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PHYTOPHTHORA CINNAMOMI AND WET SOIL IN RELATION TO THE DYING-BACK OF AVOCADO TREES[1, 2]

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INTRODUCTION

A dying-back or decline of avocado trees has become a serious problem to growers in some parts of southern California during the last few years.[4] The trees affected are usually those that are fairly old (ten or more years of age), and the trouble may occur in isolated trees or, more commonly, in groups of trees in an orchard.

Horne (7)[5] describes this decline under the various names of melanorhiza, water injury, asphyxiation, apoplexy, and collapse, and associates it with such conditions as excess water, lack of aeration, and heavy sub- soils, not with any particular organisms.

Affected trees appear to lose vitality; they become sparsely foliated, fail to produce crops, and their branches begin to die back. Such trees have been seen occasionally growing in sandy soil where drainage conditions would appear to be good. But in many instances, when holes were dug alongside of these trees, an impervious subsoil was found about 2 feet below the surface.

The possibility that at times the decline of the trees is caused by too much water, cannot be overlooked. In one instance, a hole approximately 3 feet deep was dug in an affected orchard some 10 days after a period of continuous, fairly heavy rain in midwinter. In about 15 minutes, water began to ooze out of the sides of the hole, at a depth of about 2 feet from the surface of the ground, and to trickle to the bottom.

Roots of most of the trees examined were found to be blackened and dead, especially the fibrous roots and those up to ⅛ inch in diameter. Larger roots, ¼ to ½ inch in diameter, also, were sometimes soft, brown, and rotten and had a disagreeable odor. When the thin bark of the large roots was scraped with a knife, brown lesions ¼ to ¾ inch in size were often seen, usually at the junction of a small root which was dead. When the thin bark of healthy roots is scraped, the underlying tissue is found to be white and crisp; in affected roots this tissue is brown and soft.

A few large trees have been known to die suddenly. One such tree was a twenty-five-year-old avocado with a trunk nearly 18 inches in diameter. All the leaves of this tree withered and died suddenly during the month of September, 1939, after a period of

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[2] Paper No. 455, University of California Citrus Experiment Station, Riverside, California.
[3] Plant Pathologist, Union of South Africa Department of Agriculture. On Commonwealth Fellowship in collaboration with the Division of Plant Pathology, University of California Citrus Experiment Station, Riverside, California, September, 1939, to June, 1940.
[4] Mr. M. B. Rounds places the number of acres of avocados affected with this trouble, conservatively, at 500.
[5] Italic numbers in parentheses refer to "Literature Cited" at the end of this paper.

particularly hot weather, and many of its roots were found to be blackened and dead. The theory was advanced that the tree, which was standing in a slight depression, had, during the winter, received too much water; that many roots had consequently become infected with fungi and had died; and that, possibly, the sudden heat had caused excessive transpiration, with which the reduced root system could not cope.

FUNGI FOUND ON ROOTS OF AVOCADO

Cultures were made from 156 roots from affected avocado trees growing in seven different localities. In each case, cultures were made from fibrous roots, from small roots ⅛ inch in diameter, and from larger ones ¼ to ½ inch in diameter; cultures were also made from lesions on the , big roots. A *Phytophthora* species was found on 37 roots from six of the seven localities, *Pythium* species were found on 21 roots from all seven localities, and *Fusarium* species on most of the remaining 98 roots from all localities. The *Phytophthora* species was found generally in the lesions and on the larger-sized roots—very seldom on the fibrous roots. The *Pythium* species were usually on the fibrous and smaller-sized roots.

The *Phytophthora* species found in the cultures was identified as *Phytophthora Cinnamomi* Rands. The *Pythium* species were identified as *Pythium vexans* de Bary (on 20 roots) and *Pythium ultimum* Trow (on 1 root). Two other fungi which very frequently appeared in these cultures were *Fusarium oxysporum* Schl. and *Cylindrocarpon radicicola* Wr.[6]

PHYTOPHTHORA CINNAMOMI RANDS

This is the first record of *Phytophthora Cinnamomi* on avocados in the United States. All the cultures obtained were found to be similar. The fungus grows well on various culture media and produces a tough, wiry, aerial mycelium.

Hyphae are as much as 8 μ in diameter and covered with irregularly shaped protrusions, with numerous septations in the hyphae in older cultures. Chlamydospores occur in bunches on short stalks and are usually spherical and thin-walled. In diameter, they range from 18 to 48 μ, are commonly 42, and average 37.8 μ. Oogenia are spherical and terminal; they range from 27 to 48 μ, and average 37 μ in diameter. In color, they are golden brown. The oöspore practically fills the oögonium and is spherical and thick-walled. Antheridia are rounded, about 12 μ in diameter, and amphigynous. Sporangia are thin-walled, nonpapillate, and produced on long, thin hyphae; they vary from 30 to 80 X 20 to 45 μ in. size. In one batch of material they were commonly 40 X 25 μ; in another, 60 X 40 μ,; in a third, 75 X 45 μ. The sporangial stalk may continue to grow through and out of an empty sporangium and produce another; or, more commonly, new sporangia may develop within the old, empty sporangium. Sporangia were produced in abundance when the fungus, grown on sterilized wheat, was placed in running water. As many as 16 zoöspores were seen in a sporangium. They are actively

[6] These two fungi were identified by W. C. Snyder, Assistant Professor of Plant Pathology and Assistant Plant Pathologist in the Experiment Station.

motile on liberation and soon round off to a diameter of 10 µ.

Rands (10) in his description of this fungus gives measurements of chlamydospores as 28 to 60 µ, average 41 µ; sporangia, 25 to 100 X18 to 43 µ, average 57 X 33 µ; oöspores were not observed. Ashby (1) found that oögonia averaged 32 µ in diameter. Tucker (11) obtained oögonia 28 µ in diameter. Thus, except for larger oögonia, the description of the fungus found in the avocado cultures is very similar to other descriptions of *Phytophthora Cinnamomi.* The oögonia obtained in the present study were from 3-month-old cultures in oatmeal tubes, which had been standing in the laboratory during the winter months.

Phytophthora Cinnamomi had previously been obtained from the roots of avocado trees suffering from dieback in South Africa (14). The fungus was very similar to that described above: the chlamydospores ranged from 26 to 43 µ and were commonly 32 µ in diameter; oögonia were from 30 to 52 µ in diameter and averaged 41.4 µ; sporangia were 39 to 66 X 26 to 40 µ, commonly 50 X 32 µ.

There appears to be considerable confusion in literature with regard to the taxonomy of *Phytophthora Cinnamomi* and *P. cambivora* (Petri) Buis. The latter is responsible for the "ink disease" of chestnuts in Europe. White *(16)* and Mehrlich (8) agree that the two fungi are but strains of the same species and hence retain the prior name of *P. cambivora.* Tucker,[7] however, states that he is inclined to agree with Ashby (2) in his retention of the two species, and this view has been adopted in the present study.

Phytophthora Cinnamomi has been recorded as follows: on cinnamon *(Cinnamomum BurmanniBl.)* in Sumatra (10); on chestnut *(Castanea sativa* Mill.) in England (4); on avocado *(Persea americana* Mill.) in Puerto Rico (11) and in South Africa (13); on American chestnut *(Castanea dentata* [Marsh] Borkh.), hairy chestnut *(C. mollissima* Blume), Japanese chestnut *(C. crenata* Blume), Japanese yew *(Taxus cuspidata* Sieb, and Zuce.), Norway spruce *(Picea Abies* [L.] Karst.), red pine *(Pinus resinosa* Ait.), Scotch pine *(P. sylvestris* L.), Colorado spruce *(Piceapungens* Bngelm.), black walnut *(Juglans nigra* L.), Persian walnut (*J. regia* L.), birch *(Betula papyrifera* Marsh), oak *(Quercus borealis* Michx., *Q. montana* Willd., *Q. alba* L.), plane *(Platanus orientalis* L.), and locust *(Robinia Pseudo-Acacia* L.) in the southeastern United States (3); on rhododendrons *(Rhododendron californicum* Hook., *R. carolinianum* Eehd., *R. ponticum* L.) in the United States (16); on walnut in Australia; on heath *(Erica* sp.) in the United States and *(Erica hyemalis* Nichols, *E. nivalis* Andr., X *E. Willmorei* Knowles and Westc.) in England (9); and on sour orange *(Citrus Aurantium* L.) infected with gummosis in Brazil (5). *P. Cinnamomi* has also been reported in connection with wilt produced by inoculation in *Antirrhinum, Calceolaria, Schizanthus,* and beech *(Fagus* sp.) seedlings in England (9) ; and as causing a rot of pineapples *(Ananas sativus* Schult.) in Hawaii, Queensland, Costa Rica, Jamaica, Cuba, Haiti, and the Philippines (5). The fungus was recently isolated by W. T. Horne from lesions or cankers on the trunk of a Nabal avocado tree that was dying in San Diego County, California.

Temperature Requirements.—This fungus makes good growth over a fairly wide range of temperatures. The strain from South Africa grew well at temperatures ranging from

[7] Tucker, C. M., in letter to author dated April 27, 1940.

16° to 31° C, while that from citrus in Brazil made good growth also at 34°, the optimum for the former being 25° and for the latter, between 28° and 31° (15). The temperature requirements for the California fungus were not determined, but they are probably somewhat similar to those given above.

Soil Acidity in Relation to Phytophthora Cinnamomi.—White (16), in a study of rhododendron wilt caused by *Phytophthora Cinnamomi,* found that 60 to 100 per cent infection took place in infected soils ranging in pH value from 4.0 to 7.3. In a plot having a pH value below 4.0, only 1 plant out of 15 wilted; and in plots having a pH value above 7.3, there was 33 per cent mortality.

According to Haas (6), avocado seedlings grow better both in culture solutions and in soils having low pH values, the lowest tested being pH 4.5.

PYTHIUM SPECIES

Pythium vexans de Bary has not been previously recorded from avocado. This fungus was isolated from 20 different avocado roots from seven localities in southern California. It grows well on most culture media and has a distinctive type of growth suggestive of combed silk. The hyphal main branches are as much as 6 μ in diameter; side branches are thin (2 μ), and the tips are curly. Oögonia are spherical and terminal, usually on short side branches; commonly 18 to 22 μ they average 20 μ in diameter. Antheridia have a large surface in contact with the oogonia and are usually funnel-shaped; they usually have a fairly long branch and may arise from a hypha not directly connected to the oögonium. Sporangia are generally spherical and terminal on short stalks (occasionally intercalar) 15 to 27 μ mostly 21 μ in diameter. Zoöspores are produced very readily, the evacuation tube being usually one half to one third as long as the diameter of the sporangium. Zoöspores were 7 to 8 μ in size, and the number produced in various sporangia ranged from 7 to 12.

This description agrees very closely with that of de Bary and with that of Braun (2) for the fungus he described as *Pythium complectens* Braun, which name, according to Middleton,[8] should be discarded in favor of P. *vexans.*

Pythium vexans was found in South Africa on papaya, or pawpaw *(Carica papaya* L.) infected with foot rot, and on perennial statice, or thrift *(Armeria* sp.), infected with wilt or crown rot (14). Middleton (see footnote 8) lists this fungus from the following hosts: alfalfa *(Medicago sativa* L.), sugar cane *(Saccharum officinarum* L.), durian *(Durio zibethinus* L.), pan *(Piper betle* L.), pipri *(P. longum* L.), stock *(Mathiolaincana* [L.] B. Br.), castor bean *(Ricinus communisii.),* geranium *(Pelargonium* sp.), coleus *(Coleus* sp.), flax *(Linum usitatis- simum* L.), rocket larkspur *(Delphinium Ajacis* L.), ginger *(Zingiber officinale* Eoscoe), rubber *(Hevea brasiliensis* Muell.), carnation *(Dianthus Caryophyllus* L.), potato *(Solanum tuberosum* L.), and spinach *(Spinacea oleracea* L.). It was recently isolated on several occasions from the fibrous roots of citrus trees suffering from decline in California (15).

[8] Middleton, John T. Taxonomy of the genus *Pythium* Pringsheim. Thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy, University of Missouri, 1940. (Typewritten.) Copy on file in the Library of the University of Missouri, Columbia.

Pythium ultimum Trow was isolated from 1 root only. This is the first record of its occurrence on avocados. The fungus was typical of the species. *Pythium ultimum* is found commonly on citrus (15), but as it apparently plays little or no part in this avocado trouble, it is not discussed further in the present paper.

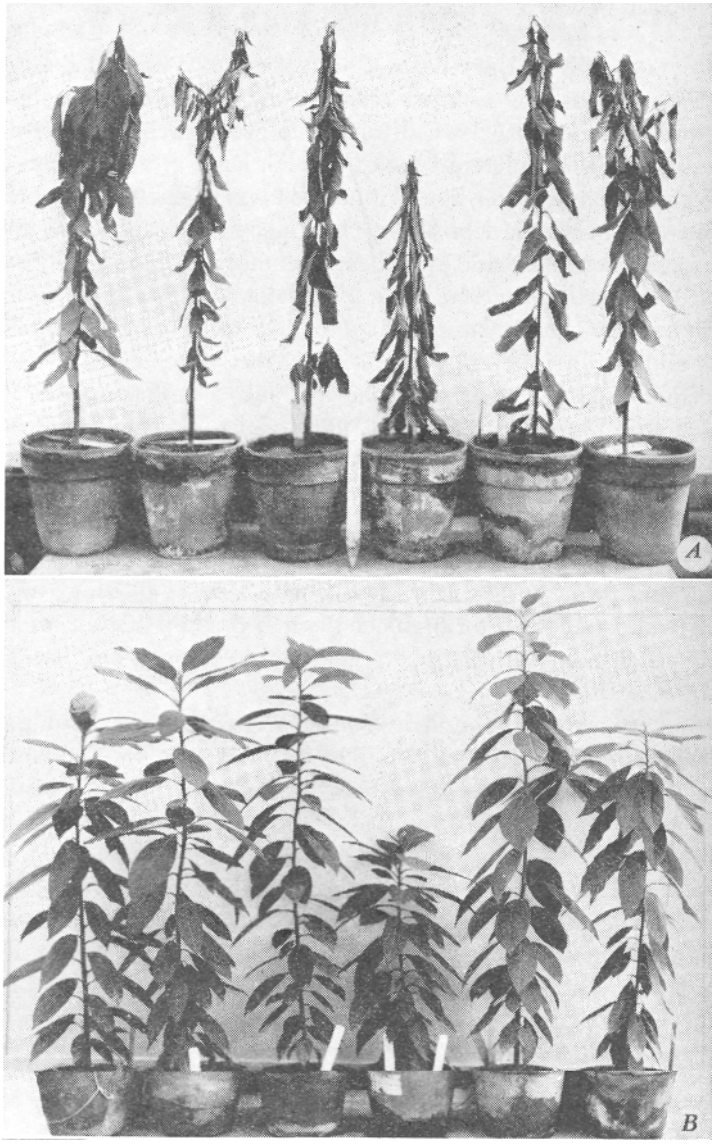

Fig. 1. *A*, *Phytophthora Cinnamomi* was added to the soil of each of these pots; a month later the 3 pots on the left were submerged for 2 days, the other 3 for 3 days. The pots were photographed 1 week later; by this time the avocado plants had wilted and died. *B*, No fungus was added to the soil in these pots; the 3 pots on the left were submerged for 3 days, the other 3 for 9 days. None of the plants subsequently showed any ill effects.

INOCULATION EXPERIMENTS

Previous inoculation experiments by the writer, in Africa, had indicated that under normal soil conditions *Phytophthora Cinnamomi* does not affect avocado plants

adversely. Tucker (see footnote 7, p. 521), also, states that avocado plants growing under healthy conditions were not affected when the fungus was added to the soil; but if the pots were allowed to stand in saucers containing 1 inch of water, the plants rapidly wilted, while uninoculated controls treated in the same manner remained healthy. A series of experiments was therefore planned with the idea of simulating possible field conditions, where, as a result of continuous heavy rains or faulty irrigation practice, the soil becomes flooded and waterlogged for a short period of time. Tests were primarily with *Phytophthora Cinnamomi,* but a few tests with *Pythium vexans* were included in experiments 1 and 2.

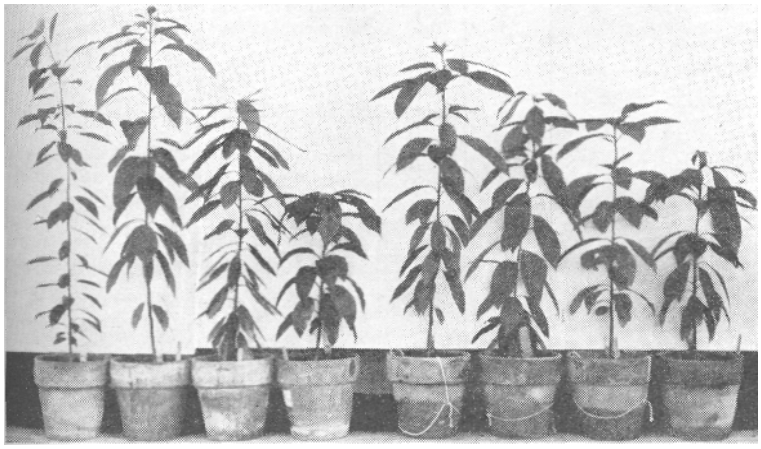

Fig. 2. *Phytophthora Cinnamomi* was added to the soil in the 4 pots on the left. Controls, on the right were untreated. Soil in all pts was watered when necessary. Six months later all avocado plants were still healthy.

Experiments 1 and 2.—For these experiments, trees two to three years old, growing in pots (Figs. 1 and 2), were used. The soil in some pots was inoculated with *Phytophthora Cinnamomi,* that in other pots was inoculated with *Pythium vexans,* and that in the control pots was untreated. The fungi were grown in tubes of sterilized wheat kernels and then introduced into a shallow hole in the top layer of the soil in the pots without injuring any roots. A month was allowed for the fungus to grow throughout the soil. Pots of each series were then immersed in larger containers of water for varying periods of time, after which the pots were lifted out of the water and allowed to drain rapidly. Results are presented in Table 1.

Experiment 3.—The soil was washed carefully from the roots of 6 avocado plants about 1 foot high. Sterilized wheat on which *Phytophthora Cinnamomi* was growing was scattered on the roots of these plants, which were then wrapped in damp paper for 2 days. Each plant was then placed in a 3-liter flask containing nutrient solution. Air was bubbled through the solution in 3 flasks, but not through that in the other 3.

Six other plants were used as controls. These plants were given the same treatment as that described in the preceding paragraph, except that there was no fungus on the wheat which was scattered on the roots.

All plants were kept in the laboratory, where temperatures reached about 23.9° C (75° F) and there was little air movement, so that transpiration was low.

Table 1. Effect on potted avocado plants of inoculation of soil and submersion of roots water for various periods of time.

Experiment no., inoculation treatment, and test no.	Plants *(number)*	Time submerged *(days)*	Results
Experiment 1:			
No fungus added to soil (controls):			
Test 1	4	0	Remained healthy; roots normal
Test 2	4	1	Remained healthy; roots normal
Test 3	4	3	Remained healthy; roots normal
Phytophthora Cinnamomi added to soil:			
Test 1	4	0	Three months later, all plants healthy; a few roots black and dead
Test 2	4	1	After 1 week, 2 plants slightly wilted (showed complete recovery after 2 months); 2 plants severely wilted and showing large number of roots blackened
Test 3	4	3	After 1 week, 2 plants dead, 2 severely wilted; roots mostly black and dead; lesions on main taproots; fungus recovered from most roots
Pythium vexans added to soil:			
Test 1	4	0	Remained healthy
Test 2	4	3	Remained healthy, except 1 plant which showed slight wilt after 1 week but recovered
Experiment 2:			
No fungus added to soil (controls):			
Test 1	4	3	Remained healthy; roots normal
Test 2	4	6	Remained healthy; roots normal
Test 3	4	9	Remained healthy; roots normal, except 1 plant which wilted and died 1 week later (*Pythium ultimum* isolated from blackened roots of this plant)
Phytophthora Cinnamomi added to soil:			
Test 1	6	2	Plants wilted after submersion; 2 plants recovered; 4 plants dead 1 week later; *Phytophthora Cinnamomi* recovered from most dead roots
Test 2	6	3	Plants wilted after submersion; all dead 1 week later
Pythium vexans added to soil:			
Test 1	4	2	Remained healthy
Test 2	4	3	Remained healthy

Table 2. Effect of inoculation with *Phytophthora Cinnamomi* on avocado plants grown in solution in flasks.

Experiment no., inoculation treatment, and test no.	Plants *(number)*	Treatment of nutrient solution	Results
Experiment 3 (in laboratory; temperature about 23.9˚C [75˚F]):			
No treatment (controls):			
Test 1	3	Aerated	All plants remained healthy, but those aerated were more robust and developed more new roots than those not aerated
Test 2	3	Nonaerated	
Phytophthora Cinnamomi:			
Test 1	3	Aerated	After 1 week, all plants showed wilt and brown roots; after 2 weeks, all plants were dead
Test 2	3	Nonaerated	
Experiment 4 (in greenhouse; temperature about 32.2˚ to 37.8˚C [90˚ to 100˚F]):			
No treatment (controls):			
Test 1	3	Aerated	All plants remained healthy, but those aerated had grown and produced more roots than those not aerated
Test 2	3	Nonaerated	
Phytophthora Cinnamomi:			
Test 1	3	Aerated	Wilted more slowly than similarly treated plants of experiment 3; dead after 3 weeks
Test 2	3	Nonaerated	

Results of these tests are presented in Table 2.

Experiment 4.—The soil was washed carefully from the roots of 12 avocado plants about 1 foot high. Bach plant was placed in a 1-liter flask containing nutrient solution, and air was bubbled through the solution in all the flasks for 1 week.

Phytophthora Cinnamomi grown on sterilized alfalfa stalks and stimulated to produce sporangia and zoöspores freely by placing in running water,[9] was inserted in the neck of each of 6 flasks; sterilized stalks with- out the fungus were placed in the other 6 flasks, which served as controls. Air was bubbled through the solution in 3 of the flasks in each series, but not through that in the other 3.

All plants were kept in the greenhouse, where temperatures reached 32.2° to 37.8° C (90° to 100° F) daily and transpiration was high.

For the results of these tests see Table 2 and Figure 3.

Conclusions.—If not overwatered, avocado plants can apparently remain in soil inoculated with *Phytophthora Cinnamomi* for at least 3 months without showing any ill effects; and when *Phytophthora Cinnamomi* was not present in the soil, the plants could be submerged for periods of 3, 6, or even 9 consecutive days without suffering any ill

[9] Method from L. J. Klotz.

effects. But if this fungus is in the soil and the roots and soil are submerged for 2 or 3 days (even 1 day is apparently sufficient), the plants are liable to attack; the roots turn black, and the plants rapidly wilt and die.

Plants in soil containing *Pythium vexans* showed no ill effects from 2 or 3 days' submersion.

Plants growing in a solution without aeration for a period of 3 weeks made little foliage or root growth, but otherwise appeared to remain normal. Those well-aerated produced new foliage and large numbers of roots. Zoöspores and mycelium of *Phytophthora Cinnamomi* added to plants growing in solution caused wilting and death, irrespective of whether the solution was aerated or not.

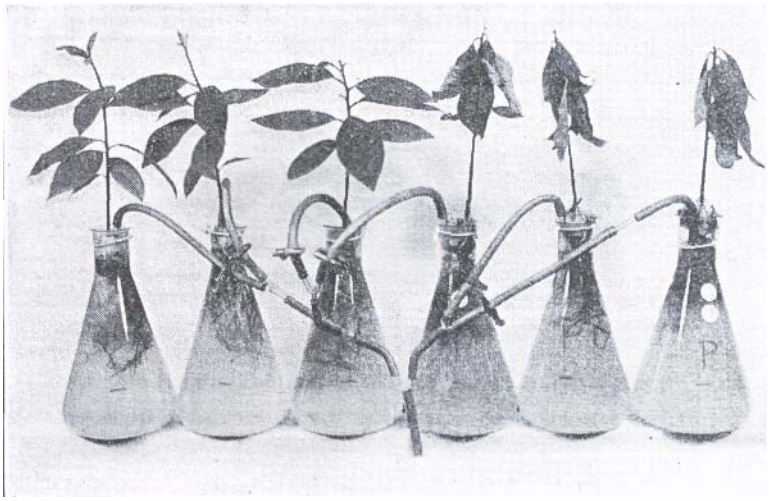

Fig. 3. Avocado plants in flasks containing nutrient solution through which air was bubbled continuously. *Phytophthora Cinnamomi* was placed in contact with the roots of the 3 plants on the right. The photograph was taken 10 days later, by which time these 3 plants had wilted and died. In a second similar series, not aerated, the results were indistinguishable from those shown here.

DISCUSSION

That avocado trees cannot stand excessive water at their roots appears to be recognized fact.[10] Dying-back, or decline, of the trees can generally be expected under such a condition, whether this is the result of faulty irrigation practice, heavy or continuous rains, a leak in a pipe line, or lack of drainage due to impervious subsoil fairly near the surface. Dying-back may occur even in sandy soils under excessively wet conditions. Many of the roots may be destroyed without apparently affecting the tree until several months later, when, with drier weather, the depleted stock of roots is unable to supply the tree adequately with nourishment, and dying-back becomes evident. The cause of the decline may then appear baffling, for at that time no sign of the excessive water conditions can be observed or would perhaps even be suspected.

The results of the present experiments may possibly throw some light on the problem.

[10] This was emphasized by Dr. J. E. Coit in a lecture to the Avocado Department of the Los Angeles Farm Bureau at Whittier, California, February, 1940.

Too much water, alone, may not be the cause of the death of the roots, for it would seem that the fungus *Phytophthora Cinnamomi* plays an important part. The results of these experiments have confirmed those of earlier tests (12, 13) and show that this fungus does not attack the roots or affect the health of plants grown in soil where drainage is good and water is not excessive. But when the roots are allowed to stand in nonmoving water for even as short a period of time as 24 hours, they become susceptible to attack by the fungus; and the longer the period, the more drastic the results. On the other hand, roots immersed for 3 days in experiment 1 and for 9 days in experiment 2, in soil in which *Phytophthora Cinnamomi* was not present, were not affected at all. In fact, Horne (7) states that the roots of 2 healthy potted plants were immersed, and only after the eighteenth day did they wilt and subsequently die.

Apparently, avocado roots can stand immersion for certain lengths of time without harmful effects, unless *Phytophthora Cinnamomi* is present, when immersion, even for a short time, will cause injury. One may speculate that, with a lack of oxygen, cell activity and normal respiratory processes may cease, accumulations of substances in the cells may take place, or the outer layer cells of the root may be weakened or killed. Under moist conditions, zoöspores of the fungus would be produced. These zoöspores might be more virulent than the fungus mycelium in attacking the roots; but this hardly seems likely, for in a heavy soil saturated with water they would probably only be able to swim about on the soil surface. It remains to be determined in what manner the fungus brings about the injury. Dead roots of the wilted plants were found to be permeated with hyphae. If unfavorable conditions are not prolonged beyond a safe limit and if no fungus is present, the vital processes which have been slowed up or stopped in the cells apparently resume normal operation when normal soil conditions are restored, without injury to the roots.

Experiments showed that *Pythium vexans* was unable to attack and harm roots immersed for as long as 3 days. It is likely, therefore, that this fungus, although found frequently in the cultures, grows in weakened or dead roots, or in those attacked by *Phytophthora Cinnamomi.*

Pythium ultimum was found on only 1 root and was disregarded in this investigation.

No tests for the pathogenicity of *Fusarium oxysporum* and *Cylindrocarpon radicicola* were carried out, but it is suspected that they would prove no more harmful than *Pythium vexans.*

SUMMARY

Dying-back, or decline, of avocados in southern California appears to be commonly associated with excessive moisture.

Roots of affected trees are frequently blackened and dead, and the larger roots may have brown lesions on them. Two fungi, *Phytophthora Cinnamomi* Rands and *Pythium vexans* de Bary, were commonly isolated from such roots.

Phytophthora Cinnamomi had previously been recorded from avocados only in South África and in Puerto Rico.

In inoculation experiments it was found that if the plants were watered normally, *Phytophthora Cinnamomi* could be present in the soil for at least 6 months without affecting them seriously. If the roots of the plants and the soil were flooded or submerged for 2 or 3 days, or for but 24 hours, however, the fungus caused injury to the roots, followed by rapid wilting and subsequent death of the plants.

Control plants, in tests where no fungus was present, could withstand such flooding for as long as 9 days without suffering any subsequent harm.

The results of tests with *Pythium vexans* indicate that this fungus does not injure the roots but probably grows only in weakened or dead roots or in those already attacked by *Phytophthora Cinnamomi.*

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