Thermal Sensitivity of Three Species of *Phytophthora* and the Effect of Soil Solarization on Their Survival

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ABSTRACT

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Heat sensitivity and the effect of soil solarization on the survival of hyphae and spores of *Phytophthora cinnamomi*, *P. cactorum*, and *P. megasperma* were determined in inoculated walnut twigs and artificially infested Reiff silty clay loam soil. Viable chlamydospores of *P. cinnamomi* were not detected in infested soil exposed to 45 C for 20 min. In contrast, oospores of a high-temperature isolate of *P. megasperma* survived exposure for 30 min at 45 C, whereas *P. cactorum* was killed within 30 min at 45 C. In field studies, solarized soil reached a maximum temperature of 45 C at the 15-cm depth and 33 C at the 45-cm depth, compared with nonsolarized soil where maximum temperatures of 31 and 28 C were recorded at 15 and 45 cm, respectively. No activity of *P. cinnamomi* was detected in infested soil after 2 wk at the 30-cm depth or after 4 wk at the 45-cm depth in solarized soil, whereas there was little or no reduction in survival in nonsolarized soil. *P. cactorum* withstood the effects of soil solarization at the 30- and 45-cm depths but was killed within 2 wk at the 15-cm depth, with little or no change in the percentages of infection of peach leaf disks used as bait in nonsolarized soil. Some propagules of the high-temperature isolate of *P. megasperma* survived the treatment, although the percentage of leaf disk infection was greatly reduced after soil solarization at the 15-cm depth during 4 wk. The heat sensitivity of the isolates of *Phytophthora* in laboratory experiments closely reflected their inactivation in solarized soil and indicated the possible use of soil solarization for management of these pathogens.

Species of *Phytophthora* are among the most important plant pathogens in different crops under different cropping systems (9–11,14). *Phytophthora cinnamomi* Rands, *P. cactorum* (Lebert & Cohn) J. Schröt., and *P. megasperma* Drechs. cause major losses in many herbaceous and perennial crops and agricultural regions worldwide (1,2,11,25,26). Root and crown rot diseases of fruit trees often involve a complex of several pathogenic *Phytophthora* spp. in a single host (11). Soilborne species of *Phytophthora* can be disseminated in soil on cultivation equipment, in planting stock (9,11,26), and in runoff and irrigation water (11,13). Once established in soil, their eradication is difficult (11).

Several approaches are used to minimize losses caused by Phytophthora root and crown rot in perennial crops, including soil-water management (10,12) and planting trees in raised beds (19). Preplant soil fumigation has also been used, but its effectiveness is limited by reinfestation of soil after the treatment (12). Another approach involves soil solarization, either for preplant or postplant management of soilborne diseases. It has the added advantages of being much less expensive than soil fumigation and causes an increased growth response and yield of crop plants (4,7,8,17,21–23) and the control of most weed species (23). However, water management is the main approach for cultural control of *Phytophthora* spp., although soil fumigation and soil solarization have also been effective (1,16). Among the *Phytophthora* spp. that have been controlled by soil solarization are *P. cambivora* (Petri) Buisman in cherry (24), *P. cryptogea* Pethybr. & Lafferty in gerbera (5), and *P. cinnamomi* in avocado in naturally infested soils (16).

The objectives of our study were to compare the thermal sensitivity of *P. cinnamomi*, *P. cactorum*, and *P. megasperma* in inoculated walnut twigs and in artificially infested soil and to determine the effect of soil solarization on the survival of these species in infested soil at different depths.

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MATERIALS AND METHODS

Isolates of *Phytophthora* species. Isolates of *Phytophthora* spp. were provided by S. M. Mircetich (University of California, Davis). They consisted of a peach isolate (2-1-4) of *P. cinnamomi*, an isolate (APP 204-C) of *P. cactorum* from apple, and two isolates (22-2-3 and 22-2-5) of *P. megasperma* from peach. All were pathogenic on English walnut (9). Isolates 22-2-3 and 22-2-5 correspond to types having low optimal temperatures and large oogonia and high optimal temperatures and small oogonia, respectively, previously described by Wilcox and Mircetich (25). The optimal temperature for growth of the low-temperature group of *P. megasperma* is 24 C, with poor growth at 30 C and no growth at 33 C. In contrast, the optimal temperature for growth of the high-temperature group is 30 C, with vigorous growth at 33 C and poor growth at 36 C. All isolates of *Phytophthora* spp. used were maintained on PARP selective agar medium (6) in darkness at 20 C. The method of Mircetich et al (15) was used for the preparation of chlamydospores from *P. cinnamomi*, whereas oospore production by *P. cactorum* and *P. megasperma* was induced by the method of Sneh (20).

Thermal sensitivity of the *Phytophthora* isolates under controlled conditions. Oospores and chlamydospores were mixed with moist soil (Reiff silty clay loam, approximately 70% field capacity) to give approximately 600 cfu/g of soil. Infested soil (25 cm^3) was placed in polyethylene bags, which then were partially evacuated to reduce air insulation, and the soil was spread in the bags to make a thin layer (1–2 mm) deep. The bags of soil then were immersed in water at 30, 35, 40, or 45 C for 5, 10, 20, or 30 min. After treatment, the infested soil was placed in petri dishes and flooded with tap water. Survival of propagules was determined by placing 10 leaf disks (6 mm diameter) from young Lovell peach leaves (*Prunus persica* (L.) Batsch) on the flooded soil at 18 C for 48 hr; disks then were plated onto PARP and incubated at 21 C. Each treatment was replicated three times. Percent incidence of infected leaf disks (disks from which *Phytophthora* colonies developed) was used to determine survival of the *Phytophthora* spp.

The laboratory experiment on thermal sensitivity of the *Phytophthora* spp. (all pathogens of English walnut) was repeated using inoculated walnut twigs according to the method of Matheron and Mircetich (9). The isolates were grown on V8 juice agar (10) for 4 days at 21 C, then agar disks (6 mm diameter) were cut from the edges of the colonies for inoculation of freshly cut walnut twigs. The English walnut twigs, approximately 1 cm in diameter and 20 cm long, were inoculated by placing an agar disk with

mycelium in a circular bark opening midway between the ends of the twigs. Inoculated twigs were incubated in moist chambers for 5 days at 21 C, during which time cankers ranging from 2 to 4 cm long developed. Twigs then were placed in plastic bags, which were partially evacuated and sealed before immersion in water at 30, 35, 40, or 45 C for 5, 10, 20, or 30 min. To determine the effect of the temperature × time treatments on the survival of isolates of *Phytophthora*, 10 5-mm pieces of bark tissue from the margins of the cankers from three replicate twigs were plated on PARP and incubated for 1 wk at 21 C. Microscopic examination was used to determine the percentage of tissue fragments from which isolates of *Phytophthora* developed.

Sensitivity of the *Phytophthora* isolates to soil solarization. Comparisons of the thermal sensitivity of the *Phytophthora* isolates were also made under field conditions. Inocula were prepared as previously described (14) with minor modifications. Individual isolates were grown for 4 wk at 22–24 C in 0.5-L canning jars containing 250 cm^3 of vermiculite and 20 cm^3 of whole oats saturated with 125 ml of broth (200 ml of V8 juice, 2 g of $CaCO_3$, and 800 ml of distilled water). Inocula were mixed with an equal volume of sterile sandy loam soil (1:1). The mixtures (25 cm^3 each) containing hyphae and chlamydospores or oospores were wrapped in nylon coat lining (40 fibers per centimeter) for burial at different depths in field plots.

Two experiments in the same field area were made at Davis, CA, in which the soil (Reiff silty clay loam) was solarized from 5 July to 6 August. Nylon bags with the hyphae and chlamydospores of *P. cinnamomi* and hyphae and oospores of *P. cactorum* or *P. megasperma* (high-temperature isolate 22-2-5) were buried in moist soil (approximately 70% field capacity) at depths of 15, 30, and 45 cm in six solarized and six nonsolarized plots (12 m^2) in each field experiment. Six solarized plots were covered with transparent polyethylene sheeting (25 μm thick) and the edges of the sheeting were anchored in soil; the remaining six plots were left uncovered (nonsolarized). Soil temperatures were monitored at 1-hr intervals throughout the experimental period in one replicate each of solarized and nonsolarized soil at depths where the fungal inocula were buried.

Isolate survival was determined by removing and plating soil from the nylon bags at both 2 and 4 wk after initiating solarization in both field experiments onto PARP. Controls consisted of samples of inocula of the isolates maintained in the nylon bags in the laboratory in moist condition at 22–24 C during the experimental period. The 25-cm^3 soil samples of the individual treatments were placed in petri dishes and flooded with tap water. Twenty 6-mm-diameter Lovell peach leaf disks were placed on the surface of the flooded soil in each dish and incubated for 48 hr at 18 C. There were six replicates per treatment. Leaf disks were then plated on PARP. The number of leaf disks from which isolates of the *Phytophthora* spp. developed was determined every other day for 1 wk. Data are expressed as the percentage of disks from which the colonies of *Phytophthora* were recovered.

RESULTS

Thermal sensitivity of the *Phytophthora* species under controlled conditions. Propagules of *P. cinnamomi* (mainly chlamydospores) and the low-temperature isolate of *P. megasperma* (mainly oospores) were killed in moist soil and infected walnut twigs within 20 min at 45 C (Table 1). In contrast, 30 min at 45 C was needed to kill all propagules of *P. cactorum*, whereas propagules of *P. megasperma* (high-temperature isolate) were still viable after 30 min at 45 C. Propagule survival was a function of time × temperature relationships; with increasing temperature and time, the incidence of leaf disks infected by the *Phytophthora* spp. from moist soil was progressively lower. Moreover, thermal inactivation of the isolates of *Phytophthora* spp. in walnut twigs was similar to that in moist soil and was inversely related to the exposure time and tem-

Table 1. Percent recovery of chlamydospores of *Phytophthora cinnamomi* and oospores of *P. cactorum* and *P. megasperma* (high- and low-temperature isolates) at four temperatures in moist soil and walnut twigs

Phytophthora species	Temperature (C)	Moist soil[a]				Walnut twigs[b]			
		5	10	20	30	5	10	20	30
P. megasperma (high temperature)	30	93[c]	90	73	67	87	83	77	63
	35	93	87	73	60	83	77	70	47
	40	90	77	53	27	83	73	57	17
	45	83	57	10	6	83	60	13	3
Control		100	100	100	97	100	97	97	97
P. megasperma (low temperature)	30	93	83	63	57	93	70	60	47
	35	83	73	57	47	83	60	50	37
	40	73	67	33	3	73	60	27	3
	45	67	47	0	0	63	37	0	0
Control		100	100	97	97	100	100	97	93
P. cactorum	30	97	87	73	63	93	77	67	63
	35	97	83	70	50	83	73	63	47
	40	93	76	53	23	77	57	47	17
	45	77	53	7	0	73	47	7	0
Control		100	100	97	93	100	100	97	97
P. cinnamomi	30	93	77	67	57	90	83	63	47
	35	93	77	63	47	87	80	60	37
	40	90	57	40	13	87	70	33	4
	45	73	47	0	0	80	60	0	0
Control		100	100	100	97	100	100	97	97

[a] Percentage of peach leaf disks from which colonies developed when plated on PARP selective medium. Before plating, disks were placed in flooded soil samples for 48 hr.
[b] Percentage of infected bark pieces from which colonies of *Phytophthora* spp. developed on agar medium after heat treatments.
[c] Average of three replicates per treatment.

Table 2. Factorial analyses of variance on the effect of temperature × time on the percent recovery of isolates of *Phytophthora cinnamoni*, *P. cactorum*, and *P. megasperma* from moist soil and walnut twigs[a]

Source	df	Sum of squares	
		Moist soil	Walnut twigs
Species	3	5,054.17***[b]	4,318.91***
Time	3	84,508.33***	87,218.91***
Temperature	3	59,283.33***	44,786.42***
Replications	2	232.29*	400.04**
Species × time	9	679.17*	2,450.08***
Species × temperature	9	754.17*	45.10
Species × replications	6	567.71*	523.46*
Time × temperature	9	12,333.33***	13,435.92***
Time × replications	6	101.04	360.96
Temperature × replications	6	376.04	508.46*
Species × time × temperature	27	1,112.50	1,507.75
Error	108		

[a] Analysis of variance was done on data from Table 1 using the type III sums of squares method of the general linear models procedure of SAS.
[b] * = Effects significant at $P \leq 0.05$, ** = significant at $P < 0.01$, and *** = significant at $P < 0.001$.

perature (Table 1). Based on the percent recovery from pieces of bark tissue, *P. megasperma* (high-temperature isolate) survived at all temperatures; however, exposure at 45 C for 20 and 30 min resulted in the greatest reduction in recovery compared with untreated infected tissue. In contrast, *P. cinnamomi*, *P. cactorum*, and *P. megasperma* (low-temperature isolate) were not recovered when infected tissue was exposed for 30 min at 45 C. Linear regression analyses of the percent survival of the isolates in walnut tissue were similar to those for survival in soil (*data not shown*). Slope values ranged from −0.198 to −4.668 and coefficients of determination were significant.

Factorial analyses of variance on the effect of temperature and time on the survival of the *Phytophthora* spp. in moist soil and walnut twigs indicated highly significant interactions ($P \leq 0.0001$) among species, time, and temperature (Table 2).

Survival of *Phytophthora* spp. during soil solarization. Survival of the isolates of *Phytophthora* spp. was dependent on the soil temperatures achieved during the solarization period. Soil temperatures were recorded hourly at 15-, 30-, and 45-cm soil depths in both solarized and nonsolarized plots in each field experiment, and daily mean temperature fluctuations are shown in Figure 1. The maximum temperature in the solarized plots was 45 C at 1600 hr at the 15-cm depth, whereas 32 C was reached in nonsolarized soil at the same depth. At 30 cm in solarized soil, the maximum temperature was 37 C, whereas the maximum temperature was less than 30 C in nonsolarized soil.

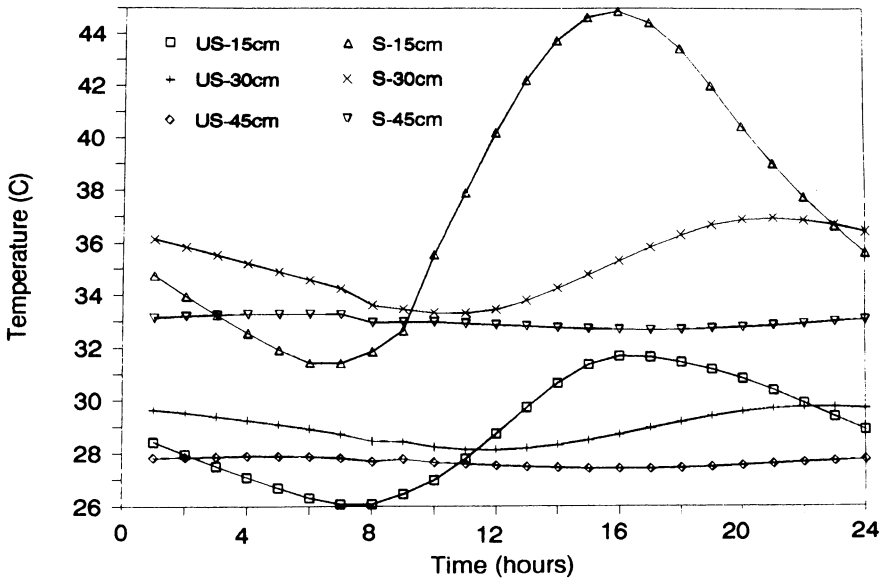

Fig. 1. Daily mean temperature fluctuations (5 July to 6 August 1989) in solarized (S) and unsolarized (US) field sites at depths of 15, 30, and 45 cm. Each value is an average of two measurements in two field sites.

Table 3. Effect of soil solarization (using three soil depths and two time periods) on percent recovery of *Phytophthora cinnamomi*, *P. cactorum*, and *P. megasperma* (high-temperature isolate)

Treatment	Depth (cm)	*P. cinnamomi*		*P. cactorum*		*P. megasperma*	
		2 wk	4 wk	2wk	4 wk	2 wk	4wk
Field site 1							
Solarized[a]	15	0.0[b]	0.0	0.0	0.0	26.7	1.7
	30	0.0	0.0	10.0	3.3	76.7	40.0
	45	38.3	0.0	55.0	13.3	86.7	56.7
Nonsolarized	15	96.7	88.3	96.7	90.0	100.0	93.3
	30	95.0	91.7	100.0	93.3	98.3	95.0
	45	100.0	93.3	100.0	95.0	100.0	98.3
Control[c]		95.0	96.7	96.7	98.3	100.0	98.7
Field site 2							
Solarized	15	0.0	0.0	0.0	5.0	23.3	15.0
	30	0.0	0.0	8.3	15.0	63.3	48.3
	45	20.0	3.3	21.7	26.7	91.7	53.3
Nonsolarized	15	93.3	90.0	100.0	95.0	100.0	98.3
	30	93.3	93.3	95.0	95.0	93.3	98.3
	45	90.0	95.0	91.7	100.0	96.7	100.0
Control[c]		100.0	96.7	98.3	100.0	98.3	95.0

[a] Transparent polyethylene tarps 25-μm thick were placed on the soil on 7 July and removed 6 August 1989 at Davis, CA.
[b] Percentage of peach leaf disks from which colonies developed when plated on PARP selective medium. Before plating, disks were placed in flooded soil samples for 48 hr. Average of six replicates per treatment.
[c] The controls were maintained in laboratory at 22–24 C.

Among the isolates of *Phytophthora*, *P. cinnamomi* was most sensitive to soil solarization in both field experiments; propagules were completely inactivated within 2 wk at both the 15- and 30-cm depths (Table 3). *P. cactorum* was fairly sensitive to soil solarization, and all propagules were inactivated within 2 wk at the 15-cm depth at field site 1; however, the results differed in field site 2. In the soil samples retrieved after 2 wk, no colonies were recovered from the leaf disks, whereas colonies developed from 5% of the leaf disks at 4 wk.

The only isolate of *P. megasperma* used in the field tests was the high-temperature isolate; it survived 4 wk of soil solarization at all soil depths (Table 3), with 85 and 98% reductions in colonization of the leaf disks at the 15-cm depth in field sites 1 and 2, respectively.

Factorial analyses of variance on the effect of soil solarization after 2 and 4 wk on the survival of the *Phytophthora* spp. indicated highly significant relationships among time, species, soil depths, and blocks ($P \leq 0.0001$) for field site 1. Also, for field site 2, the interactions of species, soil depth, and blocks were significant (Table 4). In site 2, time was not a significant factor. Within 2 wk, soil solarization had reduced the survival of the *Phytophthora* spp. as effectively as 4 wk of solarization. Differences among the blocks were highly significant, i.e., in solarized blocks the survival of the *Phytophthora* spp. was 20–40%, whereas in nonsolarized blocks it was 94–96%.

DISCUSSION

Our results were similar to those of Barbercheck and von Broembsen (1) regarding thermal sensitivity of *P. cinnamomi* in moist soil. In their study, however, chlamydospores of the two isolates of *P. cinnamomi* were inactivated by exposure to 38 C for 30 min and at 44 C for 10 min. Additionally, all propagules of *P. cinnamomi* were eradicated in solarized soil from all colonized wheat grains buried at depths of 5, 10, and 30 cm for 6 wk. Also, in the fallow treatment (nonsolarized soil), 84–99% of the propagules were killed after 3 and 4 wk, respectively. In our study, the isolate of *P. cinnamomi* used was slightly less heat sensitive than the isolates they used (1); moreover, in fallowed soil, the population of viable propagules remained similar to the untreated control inoculum kept in the laboratory. In earlier studies on the heat sensitivity of *P. cinnamomi*, Zentmyer (34) found that isolates from different areas of the world differed in their mini-

mal, optimal, and maximal temperatures for growth. It was apparent from our studies and those by Pinkas and Katan (16) and Benson (2) that *P. cinnamomi* is sensitive to soil temperatures and times of exposure that are associated with soil solarization.

Other species of *Phytophthora* have also been controlled by soil solarization (5,24), and, among fungi tested tor their thermal sensitivity, members of this genus are highly sensitive (17,23). Root rot of gerbera, caused by *P. cryptogea*, was reduced to 50% compared with control plants, and the pathogen was eradicated to a depth of 30 cm by solarization in western Australia (5). In a cherry orchard (cultivar Mahaleb rootstock) with root and crown rot caused by *P. cambivora*, Wicks (24) found that soil solarization controlled infection of trees in an irrigated orchard for more than 12 mo. Soil temperatures greater than 40 C seldom were recorded at a depth of 10 cm in the solarized soil; however, in laboratory studies, a 6-hr exposure at 45 C was lethal to hyphae and sporangia of two isolates from almond and two from cherry. However, isolate P5 from almond was not inhibited by four 6-hr exposures at 40 C. Other isolates also varied in sensitivity to exposure at temperatures of 35 and 40 C during one to four 6-hr periods but were more sensitive than isolate P5. In contrast to the reduction in infections in cherry, solarization was not effective in nonirrigated almond (cultivar Mission) orchards, possibly because of suboptimal levels of soil moisture. Moreover, soil solarization had no significant effect on established infections in either cherry or almond roots (24). These studies indicate the importance of variables such as thermal sensitivity of the pathogens, soil moisture, and soil temperatures actually achieved during solarization in its effectiveness for the control of soilborne pathogens (8,23).

In our study, the thermal sensitivity of the isolates in infested soil was similar to their heat sensitivity in infected walnut twigs. Temperature × time exposures that reduced the recovery of the isolates more than 95% from walnut bark tissue and from peach leaf leaf disks in flooded soil samples under laboratory conditions reflected the killing thresholds under field conditions. The linear relationship between death rate of fungal structures as a function of exposure time and temperature has been reported and discussed in several studies (3,17,18). These researchers also observed a linear relationship when the logarithms of the time required to kill 50 or 90% of the propagules were plotted against the reciprocals of the corresponding temperatures.

The marked reduction in recovery of the isolates of *Phytophthora* in soil samples buried in solarized plots was apparently attributable to the direct effect of elevate soil temperatures on the fungal propagules. Results of experiments on temperature sensitivity of the *Phytophthora* spp. in laboratory studies closely reflected their inactivation in solar-heated soil under transparent polyethylene sheeting. Moreover, as reported by other workers (1,5,16,24), soil solarization has potential for the nonchemical management of soilborne diseases caused by species of *Phytophthora*. Further investigations are needed to determine the conditions and host-pathogen combinations in which soil solarization may be an effective and practical method for control of soilborne diseases of perennial fruit crops.

Table 4. Factorial analyses of variance on the effect of soil solarization on recovery after 2 and 4 wk of isolates of *Phytophthora cinnamoni*, *P. cactorum*, and *P. megasperma* at three soil depths[a]

Source	df	Sum of squares	
		Site 1	Site 2
Time	1	8,689.35***[b]	6,446.30
Species	2	21,823.15***	58,125.00***
Depth	2	15,270.37***	26,944.44**
Block	5	289,057.87***	243,750.00***
Replications	1	104.17	3,266.67
Time × species × depth × block	20	1,370.37	81,903.70
Time × species	2	650.93**	14,200.93
Time × depth	2	1,837.04***	9,848.15
Time × block	5	3,157.87***	22,970.37
Time × species × depth	4	1,201.85***	19,862.96
Time × species × block	10	2,210.19***	47,999.07
Time × depth × block	10	3,007.41***	39,918.52
Species × depth	4	3,696.30***	25,855.56
Species × block	10	15,837.96***	73,975.00*
Species × depth × block	20	4,875.93***	88,644.44
Depth × block	10	11,507.41***	56,688.89
Error	107		

[a] Analysis of variance was done on data in Table 3 using the type III sums of squares method of the general linear model procedure of SAS.

[b] * = Effects significant at $P \leq 0.05$, ** = significant at $P < 0.01$, and *** = significant at $P < 0.001$.

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