead (100% necrosis).

^yLS means within a column with the same lowercase letter are not different according to an adjusted Tukey's Studentized range test at $P \leq 0.05$.

^xLS means within a row with the same uppercase letter are not different according to an adjusted Tukey's Studentized range test at $P \leq 0.05$.

^wFlooding levels: absent, present (soil continually near saturation).

rates. Under flooded conditions, exposure to *Phytophthora* resulted in a similar gradient of true fir mortality as seen in the 2009 study, with fraser fir having the highest mortality, canaan fir having lower mortality, and nordmann fir having the lowest mortality (Fig. 3).

In the 2010 outdoor planting box experiment, fraser fir was highly susceptible to *P. cactorum* and *P. drechsleri*. Canaan fir was resistant to *P. cactorum* and *P. drechsleri* under non-flooded conditions but was susceptible under flooded conditions. Nordmann fir was highly resistant to *P. cactorum* and *P. drechsleri* in

flooded and non-flooded conditions. Root plating resulted in recovery of both species of *Phytophthora* from fraser fir and canaan fir roots, whereas no *Phytophthora* were recovered from nordmann fir roots. Nordmann fir had diseased roots with severe discoloration and loss of structural integrity in the flooded treatments but no *Phytophthora* were isolated from those roots.

In these two inoculation experiments, canaan fir showed strong resistance to PRR incited by *P. cactorum* or *P. drechsleri* in non-flooded settings and more resistance to PRR in flooded settings than fraser fir. This resistance

to *P. cactorum* and *P. drechsleri* in non-flooded conditions is considerably higher than the resistance of canaan fir to *P. cinnamomi* observed by Benson et al. (1998b). The heavy watering that occurred in the Benson et al. (1998b) experiments was not as severe as the flooding treatments used in this study, yet produced similar results. The level of soil moisture or duration of flooding at which canaan fir becomes susceptible to *P. cactorum* or *P. drechsleri* is not known. This is of critical importance in determining the suitability of canaan fir for use in production sites with poorly drained soils. Canaan fir is very variable in morphological traits and postharvest needle retention (Bates et al., 2004) and shows some differences in susceptibility to *P. cinnamomi* between seed sources (Benson et al., 1998b). With selection for tolerance of poorly drained soils and resistance to PRR, canaan fir could allow true fir production on sites not suited for fraser fir.

Nordmann fir showed strong resistance to *P. cactorum* and *P. drechsleri* in these inoculation experiments. Benson et al. (1998a) reported susceptibility of nordmann fir to PRR incited by *P. cinnamomi*. The resistance to PRR incited by *P. cactorum* or *P. drechsleri* observed in this study may be a result of differences in virulence of *Phytophthora* species to nordmann fir, genetic and phenotypic variation in the nordmann fir used in the studies, or differences in environmental conditions. *Phytophthora cactorum* and *P. drechsleri* have broad host ranges but are known to have differences in pathogenicity to different hosts (Chastagner, 2001; Erwin and Ribeiro, 1996). Nordmann fir has been reported susceptible to a *Phytophthora* species similar to *P. inundata* in Norway (Talge et al., 2007), and in Hungary, a *Phytophthora* species lacking a name consistent with nomenclatural rules (currently referred to as *P. niederhauserii*) has been reported to cause sporadic disease in nordmann fir in a nursery setting (Józsa, et al., 2010). Nordmann fir is known to be variable in morphological and postharvest traits (Madsen, 1994; Nielsen and Chastagner, 2005), resistance to *Phytophthora* may also be a variable trait.

Although nordmann fir showed strong resistance to PRR in this study, the length of time the plants were

Fig. 3. True fir mortality over time in transplants exposed to *Phytophthora* treatments and flooding, 2010. Weekly mortality means between fir species within treatments with the same letter are not different according to an adjusted Tukey's Studentized range test ($P \leq 0.05$). Flooding treatment = continuous soil moisture near saturation.

under study was limited to a portion of one growing season. Environmental conditions during these experiments were favorable for PRR development. Substrate or soil saturation occurred to promote the release of zoospores. Soil temperatures were in the active range of *P. cactorum* and *P. drechsleri*, with considerable time near the optimal temperature of 25 °C for *P. cactorum* (Erwin and Ribeiro, 1996). Questions remain regarding the long-term effect of exposure to PRR on survival, growth rate, and development of nordmann fir. In addition, questions also exist about the growth rate and hardiness of nordmann fir in Christmas tree production in the eastern United States (Jones and Cregg, 2006). Nordmann fir is a popular Christmas tree crop in Europe (Chastagner and Benson, 2000), but the response of consumers in the eastern United States to differences in branch and needle morphology between nordmann fir and fraser fir is not known.

Applying results of true fir levels of resistance to *Phytophthora* species observed in greenhouse and box studies to field outcomes must be done with caution. In production settings, many variables could lead to reduction in the resistance observed in this study,

including exposure to other species or isolates of *Phytophthora* not tested in this study and environmental conditions that are more favorable to disease.

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