Association of Phytophthora cinnamomi with Ohia Decline on the Island of Hawaii

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ABSTRACT

Ohia (*Metrosideros collina* subsp. *polymorpha*) seedlings transplanted to soils collected from declining forests became infected with *Phytophthora cinnamomi*; inoculation of healthy ohia trees in the field with soils and roots from declining forests resulted in root necrosis and *P. cinnamomi* was isolated. *Phytophthora cinnamomi* was recovered from 96% of the decline areas and from 24% of the apparently healthy areas sampled throughout the island of Hawaii. Lupine baiting and the use of soil dilution plates indicated little difference between population of the fungus in soil of declining and healthy forests. Addition of nutrients to ohia trees in the greenhouse had little effect on subsequent root infection by *P. cinnamomi*, and the fungus was recovered from soil in areas where declining ohia trees produced new growth following application of complete fertilizer. Fungicides reduced infection of ohia trees and lupine by *P. cinnamomi* in greenhouse and laboratory experiments. Broadcast applications of fungicides plus complete fertilizer to declining ohia trees resulted in a greater growth response than application of complete fertilizer only.

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Ohia [*Metrosideros collina* (Forst.) Gray subsp. *polymorpha* (Gaud.) Rock] forests on the island of Hawaii are declining at an increasing rate (18). Pathogenicity of *Phytophthora cinnamomi* Rands on ohia trees has been established (9) and the fungus was isolated from declining as well as healthy forests (2, 9, 11). This fungus has been associated with major declines of other forest trees, including *Castanea dentata* (7) and *Pinus echinata* (4) in the United States, *P. radiata* in New Zealand (16), *Eucalyptus marginata* in southwestern Australia (19), and native forest species in the Brisbane Ranges (24) and coastal Victoria (14) in Australia. Environmental factors influence the contribution of *P. cinnamomi* to tree decline (17). Addition of complete fertilizer to declining ohia trees alleviated the decline symptoms (10). Our objective in the present study was to determine the association and significance of *P. cinnamomi* in the decline of native ohia forests. A preliminary report has been published (11).

MATERIALS AND METHODS.—*Site descriptions.*—Ohia forests studied ranged from mature ohia-treefern rainforests to stands of younger ohia trees on more recent lava flows. Rainfall ranged from 190 to 630 cm/year. Soils were mainly thin layers of organic material or volcanic ash accumulated on pahoehoe (massive lava with relatively smooth surface) or aa (small porous lava with rough surface) rock. Soil depth and drainage differed widely within short distances. Ohia forests were considered to be declining if an average of 10% or more of ohia branches in the stand showed dieback, and considered healthy if dieback of ohia branches was less than 10%.

Decline survey.—Five areas of declining ohia forests were surveyed to determine the relative conditions of different height classes of ohia trees. In each area, three transects (30 m long and 90 degrees apart) were run from a random starting point. All ohia within 0.9 m on each side of the transects were recorded. The percentage of crown dieback for each tree was estimated visually and recorded by tree-size class, as were the number of dead trees in each size class.

Inoculation tests.—Sixteen- to 24-month-old ohia seedlings (15- 20 cm in height) grown from seed in vermiculite, or healthy ohia trees (1.5 m in height) transplanted from an area in the field where *P. cinnamomi* had not been isolated, were used for inoculation tests in the greenhouse. In one test, seedlings were transplanted to individual 1.5-liter containers with 1 liter of test soil in each. Soils used included those collected from two areas of decline and from one area known to contain *P. cinnamomi,* but with no aboveground symptoms of decline. Autoclaved soils from the two areas of decline and natural soil free of *P. cinnamomi* were used as controls. Nine seedlings were used for each treatment. In a second test, 15 ohia trees were transplanted individually to 10-liter containers with aa rock. Each of five containers received 450 g of washed ohia root tissues collected from one of three source areas, two forest areas with decline and one area of healthy forest.

In a field test, roots of nine healthy ohia trees (2.1-2.4 m in height) from an area in which *P. cinnamomi* had not been isolated, were surrounded with soils collected from two areas of healthy forest and from one forest area with decline. Three lateral roots on each of three trees were used for soils from each location. Each lateral was uncovered from aa rock, a plastic bag placed underneath, and then 100 g of soil placed around the lateral. The roots were then covered with aa rock and examined 4 months later.

Root and soil sampling.—Tests for association of *P. cinnamomi* with ohia trees were made by root isolation and soil baiting at 35 decline locations, and by soil baiting only at an additional 95 locations. Root tissues collected directly from five trees at each location were washed under running tap water, surface-sterilized with 0.5% NaOCl, and plated on selective medium (15). At least 100 root pieces from each tree were plated. Soil samples from 75 areas of decline and 55 areas of healthy ohia forest were tested for the presence of *P. cinnamomi* by baiting with lupine (*Lupinus angustifolius* L.) radicles (6). In preliminary experiments, pineapple heart leaves (1) and apple (3) were also tested as baits, but lupine radicles were the most efficient. One to three samples were taken from each area and baited separately. Each sample was a composite of three to five subsamples of roots and soil 0 to 10 cm beneath vegetation. Each sample was mixed and baited within 48 hours after collection. Unless stated otherwise, 250 ml of distilled water was added to 100 g of test soil in a 400 ml beaker, and five lupine seedlings were suspended with the radicles, 2-3 cm long, submerged in the water. After 48 hours, lupine roots were excised, washed in 0.5% NaOCl, and plated on selective medium. The presence of *P. cinnamomi* was detected by its characteristic mycelium and chlamydospores. Baiting was repeated at least once with freshly collected soil from the same area if *P. cinnamomi* was not initially recovered.

Population of Phytophthora cinnamomi in soil.—The population of *P. cinnamomi* in soils was determined in two ways. First, a modification of Tsao's (21) method of serially diluting soil to determine the dilution end point was used. Each soil sample was screened to remove rocks and undecomposed organic matter and 100, 10, 1, 0.1, and 0.01 g of the screened soil were added to 150-ml quantities of distilled water in 400-ml beakers and baited with lupine. Duplicate serial dilutions were made and baited for each soil sample. For direct colony counts, we used selective medium (15) but with 4% agar, 50 μg/ml rose bengal, and 72 hours of incubation at 20 C as suggested by Hendrix and Kuhlman (8). Each plate received 0.5 g of test soil, and then was flooded with 10 ml of distilled water (15). After incubation for 72 hours, the soil was washed from the plates and colonies of *P. cinnamomi* were counted with a microscope by inverting the petri plate. Ten plates were used per soil sample. With both methods, new soil samples were collected from the same locations and the procedures repeated.

Effect of fertilization.—Thirty soil samples were collected randomly from a 15.3 × 30.5-m plot in a decline area treated with a complete fertilizer (Keaau 19, composed of 12.14% N, 27.33% P, 7.27% K, 0.23% CaO, 0.24% Mn, 0.22% Zn, 0.023% B, 3.69% Mg, 7.09% S, 0.23% Cu, 0.23% Fe, and 0.0199% Mo) 17 months previously (10). Thirty soil samples from an untreated control plot 61 m away and from each of two additional untreated plots in the same vicinity were also collected. The samples were baited with lupine for *P. cinnamomi.*

To study the effect of fertilization on subsequent root infection, 12 healthy ohia trees collected from the field in an area not infested with *P. cinnamomi* and transplanted to vermiculite and aa rock in 10-liter containers 4 weeks previously were used. Six of the trees received 15 g of complete fertilizer and six trees were left untreated. Four weeks later, all 12 trees were inoculated with 1-week-old

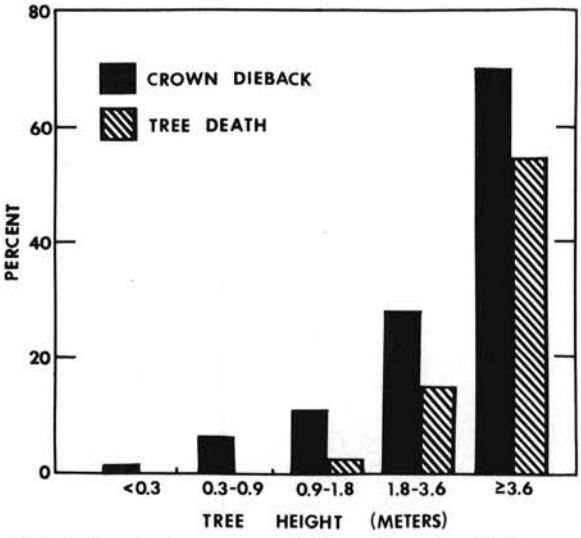

Fig. 1. Relation between tree height and severity of ohia tree decline in five areas of declining forest. The numbers of trees in each height class, starting with trees less than 0.3 meters, were 247, 235, 170, 108, and 101, respectively.

cultures of *P. cinnamomi* in 20% V-8 juice broth. The broth and mycelium were ground in an Omni-mixer for 2 minutes at 3,100 rpm and 100 ml of the mixture added to each tree. The containers were flooded for 24 hours, and then watered normally. Three months after inoculation, 100 root pieces (2 cm in length) were removed from each tree, surface-sterilized, and plated on selective medium.

Effect of fungicides.—Dexon (*p*-dimethylaminobenzenediazo sodium sulfonate), Benlate (methyl 1-(butylcarbamoyl)-2-benzimidazolecarbamate), and Difolatan [cis-*N*-(1,2,2-tetrachloroethyl) thio 4 - cylcohexane - 1,2-dicarboximide] were added to 20% V-8 juice agar at about 45 C. Chlamydospore germination of *P. cinnamomi* was tested on agar containing 10, 50, and 100 μg/ml active ingredient of Benlate. Effect on mycelial growth was tested by inoculating the centers of petri plates containing 12.5, 25, 50, or 100 μg/ml active ingredient of Dexon, Benlate, or Difolatan and measuring colony diameter after 3 days of incubation at 24 C in the dark. Dexon, Benlate, and Difolatan at 1, 10, 50, and 100 μg/ml active ingredient were added to 200-ml volumes of water and mixed with 50 g of soil naturally-infested with *P. cinnamomi*; the soil was baited with lupine.

Declining (twig and branch dieback affecting one-quarter to one-half of the tree) ohia trees, 1.2-2.4 m in height and 2.5-7.6 cm in diameter 30 cm aboveground, were used for field tests of fungicides. Trees were selected for uniformity of size and natural varieties within the species. Complete fertilizer was broadcast within a circular plot of 0.91 m radius, cleared of vegetation, around each tree. The chemicals tested included Nemagon granular (1, 2-dibromo-3-chloropropane) at a rate of 38 g/tree (100 lb active/acre) Difolatan at 8 ml/tree (40 lb active/acre), Benlate at 19 g/tree (100 lb active/acre), and Dexon at 9.5 g/tree (35 lb active/acre). Each fungicide was thoroughly mixed with 900 g of vermiculite and broadcast on a 0.91-m radius plot around

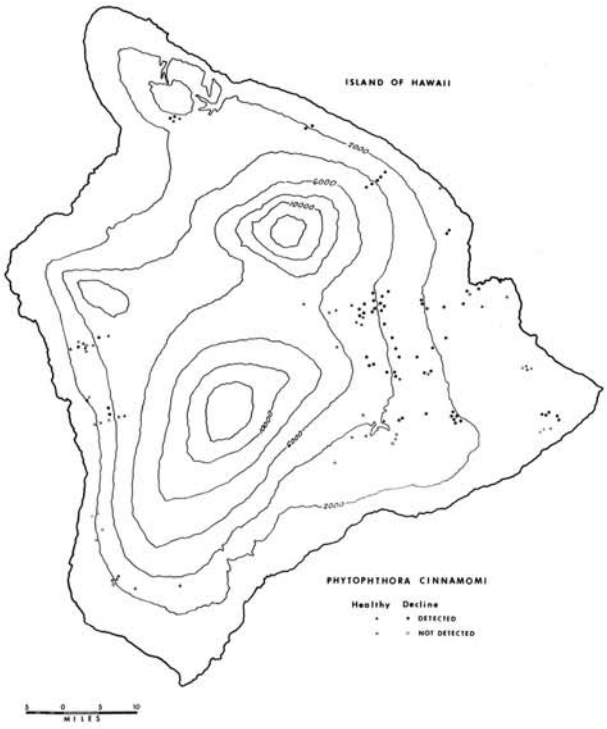

Fig. 2. Distribution of *Phytophthora cinnamomi* as detected by a lupine baiting technique in healthy and declining ohia forests on the island of Hawaii.

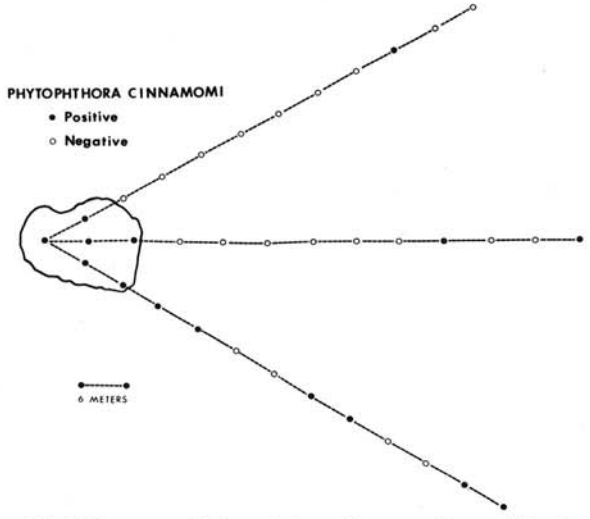

Fig. 3. Recovery of *Phytophthora cinnamomi* from soil by the lupine baiting technique at points in an area of ohia decline (within the dark line) and out into healthy ohia forest.

each tree. After application, the vermiculite with the adsorbed fungicide was covered with debris to protect it from direct sunlight. Control trees received vermiculite and debris only. The nematicide was broadcast directly and worked into the surface soil with a pick. All chemicals were applied during rainy periods. Eight to 9 weeks after treatment, the number of new lateral leaf buds produced on stems and branches were counted. Uptake of Difolatan and Benlate by ohia roots was determined by excising 10 root pieces from each of five trees treated with each fungicide and placing them on potato-dextrose agar seeded with conidia of *Mucor ramannianus* Möller for Difolatan and *Penicillium frequentans* Westling for Benlate. Resulting zones of inhibition were compared with standards obtained by the filter paper disk method (22).

In another test, ohia trees (1.5 m in height, from an area not infested with *P. cinnamomi*) were transplanted to aa rock and vermiculite in individual 10-liter containers. Six weeks later the following treatments were applied to each of three trees: Difolatan (2 ml/tree), Benlate (4.75 g/tree), and Dexon (2.4 g/tree) individually, a combination of the three fungicides, and no treatment. Eight weeks later the fungicides were applied again to the same trees, and one week later all trees were inoculated with *P. cinnamomi* as previously described. Eight weeks after inoculation, 50 root pieces from each tree were plated on selective medium. The experiment was repeated.

Analyses of variance were applied to appropriate data, and differences between means were determined using Duncan's multiple range test.

RESULTS.—*Tree height versus severity of decline.*—The average percentage of crown dieback and the percentage of dead trees in five areas of decline were directly correlated with tree height (Fig. 1). Ohia less than 0.3 m in height were generally healthy in appearance, whereas about 70% crown dieback occurred on trees 3.6 m or taller. None of the ohia less than 0.9 m in hieght were dead, but more than 50% of the trees 3.6 m or taller were dead in the same areas of decline.

Inoculation tests.—*Phytophthora cinnamomi* in soils collected from two areas of decline infected ohia seedlings in the greenhouse. Three of 18 seedlings wilted after 2 weeks and *P. cinnamomi* was isolated from their necrotic roots. The fungus was also recovered from roots of the remaining 15 nonwilted seedlings after 4 weeks. Seedlings transferred to autoclaved soil from the same two areas, or to natural soil free of *P. cinnamomi*, remained healthy throughout the experiment and *P. cinnamomi* was not recovered. *Phytophthora cinnamomi* in soil from one area of nondeclining forest also infected all nine ohia seedlings tested. Root necrosis was evident after 4 months and *P. cinnamomi* was isolated.

Roots of all ohia trees transplanted to aa rock with root tissues from two areas of decline became infected with *P. cinnamomi*. The fungus was not recovered from roots of five trees transplanted to aa rock with root tissues from one area of nondeclining forest.

Phytophthora cinnamomi in soil collected from a decline area infected roots of ohia trees in the field. No aboveground symptoms were observed after 4 months, but extensive root necrosis was evident and *P. cinnamomi* was isolated from all roots. Roots covered with soils from two areas of healthy forest were not necrotic and *P. cinnamomi* was not isolated.

Recovery of Phytophthora cinnamomi from ohia roots.—*Phytophthora cinnamomi* was recovered from roots of declining ohia trees at 32 of the 35 decline areas sampled. Of the root pieces plated, 5% to 30% contained the fungus. *Phytophthora cinnamomi* was not isolated from roots of declining trees in the remaining three

decline areas. The fungus was also occasionally isolated from necrotic rootlets from some healthy trees in both declining and healthy forests. Seven of 28 seedlings with no aboveground symptoms of decline collected from three areas with declining ohia trees in the overstory were infected with *P. cinnamomi.*

Presence of Phytophthora cinnamomi in healthy and declining ohia forests.—Phytophthora cinnamomi was widely distributed throughout the island (Fig. 2). It was recovered from 72 of the 75 areas where ohia were declining. The three areas of decline from which *P. cinnamomi* was not recovered by soil baiting or root isolation were in the Hawaii Volcanoes National Park, the Manuka State Park, and the Kahaluu Forest Researve. Soil samples from the third location were baited and root isolations were made on six occasions during a period of 8 months with no success. Although *P. cinnamomi* was not recovered from the decline center or margin at the third location, it was recovered from soil in healthy forest 91 m away from the decline margin. The fungus was recovered from 13 or 55 areas described as healthy.

In one area (42 m^2) of decline, three permanent lines were run from the decline center out 72 m into the healthy forest. Soil samples were taken every 6 m along each line and baited with lupine. *Phytophthora cinnamomi* was present in the decline center and margin but it was also present at 9 of 29 sample points in the healthy forest (Fig. 3).

Populations of Phytophthora cinnamomi in healthy and decline areas.—At one location, there were two decline areas, 60 m apart, in a healthy forest. Soils were collected and baited at six points on a line running from healthy forest through the first area of decline, healthy forest, and the second area of decline. There was no indication that *P. cinnamomi* was present in greater numbers in the decline centers or margins than in the healthy forest (Table 1).

An additional three locations, each with a recognizable boundary between declining and healthy trees, were located and soil samples taken from the margin of decline and from 72 m out into healthy forest. With the baiting method, the dilution end point of *P. cinnamomi* was higher in the healthy forest than at the decline margin at two of the locations and was the same at the third (Table 2). With the soil dilution plate method the population of *P. cinnamomi* in soil was higher at the decline margin than in healthy forest at one location, but was about the same at the other two locations.

Effect of fertilization.—Phytophthora cinnamomi was recovered from 87% of soil samples taken from the fertilized plot, and from 63 to 100% of samples from nontreated plots. Although fertilization alleviated decline symptoms in the field (10), it did not affect subsequent infection of ohia trees by *P. cinnamomi* in greenhouse tests. The percentage of roots of fertilized and nonfertilized trees infected by *P. cinnamomi* following inoculation in the greenhouse was 16 and 14%, respectively.

Effect of fungicides.—The diameter growth of colonies of *P. cinnamomi* in petri plates was reduced by 92, 79, and 39% with 50 μg/ml of Difolatan, Dexon, and Benlate, respectively. Benlate at 50 μg/ml reduced chlamydospore germination by 92%. The three fungicides decreased infection of lupine radicles when added to soil suspensions. Difolatan was most effective, followed by Dexon and Benlate. Lupine infection by *P. cinnamomi* was prevented by Difolatan at 1 μg/ml, Dexon at 50 μg/ml, and Benlate at 100 μg/ml. Drenching ohia trees in the greenhouse with the fungicides individually or in combination prior to inoculation with *P. cinnamomi* reduced subsequent infection of ohia roots. The fungus was recovered from 27% of the roots from trees not treated with fungicides, 0.7% of the roots treated with Dexon, and from none of the roots treated with Difolatan and Benlate individually or with a combination of the three fungicides. One week after application of fungicides in the field, ohia roots treated with Benlate and Difolatan gave average inhibition zones of 41 and 15 mm in diameter, respectively. The inhibitory effect was equal to that given by 5.7 μg of Benlate and 2.3 μg of Difolatan.

TABLE 1. Assay for *Phytophthora cinnamomi* in border zones of ohia decline in Hawaii. Detection of *P. cinnamomi* in soils collected at six points on a line running from healthy forest, through the first area of decline, healthy forest, and the second area of decline

Location	Amount of soil (g)				
	100	10	1	0.1	0.01
Healthy	+[z]	+	+	+	−
Decline Center Area 1	+	+	+	+	−
Decline Margin Area 1	+	+	−	−	−
Healthy	+	+	+	+	+
Decline Margin Area 2	+	+	+	+	+
Decline Center Area 2	+	+	+	−	−

[z] + = *Phytophthora cinnamomi* detected; − = *P. cinnamomi* not detected. Determined by the lupine baiting method.

TABLE 2. Assay[y] for *Phytophthora cinnamomi* in border zones of ohia decline in Hawaii. Detection of *P. cinnamomi* in soil from the decline margin and from soil 72 m out into healthy forest at three different locations

Location	Amount of soil (g)					Colonies/g soil[z]
	100	10	1	0.1	0.01	
No. 1 Decline	+[y]	+	−	−	−	2.0[a]
Healthy	+	+	+	+	−	2.4[a]
No. 2 Decline	+	+	−	−	−	0.9[a]
Healthy	+	+	+	−	−	1.1[a]
No. 3 Decline	+	+	+	−	−	3.8[a]
Healthy	+	+	+	−	−	2.4[b]

[y] + = *P. cinnamomi* detected; − = *P. cinnamomi* not detected. Determined by the lupine baiting method.

[z] Determined by the soil-dilution-plate method. Numbers at each location followed by the same letter are not significantly different, $P = 0.01$.

TABLE 3. Response of ohia trees in the field to a nematicide and to fungicides individually and in combination, with and without the addition of complete fertilizer

Treatment	New lateral buds produced 9 weeks after treatment[x] (no. new buds per tree)	
	Location No. 1[y]	Location No. 2[z]
Control	8 a	2 a
Nemagon	5 a	5 a
Difolatan	8 a	5 a
Benlate	4 a	3 a
Dexon	6 a	3 a
Nemagon + Difolatan + Benlate + Dexon	6 a	7 a
Fertilizer only	170 bc	85 bc
Fertilizer + Nemagon	153 b	66 b
Fertilizer + Difolatan	194 cd	113 cd
Fertilizer + Benlate	196 cd	117 cd
Fertilizer + Dexon	214 d	100 bc
Fertilizer + Nemagon + Difolatan + Benlate + Dexon	221 d	121 cd

[x]Average of nine trees per treatment. Means followed by the same letter in each column are not significantly different, $P = 0.05$.
[y]Soil known to be infested with *Phytophthora cinnamomi*.
[z]*Phytophthora cinnamomi* not recovered from soil.

TABLE 4. Response of ohia trees in the field to complete fertilizer only, and to fertilizer plus fungicides individually and in combination

Treatment	New lateral buds produced 8 weeks after treatment[x] (no. new buds per tree)	
	Location No. 1[y]	Location No. 2[z]
Control	4 a	8 a
Fertilizer only	90 b	59 b
Fertilizer + Difolatan	124 bc	77 bc
Fertilizer + Benlate	190 d	79 bc
Fertilizer + Dexon	193 d	52 b
Fertilizer + combination	182 d	94 c

[x]Average of nine trees per treatment. Means followed by the same letter in each column are not significantly different, $P = 0.05$.
[y]Soil known to be infested with *Phytophthora cinnamomi*.
[z]*Phytophthora cinnamomi* not recovered from soil.

The fungicides and Nemagon were then applied at two locations in the field as a means of determining the contribution of *P. cinnamomi* to decline. Location No. 1, a decline area at 732 m elevation, was known to have *P. cinnamomi* in the soil and in ohia roots. Location No. 2, a healthy area at 1,740 m elevation, was an area from which *P. cinnamomi* had not been recovered from soil or roots. Ohia trees in the field which were not fertilized did not respond to the chemicals individually or in combination (Table 3). Fungicides applied individually increased the response to fertilization, but the differences were not significant except for Dexon at location No. 1. The combination of fungicides and the nematicide increased the response to fertilization significantly at location No. 1, but not at location No. 2.

In a second test at the same locations, Benlate and Dexon individually, and the three fungicides in combination, significantly increased the response of ohia trees to fertilization at location No. 1 (Table 4). Responses to Difolatan were not significant. At location No. 2 the combination of fungicides, but not fungicides individually, significantly increased the response.

DISCUSSION.—Alleviation of decline symptoms by fertilization indicated that ohia trees were declining because of starvation (10), but the cause of the starvation is not known. *Pythium vexans* caused rootlet necrosis of ohia trees, but its occurrence in ohia forests was not correlated with decline (12). *Phytophthora cinnamomi* caused rootlet necrosis of ohia trees in greenhouse and field tests, and the fungus was widespread in ohia forests. Our data suggest that rootlet necrosis induced by *P. cinnamomi* is associated with declining ohia forests. However, it does not appear to be the only factor involved in ohia decline. (i) The fungus was isolated from only 5 to 30% of the sampled roots on each declining ohia tree. (ii) It was recovered from 24% of the apparently healthy forest areas sampled, but was not recovered from declining trees or from soil in three areas of decline. (iii) The population of *P. cinnamomi* as measured by lupine baiting and dilution plate methods was about the same in healthy and declining forests.

Increased response of declining ohia trees to fungicides in addition to fertilizer could be due to inhibition of *P. cinnamomi*. However, a combination of fungicides increased the fertilization response of ohia trees in the area free of *P. cinnamomi* (Table 4). Therefore, the effect of fungicides could also be interpreted as the result of stimulatory action on uptake of nutrients or reduced microbial competition for nutrients.

The contribution of *P. cinnamomi* to different tree declines varies. Ohia decline may be similar to littleleaf disease in the United States (20) and New Zealand (25)

where fertilization alleviated decline symptoms, but unlike Jarrah dieback in Western Australia (19) and dieback of eucalypt species in Eastern Australia (13) where fertilization had no effect on decline severity. Where *P. cinnamomi* is associated with tree decline in Eastern Austrialia, neither Marks et al. (14) or Weste et al. (23) recovered the fungus from nondeclining areas. We isolated *P. cinnamomi* from 24% of the apparently healthy areas of ohia forest sampled.

Although *P. cinnamomi* is an injurious root pathogen on ohia trees, its behavior in different soil environments associated with ohia forests and its interaction with other stress factors require further investigation. The contributory role of environmental factors in other tree declines involving *P. cinnamomi* has been illustrated (5, 16, 17).

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