Phytophthora cinnamomi in Hawaiian Forest Soils: Seasonal Variations in Population Levels

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ABSTRACT

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Soils from three ohia forest sites with trees showing varying degrees of decline, and from adjacent healthy and declining sites, were sampled bi-weekly for population levels of *Phytophthora cinnamomi* over an 8- to 13-mo period. Population levels varied considerably among sites and within the same site throughout the course of the study. At the three sites, the fungus generally was undetectable or its population levels were lowest in the winter months when minimum soil temperatures were near 10 C and then they increased as soil temperatures increased. Population levels decreased after extended periods of heavy rain and measurements at six of the eight monthly sampling times were significantly higher at the decline site than at the adjacent healthy site. Significant correlations between *P. cinnamomi* population levels and maximum soil temperature, minimum soil temperature, and rainfall were found at some sites but not at others. Soil matric potentials at all sites ranged from 0 to −30 mb and were seldom less than −25 mb. High water holding capacity of the soils combined with rainfall averages ranging 2,984–3,489 mm/yr apparently were favorable for sporangium formation. Zoospores were prevalent at certain times of the year.

Soil temperature and soil moisture are limiting factors in the spread of *Phytophthora cinnamomi* Rands (2,8,23). Seasonal variations in inoculum densities of *P. cinnamomi* in Victorian forests, determined by the serial dilution end point method (27), were associated with environmental factors (15,29,30) and a seasonal variation in numbers of chlamydospores has been demonstrated (31) with the soil sieving method (16). In western Australian forests, where *P. cinnamomi* is associated with dieback of jarrah (*Eucalyptus marginata* Sm.), environmental factors were measured (3,25) but no estimates of actual fungal populations were made. Population levels of other species of *Phytophthora* also are affected by seasonal variations in the soil environment (6,24).

Phytophthora cinnamomi was isolated by lupine (*Lupinus angustifolius* L.) baiting from Hawaiian forest soils where decline of ohia (*Metrosideros collina* [Forst.] Gray subsp. *polymorpha* [Gaud.] Rock) trees occurs and also from many soils supporting healthy ohia trees (11,14). Soil population levels of the pathogen also were compared in some adjacent healthy and declining tree sites (9,11) but at only one time period and no measurements of edaphic factors were made.

The objectives of this study were to measure edaphic factors at declining and nondeclining ohia forest sites; to monitor changes in population levels and propagule types of *P. cinnamomi* in relation to the edaphic factors measured; and to relate edaphic factors, population levels, and propagule types of *P. cinnamomi* to the incidence and severity of tree decline. A preliminary report has been published (12).

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MATERIALS AND METHODS

Five ohia forest sites, characterized in Table 1, were studied. Three sites with varying intensities of decline, in study areas previously described (19), were studied from January 1977, through February 1978. Two additional sites (sites 4 and 5), in an area studied previously (11) for the presence of *P. cinnamomi*, were studied from April through November 1978. Site 5 was within an approximately 16-m diameter area of severely-declining trees, surrounded by approximately 4 ha of healthy forest. Site 4 was in healthy forest 12 m from the decline margin and 24 m from site 5. Percent crown loss (the percentage of foliage missing from the crown, estimated to the nearest 10%) and number of dead trees on previously established transects (19) at sites 1, 2, and 3 were determined every 6 mo from April 1975, through April 1978. On sites 4 and 5, percent crown loss and number of dead trees within a 5-m radius of each sampling point were recorded in March 1977, and again in July 1978. Soil pH was determined by measurements of a saturated soil paste 1 hr after mixing. Percent organic carbon in soil was determined by the Walkley-Black method (28) and converted to total organic carbon by multiplying by 1.33 (7).

Continuous measurements of rainfall (remote recording tipping-bucket rain gauge [Weather Measure Corp., Sacramento, CA 95841]), air temperature and soil temperature at an 8–10 cm depth (automatic remote recording two-point thermograph, Weather-

Measure Corp.) were made at each site. Tensiometers (mercury-filled, with 1-bar high-flow porous ceramic cups [Soil Moisture Equipment Co., Santa Barbara, CA 93105]) were placed at an 8–10 cm depth at each site and read weekly to determine soil matric potential. Soil cores were taken bi-weekly at an 8–10 cm depth to determine volumetric moisture content and bulk densities. Soil moisture characteristic curves were determined with a pressure plate extractor apparatus.

Every 2 wk, one 100-g bulk soil sample was collected at a depth of 6–10 cm from within a 1 m^2 area at each of the five sites. Subsequent samples were taken from undisturbed portions from the same 1 m^2 area. Approximately 50-g subsamples were used to determine population levels of *P. cinnamomi*, and the remainder was used to determine gravimetric moisture content (three replicate 10-g samples, oven-dried at 105 C). Soils for population level assays were taken to the laboratory the same day they were collected, air-dried overnight, and then treated as described previously (13). Briefly, the assay technique involved suspending 50 g (wet weight) of soil collected 24 hr previously in 150 ml of water and dispersing the mixture in an Omni-Mixer for 30 sec. The mixture was agitated by a magnetic stirrer and a 3-ml subsample dispersed on each of 10 plates of antibiotic medium (16) but with 1% V-8 juice and 3% agar. Five additional 3-ml subsamples were dried overnight at 105 C in weighing pans to determine the average dry weight of soil per plate. The plates were incubated in the dark at 24 C for 24 hr, washed, and the number of colonies of *P. cinnamomi* and their origin (chlamydospores, organic matter, zoospores, directly-germinating sporangia, or hyphae) were determined. The plates were reexamined after 48 hr. The number of propagules recovered was converted to number of propagules per gram of oven-dried soil.

RESULTS

Population fluctuations. Population levels of *P. cinnamomi* varied considerably among sites and within the same site throughout the course of the study. The pattern of population fluctuations at sites 1, 2, and 3 were similar: lowest in the winter months, increasing in spring, and decreasing following extended periods of heavy rain (Fig. 1).

At site 1 (Fig. 1A), low numbers of chlamydospores and only a few zoospores were recovered in January and February 1977, when the minimum soil temperature frequently was below 10 C. The population level increased from two propagules per gram on 22 February to 288 propagules per gram on 8 March, following a 2-wk period when 58 cm of rain was recorded and the minimum soil temperature increased from 8 to 12 C. Of the 288 propagules recovered, 148 were zoospores. The population decreased to 68 propagules per gram on 21 March, following another 60 cm of rain, increased to 271 propagules per gram on 5 April as rainfall diminished, and decreased to 34 propagules per gram on 19 April as rainfall increased. The number of zoospores recovered decreased from 166 on 5 April to 21 on 19 April. The population increased in May and June as soil temperatures increased and only traces of rainfall were recorded. The maximum population of 330 propagules per gram, 219 of which were zoospores, was recorded on 28 June following a total of 1.8 cm of rain in May and June. The population level remained relatively stable from July through October as soil temperatures reached a maximum and rainfall was relatively constant, then decreased as soil temperatures decreased.

At site 2 (Fig. 1B) the lowest population levels generally occurred in December and January when the soil temperatures reached a minimum near 10 C. Zoospores were not recovered, or were recovered in low numbers, during those months. The population increased from four propagules per gram in January to 51 propagules per gram in February 1977, as soil temperature increased and zoospores were recovered, then dropped on 21 March to six propagules per gram following 122 cm of rain over a 4-wk period. No zoospores were recovered during that period. The population increased to the maximum level recorded (94 propagules per gram, 54 of which were zoospores) as rainfall diminished.

At the site with healthy trees (site 3, Fig. 1C) the same general

TABLE 1. Characteristics of five ohia forest sites used for study of *Phytophthora cinnamomi* population levels in relation to edaphic factors and ohia decline

Site	Elevation (m)	Crown loss (%)	Soil depth (cm)[a]	pH[b]	Organic matter (%)[b]	Bulk density[c]
1	1,112	53	0–15	4.8	62	.12–.14
2	1,265	49	0–12	4.9	68	.10–.13
3	914	26	10–30	5.6	24	.27–.28
4	1,536	26	6–18	4.7	63	.15–.16
5	1,536	83	3–10	5.0	64	.15–.16

[a] Depth from soil surface to solid underlying substrate, range of three probes in a 1 m^2 area.
[b] Average of three samples collected at an 8–10 cm depth.
[c] Range of bi-weekly determinations over an 8–13 mo period.

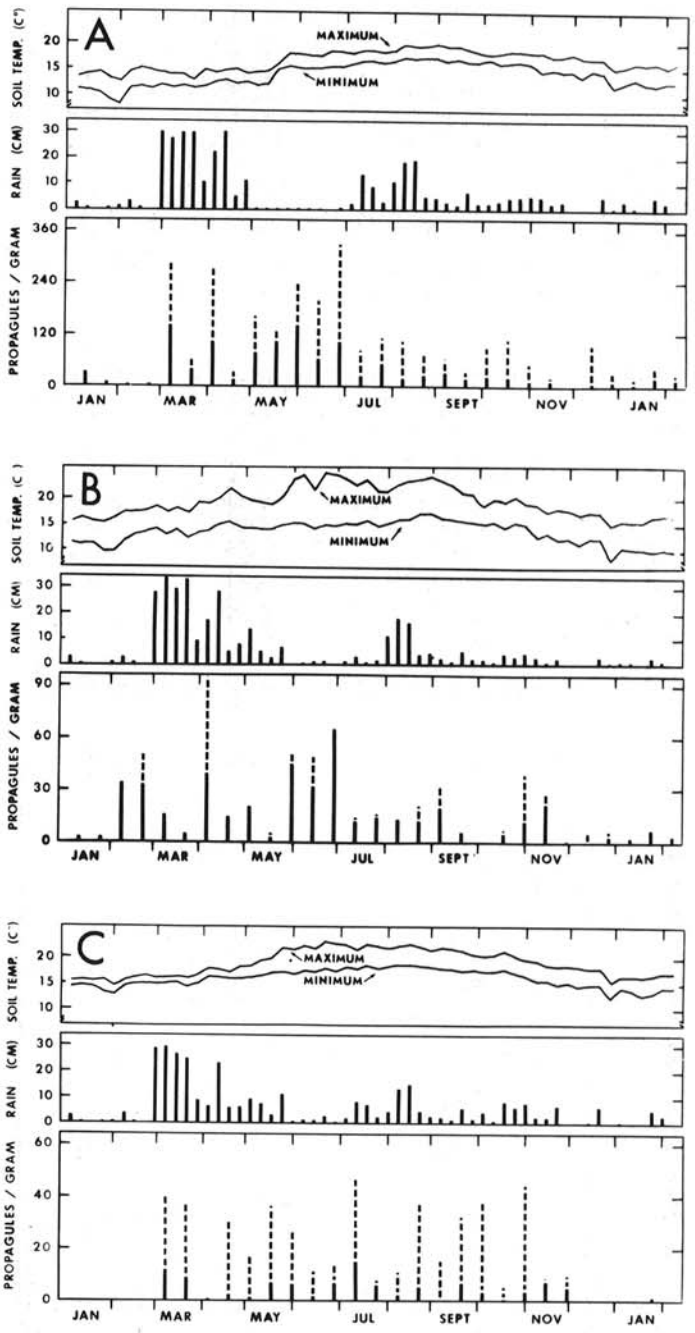

Fig. 1. Propagules per gram of *Phytophthora cinnamomi*, rainfall, and minimum and maximum soil temperatures measured over a 13-mo period at three ohia forest sites. With propagules per gram, a solid bar indicates chlamydospores, organic matter or hyphae as colony origin, and a broken bar indicates zoospores as colony origin. **A,** Site 1. **B,** Site 2. **C,** Site 3.

pattern was observed, except that the population levels were consistently lower than those at the first two sites. *P. cinnamomi* was not recovered in January, February, or December 1977, and only a few propagules were recovered in January 1978. These dates corresponded with the lowest soil temperatures and the least amounts of rain recorded. The population increased from 0 to 38 propagules per gram on 3 March as the rainy season started, and then dropped to undetectable levels on 5 April after 1 mo of heavy rain. The maximum population recovered was 48 propagules per gram on 11 July when maximum soil temperatures were recorded.

TABLE 2. Propagules of *Phytophthora cinnamomi* per gram of soil recovered from adjacent healthy and declining ohia forest sites, and total monthly rainfall, over an 8-mo period

Month	Site		Rain (cm)
	Healthy	Declining	
April	0	35.0 ± 17.2[a]	16.9
May	0.2 ± 0.7	31.2 ± 14.0	18.7
June	1.9 ± 1.2	19.4 ± 6.1	18.6
July	13.3 + 4.2	5.5 ± 2.8	28.5
August	0	0	22.5
September	0	20.3 ± 6.6	11.6
October	10.8 ± 4.8	61.3 ± 21.2	19.9
November	0	2.6 ± 1.1	33.8

[a]Propagules of *Phytophthora cinnamomi* per gram of oven dry soil, with standard deviation. Average of bi-weekly readings each month.

TABLE 3. Average of three variables measured from April through November 1978 on adjacent healthy and declining ohia forest sites

Site	Variable		
	Phytophthora cinnamomi (propagules/g)[a]	Soil moisture (% volumetric)[b]	Matric potential (mb)[a]
Healthy	3.7 A[c]	62.9 A	−12.8 A
Declining	25.9 B	75.9 B	− 6.3 B

[a]Average of 17 observations.
[b]Average of 34 observations.
[c]Numbers in each column followed by the same letter are not significantly different ($P = 0.05$) as determined by Duncan's multiple range test.

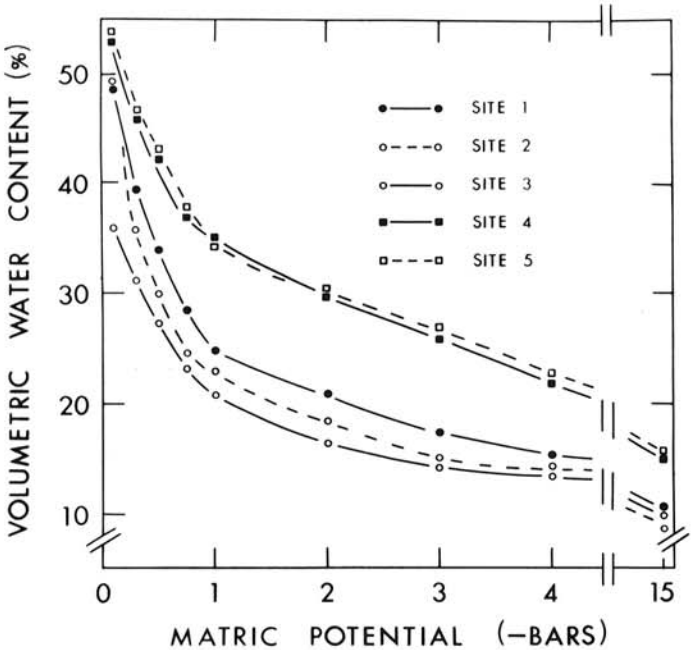

Fig. 2. Moisture characteristic curves for soil from five ohia forest sites sampled.

Population levels of *P. cinnamomi* were significantly higher at the tree decline site (site 5) than at the adjacent healthy site (site 4) during 6 of the 8 mo that measurements were taken (Table 2). Minimum soil temperatures ranged from 10 C in April to 14.2 C in July and were consistently 0.4–0.9 C lower at site 4. Population levels at both sites dropped to undetectable levels in August following 51 cm of rain in July and August. As rainfall diminished in September, *P. cinnamomi* remained undetectable in soils from the healthy site, but increased from zero to 20 propagules per gram in soil samples from the tree decline site.

Soil moisture and matric potentials. Gravimetric soil moisture contents at sites 1, 2, and 3 ranged from 330 to 950% and volumetric soil moisture contents ranged from 66 to 80%. Site 3 had consistently lower moisture and matric potentials than did sites 1 and 2. Gravimetric soil moisture contents at site 3 averaged 110 to 230% lower than at site 1, and 160 to 340% lower than at site 2. Average matric potentials were −15.6 mb at site 3, and −6.5 and −2.0 mb at sites 1 and 2, respectively. Volumetric soil moisture and matric potentials were consistently higher at the site with declining trees than at the adjacent healthy site (Table 3). No relationships among rainfall, soil moisture, and matric potential were apparent at any of the sites.

Soil moisture characteristic curves from the five sites are shown in Fig. 2. Soil from all sites retained high moisture levels at matric potentials considerably lower than those recorded in the field. The soils lost considerable amounts of water between 0 and −1 bar, but still retained 20–38% by volume. The soil moisture curves for soils from four of the five sites generally corresponded with the degree of decline at each site; soil at site 5 (83% crown loss) retained the most moisture and that at site 3 (26% crown loss) retained the least. Site 4 was an exception. Although it was considered comparatively healthy with 26% crown loss, the moisture characteristic curve was similar to soil from the adjacent declining site 5 with 83% crown loss.

Correlations between population levels, soil temperature, and rainfall. The linear relationships (26) between *P. cinnamomi* population levels and maximum soil temperature, minimum soil temperature, and rainfall on the five sites was determined. The total number of propagules and the number of zoospores only were analyzed separately (Table 4). Maximum soil temperature was correlated ($P = 0.05$) with total propagules at sites 2 and 3, and with numbers of zoospores at sites 3 and 5. Minimum soil temperature was highly correlated ($P = 0.01$) with both total propagules and number of zoospores at site 3, and correlated ($P = 0.05$) with total propagules at site 2, and with number of zoospores at site 5. Rainfall was highly correlated ($P = 0.01$) with total propagules and number of zoospores at site 3. At site 4, the correlation between rainfall and total propagules was significant ($P = 0.05$) and between rainfall and number of zoospores highly significant ($P = 0.01$). Multiple correlations (26) between total propagules or zoospores, and minimum soil temperature in combination with rainfall were not significant.

Population levels in realtion to decline intensity. Percent crown loss on 100 trees at each of the first three sites remained relatively stable over a 3-yr period. At site 1, the site with the highest overall levels of *P. cinnamomi* in the soil, percent crown loss decreased from 57 to 53% and the number of dead trees increased from zero to eight. On site 2, percent crown loss increased from 42 to 49% and the number of dead trees increased from two to 19. On site 3, the site with the lowest overall levels of *P. cinnamomi*, percent crown loss decreased from 31 to 26% and no dead trees were recorded over the 3-yr period.

On site 4, the relatively healthy site, percent crown loss on 20 trees decreased from 32 to 26% and one tree died during that period. On site 5, the decline site, percent crown loss on 19 trees remained constant at 83% and there was no increase in the number of dead trees (13).

DISCUSSION

Fluctuations in population levels of *P. cinnamomi* occurred at all the sites studied. In general, the populations were undetectable or lowest in the winter months when minimum soil temperatures were

near 10 C and increased as temperatures increased. Populations decreased during extended periods of heavy rain. Marks et al (15) and Weste and Ruppin (30) concluded that in Victorian soils low soil temperatures limited the population of *P. cinnamomi* in winter months and, when soil temperatures were favorable during the summer months, population levels were dependent on soil moisture, decreasing during dry periods and increasing after rainfall. Statistical analyses of our data suggested that factors in addition to soil temperature and moisture, alone or in combination, also are involved in population fluctuations. The highest correlations between population levels and rainfall were on sites 3 and 4, which had the deeper and better-drained soils. Although fluctuations occurred at all sites, consistently high moisture levels combined with shallow poorly-drained soils may have precluded any higher correlation between population level and rainfall. Even though Hawaiian forest soils are unfavorable for *P. cinnamomi* during only short periods of the year, reports of nonrecovery of the fungus in soils sampled during winter months or periods of heavy rain need to be re-evaluated.

The Hawaiian forest soils that we studied, are representative of large portions of ohia forest, and appear particularly suited to the requirements of *P. cinnamomi*. They differ from western Australian jarrah (*Eucalyptus marginata* Smith) forest soils in which moisture conditions are unfavorable for most of the year (25) and from Douglas-fir (*Pseudotsuga menziesii* [Mirb.]Franco) regions in the western USA where favorable moisture and temperature levels for the fungus do not occur concurrently (23). We found a rapid increase in population levels when favorable temperature returned, as also reported by Australian workers (15,30). The advantage of our plating technique over the serial dilution end point method used in Victoria (15,29,30) is that we were able to observe the types of propagules, mainly zoospores, responsible for the increase. Although free zoospores exist in the soils, zoospores occasionally were observed in clusters with empty sporangia nearby (13), indicating that the assay technique induced indirect germination of sporangia present in field soils. The soil sieving technique (16) used by Weste and Vithanage (31) is inefficient for recovering propagules less than 38-μm, which were common in our soils (13).

The actual numbers of *P. cinnamomi* propagules in soils reported here cannot be compared directly with numbers reported by others (16,31). Because bulk densities and organic content vary with soil type, reporting of population levels on a soil volume basis rather than on a soil weight basis would seem preferable.

The forest soils we studied had much higher organic matter content and water holding capacity than those studied elsewhere. The high organic matter content apparently had little adverse affect on *P. cinnamomi*, as data from other areas (1,20) had suggested. The high water holding capacity of Hawaiian forest soils, combined with high rainfall during most of the year, means that soil matric potential is seldom, if ever, a limiting factor for sporangial production and subsequent indirect germination. High soil moisture levels are retained during periods without rain. In fact, the data suggest that saturation of the shallow soils occurs during periods of high rainfall, resulting in anaerobic conditions and a decrease in population. Data gathered earlier (J. T. Kliejunas, *unpublished*) suggest that low oxygen and high methane levels are characteristic of many of the shallow, poorly-drained Hawaiian forest soils. The destructive combination of water-saturated soils with infection by *P. cinnamomi* is documented (18,25).

Various types of *P. cinnamomi* propagules were recovered. Zoospores were especially prevalent in soils at certain times of the year, indicating that Hawaiian forest soils are favorable for sporangial formation and subsequent indirect germination, and that conditions for a rapid population increase exist. The high numbers of zoospores in our soils, which seldom had matric potentials below −25 mb, agree with published reports indicating that optimum matric potentials for sporangial production and subsequent indirect germination by other *Phytophthora* spp. vary from saturation to approximately −300 mb (4,5,21,22). Chlamydospores, of a wide size range, and vesicles were also common (13). The recovery of *P. cinnamomi* colonies originating from individual pieces of hyphae and from pieces of organic matter indicated that conditions in the soil are favorable for vegetative growth or persistance of *P. cinnamomi*. The ability for long-term survival of the fungus in the unique Hawaiian forest histosols studied here is unknown, although our data indicate that the fungus apparently does not require long-term survival structures. Conditions are unfavorable for only short periods, and past work (10,17) indicates that chlamydospores of the fungus can survive for 1 yr, mycelium for 2 mo, and zoospores for 3 wk.

TABLE 4. Relation between populations of *Phytophthora cinnamomi* and soil temperature extremes at five ohia forest sites

Variable	Site	Observations (no.)	Population level of *P. cinnamomi*	
			Total	Zoospores
Maximum soil temperature[a]	1	29	.057	.140
	2	29	.370*[d]	.121
	3	29	.391*	.358*
	4	17	.087	.222
	5	17	.143	.413*
Minimum soil temperature[b]	1	29	.133	.186
	2	29	.361*	.301
	3	29	.518**	.502**
	4	17	.204	.187
	5	17	.214	.400*
Rainfall[c]	1	29	.221	.152
	2	29	.018	.027
	3	29	.574**	.537**
	4	17	.449*	.698**
	5	17	.088	.074

[a] Average maximum over a 2-wk period prior to soil sampling for *P. cinnamomi* population levels.
[b] Average minimum over a 2-wk period prior to soil sampling for *P. cinnamomi* population levels.
[c] Total rainfall over a 2-wk period prior to soil sampling for *P. cinnamomi* population levels.
[d] Asterisks: * = statistically significant at $P = 0.05$; ** = statistically significant, $P = 0.01$.

The perennial nature of ohia trees precluded finding any direct, immediate, relationship between changes in *P. cinnamomi* population levels and intensity of decline. Highly susceptible woody shrubs or trees, such as those that act as indicator species in western Australia and Victoria, are not present in ohia forests. Higher levels of *P. cinnamomi* were found on sites with more tree decline in our study, however, suggesting that the pathogen is contributing to ohia tree stress and subsequent decline.

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