The Effect of Temperature on Growth and Pathogenesis of *Phytophthora cinnamomi* and on Growth of Its Avocado Host

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ABSTRACT

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The growth curve of *Phytophthora cinnamomi* in response to temperature was similar to that of the avocado (*Persea americana*) host except at 33 C where the host grew well but the pathogen was inhibited both in growth and in sporangium production. Development of Phytophthora root rot and consequent reduction of growth of avocado seedlings was greatest at soil temperatures of 21 and 27 C under controlled conditions in naturally infested soil. Some disease developed at 15 C; at 33 C, the fungus was not pathogenic and did not affect growth of the avocado. There was a positive correlation ($R=0.966$, significant at $P=0.05$) between the reduction in root weight at the different temperatures and growth of *P. cinnamomi* at those temperatures. In the absence of the pathogen, water use by the avocado seedlings was related to top growth. In the presence of the pathogen, water use was restricted at 15, 21, and 27 C but not at 33 C. Infection of avocado seedlings was related to soil temperature at a depth of 10 cm in an avocado grove in California, with maximum infection in the summer and fall months when soil temperatures reached maximum levels of 24.5 to 25.5 C. In July, August, and September, there were at least 570 hr/mo when the soil temperature was 20 C or over; in August and September, there were 30 and 36 hr, respectively, when soil temperature was over 25 C.

Temperature is a significant factor affecting pathogenesis. Phytophthora root rot of avocado, caused by *Phytophthora cinnamomi* Rands, is a common problem in many of the subtropical and tropical areas of the world, where air temperatures can reach high levels (35–40 C) but little information is available on the soil temperatures that would more directly affect pathogenesis. This paper reports the relation between soil temperature, water use by the host, and development of this disease, as well as the effect of temperature on growth of the pathogen.

Although *P. cinnamomi* has a wide host range (13) and has been the subject of considerable research, reports of the effect of soil temperature on pathogenesis have generally been limited in scope, some merely indicating that infection occurred at moderate soil temperatures (1,3,8,11,12). Hepting (4), in summarizing requisite environmental conditions for infection by *P. cinnamomi*, noted that infection was generally slight below 15 C or above 34 C. Roth and Kuhlman (9) found that soil temperatures of 18.3 C (65 F) were required for infection of Douglas-fir seedlings, and maximum infection of the roots occurred at 26.7 C (80 F).

Hine et al (5) found that the optimum soil temperatures for heart and root rot of pineapple caused by *P. cinnamomi* in Hawaii were between 19 and 25 C; the disease developed slowly at 30 C and not at all at 36 C. Marks et al (7) reported that the pathogenicity of *P. cinnamomi* to *Eucalyptus sieberi* seedlings in greenhouse tests in Australia increased as the temperature increased from 12.5 to 22 C; seedling mortality was 100% at 22 C.

MATERIALS AND METHODS

Mexican avocado (*Persea americana* var. *drymifolia*) (Schlecht. & Cham.) Blake 'Topa Topa' seedlings were germinated in flats of steamed sand, then transplanted to 10.2-cm (4-in.)-diameter pots containing a sandy loam soil steam sterilized at 100 C for 1 hr. Soil (Fallbrook series), for use in the large containers in the temperature tanks, was collected from under 15-yr-old avocado trees affected with Phytophthora root rot in Vista, CA. The sandy loam was screened to remove large roots, mixed thoroughly, then placed in 10-L plastic containers at a moisture content of approximately 20%. Half of the soil was steamed before it was placed in the containers and the other half was not steamed. Hereafter, these soil treatments are referred to as noninfested and infested, respectively.

The avocado seedlings, 15.2–20.3 cm (6–8 in.) in height, were selected for uniformity, then transplanted into the plastic containers with the infested or the noninfested soil. The containers were placed in temperature tanks with the soil level just below the water level in the tanks. Five replicates of each soil (steamed and nonsteamed) were randomized in each tank. Tank temperatures were maintained at 9, 15, 21, 27, and 33 C. Air temperatures in the greenhouse ranged from 25 to 28 C. The soil surface was covered with 2.54 cm (1 in.) of peat moss to reduce evaporation.

Soil moisture was brought once a week to the original "field capacity" level of 20% by weighing each container and adding the required amount of demineralized water. Data on water use were thus obtained for plants growing at the different soil temperatures in infested and noninfested soil. After 12 wk, tops were removed, soil was washed from the roots, roots and tops were weighed, and roots were cultured for the presence of *P. cinnamomi*. Seedling height was measured periodically.

The relation between temperature and in vitro growth of *P. cinnamomi* (A^2 mating type isolate from avocado roots [Pc40, ATCC 32942]) was determined by growing it on potato-dextrose agar (PDA) in incubators set at intervals of 3 C from 6 to 36 C.

In a field aspect of the study, soil thermographs were placed at a depth of 10 cm under infected avocado trees with a full leaf canopy in Riverside County, CA. Temperatures were recorded for 1 yr. During this period, Mexican avocado seedlings (cultivar Topa Topa) were planted under the diseased trees. These seedlings were left in the soil for 2 mo. Upon removal, the percentage of diseased roots was estimated, and small roots were cultured to detect infection by *P. cinnamomi*. This process was repeated every 2 mo during the year. Soil moisture was maintained at adequate levels by irrigation during the dry months (April to November).

RESULTS

Soil temperature effects in greenhouse. The differences in growth of seedlings in the infested and noninfested soils in the greenhouse became obvious at the moderate soil temperatures (21 and 27 C) within 1 mo after planting. With adequate soil moisture and lack of

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stress on the foliage under greenhouse conditions, wilting was not severe in the infested soil during the duration of the experiment (Fig. 1).

When the seedlings were removed from the soil, differences in the size and condition of the root systems in the infested versus the noninfested soil were found to be substantial, particularly at 15, 21, and 27 C (Fig. 1). The effect of *P. cinnamomi* on the roots and on growth of the seedlings at the various soil temperatures was obvious from the comparison of root and top weights, and growth increments (Table 1).

Based on the average weight of tops and roots, the optimal soil temperature for growth of the avocado seedlings in noninfested soil was 27 C. At 21 C, the increase in height of the plants was nearly the same as at 27 C, but leaf size and stem diameter were smaller. The avocado seedlings made appreciable growth at 33 C, but growth at that soil temperature was considerably less than at 27 C.

Laboratory tests with the avocado isolate on PDA showed that the optimum temperature range for growth of the fungus was similar to that of the host plant (Fig. 2). The isolate used in this study did not grown at 33 C on PDA, however. Later studies (14) showed that some avocado isolates of *P. cinnamomi* grew slightly at 33 C; a few isolates from other hosts grew slightly even at 36 C. The isolate used in this study did not produce sporangia at 33 C.

The relations are obvious between temperature, growth of *P. cinnamomi*, and growth of the avocado seedlings in infested and in noninfested soil (Fig. 2). There was a positive correlation ($R = 0.966$, significant at $P = 0.05$) between the reduction in root weight (weight of roots grown in infested soil minus weight of roots grown in noninfested soil) at the different temperatures and the growth of the fungus at those temperatures (Fig. 3). Disease development, as evidenced by the parameters of root weight, top weight, and increase in height of the avocado seedlings, as well as water use by the seedlings, was directly correlated with soil temperature. The experiment in the temperature tanks was repeated, with similar results.

Soil moisture effects in the greenhouse. The amount of water used by plants also was directly correlated with temperature and with presence or absence of the pathogen (Fig. 4). Reductions in water use in the presence of *P. cinnamomi* were most significant at 15, 21, and 27 C. At 33 C, where there was little root invasion by the pathogen, water use was similar in infested and noninfested soils. There were no significant differences in root weight, top weight, height increase, and water use of inoculated and uninoculated

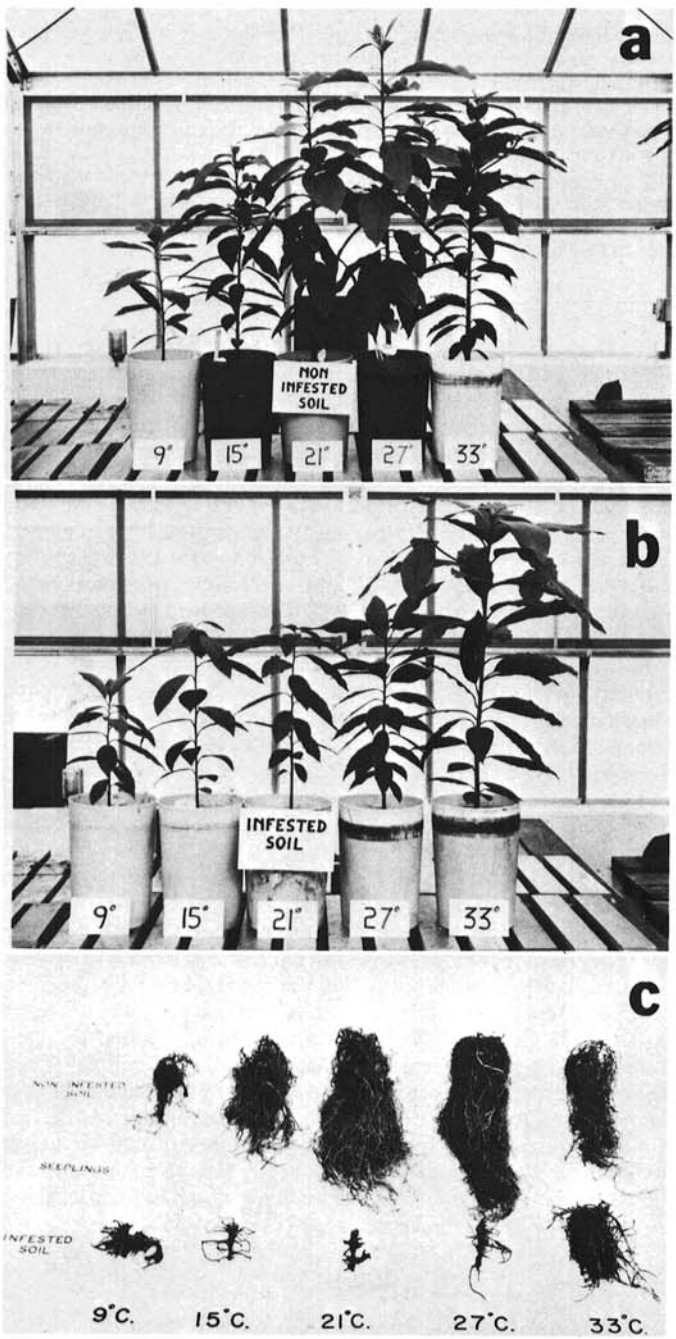

Fig. 1. Growth of avocado seedlings in soil infested with *Phytophthora cinnamomi* and in noninfested soil at different soil temperatures after 12 wk.

TABLE 1. Relation of soil temperature to growth of avocado seedlings after 12 wk in soil infested with *Phytophthora cinnamomi* and in noninfested soil

Soil temp. (C)	Weight of roots (g)		Weight of tops (g)		Increase in height (cm)	
	N[a]	I[b]	N	I	N	I
9	17.5 b[c]	12.2 b	27.4 z	32.9 z	40.0 c	5.8 c
15	68.4 b	12.1 b	68.4 z	30.5 z	31.1 b	2.7 c
21	150.4 a	20.0 b	131.4 y	30.2 z	48.2 a	0.3 c
27	209.6 a	15.3 b	186.3 x	41.8 z	50.3 a	14.2 c
33	58.1 b	56.0 b	117.9 y	122.0 y	38.9 ab	40.2 ab

[a] Noninfested soil.
[b] Soil infested with the pathogen.
[c] Duncan's multiple range, separate for each parameter (significant at $P = 0.01$). Figures followed by the same letter are not significantly different at $P = 0.01$.

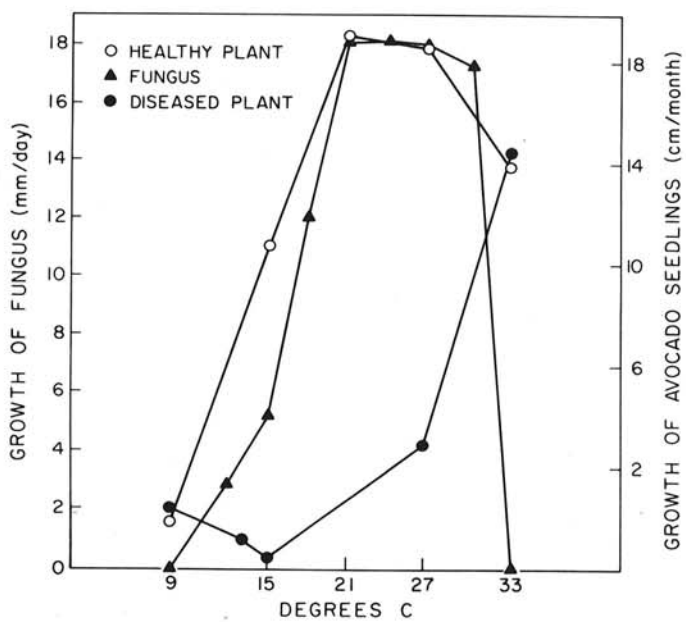

Fig. 2. Comparison of the effect of temperature on growth of *Phytophthora cinnamomi* on PDA, and on growth of avocado seedlings in infested and noninfested soil.

plants at 9 or at 33 C, according to Duncan's multiple range test, $P = 0.01$ (Table 1 and Fig. 4). At 15 C, height increases were significantly greater for noninoculated plants at $P = 0.01$, but for root weight, top weight, and water use at 15 C, healthy plants differed from inoculated plants only at $P = 0.05$. At 21 and 27 C, uninoculated plants grew significantly better (both roots and tops) and used significantly more water than did inoculated plants ($P = 0.01$).

Field studies. In the field study, soil temperatures are shown in Tables 2 and 3 together with data on the percentage of roots rotted by *P. cinnamomi* during the bimonthly infection periods at the Riverside location. No infection occurred in the winter months (January and February); infection was low during March, April, May, and June. The main infection period was from July to November when soil temperatures were the highest. Completing the year, a very slight amount of infection (0.5%) occurred in December and January.

Based on the more detailed temperature data in Table 3, months with the warmest soil temperatures were July, August, and September, when temperatures were over 20 C for essentially 24 hr/day. In August and September there were 30 and 36 hr, respectively, of soil temperatures over 25 C.

DISCUSSION

Data presented here indicate that *P. cinnamomi* can effectively reduce root and top growth of the avocado, a subtropical fruit tree, when soil temperatures range from 15 to 27 C, but when the soil temperature is maintained at 33 C, the fungus is nonpathogenic. These results are related to the growth of *P. cinnamomi* and to production of sporangia in relation to temperature.

Soil moisture conditions under irrigation in California would not be expected to limit infection by *P. cinnamomi*. Thus, it appears that temperature is the more critical limiting factor; the data here indicate optimum infection occurs when soil temperatures are above 21 C but below 33 C. This would no doubt vary somewhat with locality and exposure. In inland areas of southern California, at least as indicated by the field data, the most favorable period for infection would be in late spring, summer, and fall when soil temperatures rise to 22 to 26 C. The principal period during which infection occurred in the field study was from July to November when soil temperatures were the highest. With the 2-mo period of exposure of the plants to the infested soil it is difficult to pinpoint precisely the principal time when infection occurred. Based on the data in Table 3, it is likely that most of the infection took place in July, August, September, and early October when soil temperatures were over 15 C for 24 hr/day and over 20 C for much of the time. This is of course only one area, an inland area, in the

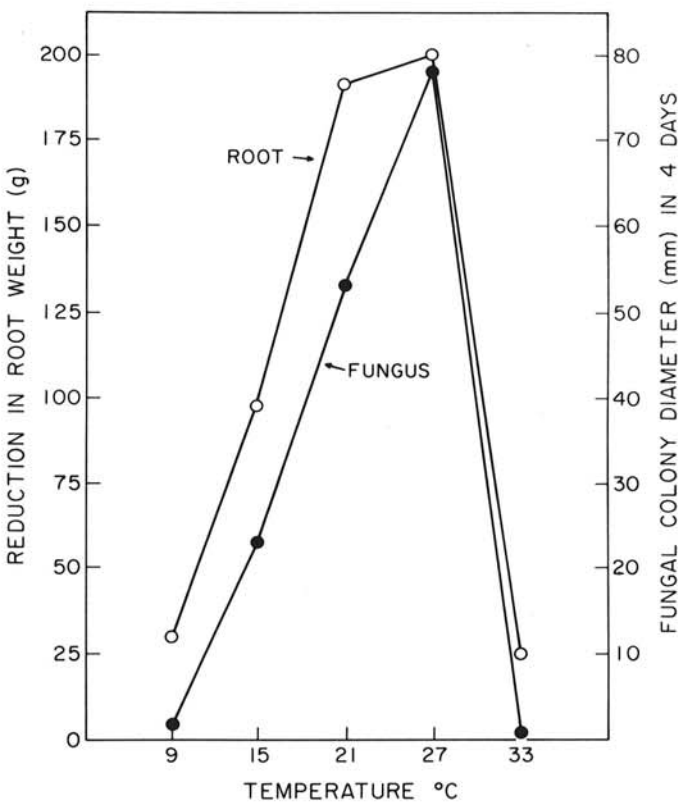

Fig. 3. Relation between soil temperature and reduction in root weight (weight of roots from noninfested soil minus weight of roots from infested soil) and growth of *Phytophthora cinnamomi* at the different temperatures ($R = 0.966$, significant at $P = 0.05$).

TABLE 2. Infection of avocado roots by *Phytophthora cinnamomi* in a field planting at Riverside, CA, over a 1-yr period in relation to soil temperatures at 10 cm depth

Infection period	Soil temperature (c)		Percent roots infected
	Maximum	Minimum	
3 Jan–5 March	15	8	0
5 March–2 May	18	6	4.9
2 May–5 July	22	12	5.4
5 July–24 Sept	26	19	24
24 Sept–27 Nov	23	14.5	31.1
27 Nov–21 Jan	17	4.5	0.5

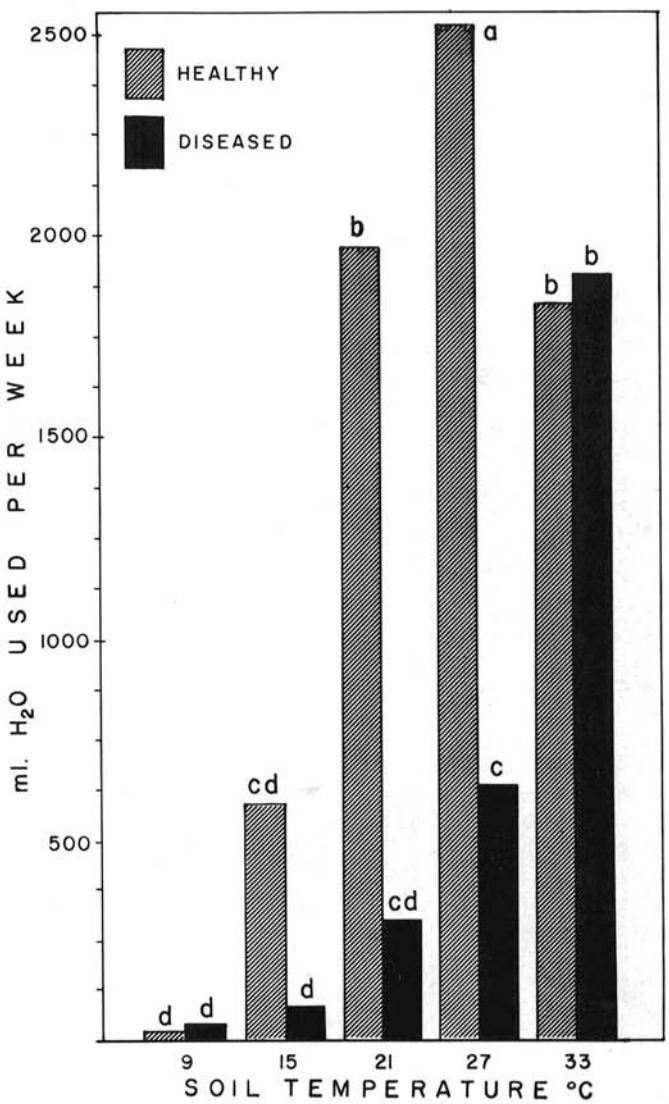

Fig. 4. Water uptake by avocado seedlings in soil infested with *Phytophthora cinnamomi* and in noninfested soil.

TABLE 3. Monthly soil temperature figures at the 10 cm depth in an avocado grove in Riverside, CA, based on total number of hours over a certain temperature in that month

Month[a]	Number of hours per month temperature (C) over:			
	10	15	20	25
January	535	0	0	0
February	660	0	0	0
March	562	0	0	0
April	720	81	0	0
May	720	370	44	0
June	720	720	62	0
July	720	720	666	0
August	720	720	710	30
September	720	720	570	36
October	720	670	10	0
November	670	10	0	0
December	665	0	0	0
January	504	0	0	0
February	400	0	0	0

[a]Total figures for each month based on 30 days or 720 hours.

southern California avocado region. In somewhat more mild coastal areas, infection might occur over a longer period including the spring months.

The data obtained from the soil temperature tank experiments indicate that some infection occurred at 15 C, but that the fungus is more effective in reducing root and top growth at 21 and 27 C. Thus, some infection would be expected in the field when soil temperatures were ranging from 10 to 15 C. In the one field study in California there were many hours per month, even in the winter, when soil temperatures were from 10 to 15 C, but little infection took place for undetermined reasons.

Reduction in water use by avocado seedlings in soil infested with the pathogen followed a similar trend to growth reduction, but percentage reduction of water use was more significant at 15 and 21 C than at 27 C. The fact that water use was greatly reduced in infested soil reflects the severe rotting of the absorbing roots and their consequent inability to take up water at the soil temperatures at which *P. cinnamomi* is active. At 33 C, roots were essentially healthy and water uptake was similar in infested and in noninfested soil. Maximum and minimum temperatures at which infection does not occur apparently can vary with the host. For example, these results differ somewhat from those of Roth and Kuhlman (9) who reported infection of Douglas fir to be at a high level at 32.2 C, and observed no infection at 15 C. They concluded that *P. cinnamomi* was unlikely to be a problem in the forests of the Pacific Northwest. When soil temperatures were above 18 C (June to October) the soil was too dry for infection. Fall rains provided adequate soil moisture but the temperature was depressed below 18 C.

The situation in avocado plantings in California contrasts sharply with that in the native forests of the Pacific Northwest because in California adequate soil moisture for infection by *P. cinnamomi* is provided in the summer and fall by irrigation. Thus, in California, temperature and moisture conditions are favorable for infection both in the summer and fall months. That such infection can occur under field conditions is indicated by the results of the field study of avocado seedling infection.

In Australian forests, there are indications of similar relationships between soil moisture and temperature to those in the Pacific Northwest. Shea (10) did not present any experimental data on the effect of temperature on infection but, based on the reports noted above (4,5,8,9), concluded that there would be long periods in lowland sites in the Jarrah forest in Western Australia when soil temperature and moisture would be suitable for infection. These periods would be primarily in spring, summer, and autumn. Canopy and litter cover would influence periods when soil temperature and moisture are suitable for infection, according to Shea (10).

The data presented here show appreciable infection of avocado at a soil temperature of 15 C in greenhouse tests. It may be necessary to reexamine some of the general statements made in relation to infection of trees in Australia, for instance, where the assumption has been broadly made that infection generally does not occur at or below 15 C.

The pathogenesis × temperature interaction affecting *P. cinnamomi* and its avocado host differs considerably from temperature responses of other soilborne pathogens. For example, in corn and wheat infected with *Gibberella*, disease development is most severe at temperatures unfavorable for the host (2). In the case of root rot of tobacco, the temperatures optimum for the pathogen, *Thielaviopsis basicola* (6) and its tobacco host were similar (28–30 C) as with the avocado and *P. cinnamomi*. However, the disease was most severe at 17–23 C, and little damage occurred at 28–30 C. The pathogen was apparently unable to attack the vigorously growing host at the higher temperatures.

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