such mixtures are to be used for plant propagation (6). Other sources suggest that steam sterilization of peat mixtures used for seeding bedding plants is not beneficial and may even cause undesirable results (2,5); however, no data were provided, nor were details of the sterilization process given. Total sterilization is not necessary for the control of most plant pathogenic fungi and bacteria (1). Pasteurization of the propagating medium with aerated steam at 60°C (140°F) provides satisfactory results and eliminates all but the most resistant fungi and bacteria.

Chemical fumigation is frequently employed to eliminate pathogens from propagation media, particularly in locations where steam is not available. Satisfactory results are often achieved when label directions are carefully followed. Special attention must be given to completely eliminate all chemical residue following treatment to prevent injury of sensitive crops.

While many plant propagators have overlooked the potential of peat moss as a carrier of disease organisms in the past, more attention should be given to this possibility. Peat moss is a valuable additive for mixtures used to propagate and grow a wide variety of plants and should not be discarded. Rather, elimination of the pathogens should become a routine part of the sanitation program.

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BIOLOGICAL CONTROL OF PHYTOPHTHORA CINNAMOMI

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Abstract. Phytophthora cinnamomi root rot of avocado is biologically controlled in Queensland, Australia by intensive cover cropping and applica-

tion of chicken manure and dolomite limestone. This is now standard practice there. Root rot of pineapple in Queensland, caused by the same fungus, is now commercially controlled by a preplanting application of sulfur to lower the soil pH below 3.8 Root rot of eucalyptus in Western Australia forests, caused by P. cinnamomi has been experimentally controlled by changing the understory from highly susceptible Banksia spp. to highly resistant Acacía spp. through controlled burning. All of these successful procedures involve both biological and ecological control by mechanisms not yet fully understood, but under further investigation.

In August 1969 I gave a lecture before the Australian Nurserymen's Association in Queensland, Australia, and included my usual request for growers and others closely associated with a given crop to tell investigators of areas where the pathogen is thought to be, but the disease is not (1). One nurseryman then told me of a healthy 30-year-old avocado grove on Tamborine Mt. surrounded by groves sustaining severe losses from root rot caused by Phytophthora cinnamomi. The grower had followed an unusual cultural regimen from the beginning and had one of the most productive groves in Queensland. The next day we went there and found a beautiful grove well protected by clouds of mosquitos. Root root was essentially non-existent, but was prevalent in nearby severely diseased groves. Soil samples were collected and baited with white pineapple leaf bases. The typical fruity odor of pineapple invaded by P. cinnamomi developed, but the fungus could not be cultured until a selective medium was used that inhibited bacterial growth. The pathogen was present, but the disease on the highly susceptible crop was not. Why?

Sterile alfalfa stem baits were placed in this soil and in soil from a badly diseased grove. One inch of the stem from the soil of the diseased grove developed an average of 311 sporangia; that from the healthy grove developed only 10. Mycelial mats placed in extracts of these soils gave similar results, and there was considerable mycelial endolysis in the suppressive soil. Filtrates from suppressive and conducive soils passed through Millipore filters to remove microorganisms gave no endolysis of P. cinnamomi mats placed in them, indicating an active microbiological relationship. Dilution plates of soils showed suppressive soils to have more pseudomonad bacteria and actinomycetes than conducive soils. After treatment with aerated steam at 140°F/30 min. and reinoculation with the fungus the soil was still suppressive, but after a 212° treatment it had completely lost its suppressiveness. This was confirmed by growing susceptible jacaranda seedlings in nontreated suppressive soil and that treated at 140° and 212°F, all inoculated uniformly with P. cinnamomi. The fungus grew through 134 in. of suppressive soil treated at 212°F/30 min. and survived there for 6 weeks; there was little survival in such soil treated at 140°F/30

min. Antagonists were diminished, but survived the 140° treatment. Disease incidence paralleled the results with mycelial mats. Suppression of the pathogen by antagonists had been protecting this grove for 30 years, and the effective biocontrol apparently was due to heat-tolerant bacteria and actinomycetes (2, 3).

Thus began a study that is still continuing to clarify the many fascinating angles of this problem. I have returned to Australia three times for a total of 23 months studying it, and it has been continuously studied there by P. Broadbent in New South Wales, K.G. Pegg in Queensland, and N. Malajczuk in Western Australia. The complex story is being clarified, but the application of the biocontrol has far outstripped our understanding of the mechanisms involved. Most of the avocado growers of Queensland and New South Wales now use this socalled "Ashburner system" and the disease losses have been greatly reduced (7). The sequence of the system: New Zealand blue lupine is planted in the fall (March-April). This is disced down in spring (October-November) when in flower, and chicken manure (2 tons/acre) broadcast, plus an NPK fertilizer (1 lb. per tree). A mixture of Lablab purpureus and corn or sorghum is immediately thickly planted. This is disced in fall, and chicken manure (2 tons/acre) and NPK (1 lb. per tree) applied. Dolomite limestone is added whenever the pH falls below 6.0. Blue lupine is then planted, and so on ad infinitum. This procedure supplies a great deal of organic matter on the surface of the soil. Surface roots are never disturbed by cultivation or plowing. These cover crops are grown in place two years before a new planting of avocados is made. The organic matter is piled around the base of young trees, but not against the trunk, for the first five years. After that, fallen leaves maintain the organic matter under the trees, but organic matter (barley straw, sorghum, or Rhodes grass hay) may be added. Use of containergrown trees free of Phytophthora is emphasized in planting (3).

Old diseased groves may be pulled and started anew with the above procedure. One such orchard (Ware) has been monitored by Pegg (7) during the four years since replanting. Population of the pathogen has been below the detectable limit for the last two years, and the trees are making excellent growth. Other diseased orchards have been severely pruned and heavy applications of straw made in addition to the cover crops. Trees injured in Ashburner's grove in the extraordinarily wet year of 1974 (150" rain; 55" in 3 days) were so treated. They put out new growth that reached 6 feet in the first year and were sizeable trees in two years.

Pegg (7) has made extensive surveys in Queensland, correlating levels of exchangeable Ca with severity of root rot on a

range of crops. Almost without exception severe root rot and low Ca levels have been linked, and high Ca with slight root rot, in hundreds of samples studied. Frequently these sites are adjoining or across the road from each other. In one instance the first row of avocado trees below a vegetable field was free of root rot, but the rest of the grove was severely damaged. Calcium and fertilizer had washed into the first row of trees from the vegetable area.

Ashburner's soil is suppressive to P. cinnamomi and P. citrophthora and lyses mycelium of Pythium ultimum. Phytophthora cinnamomi disappeared from infested soil treated by the Ashburner method in the Ware grove, but has remained in detectable amounts in Ashburner's grove, although root rot control was very good in both cases. Suppressiveness may be temporarily lost when soil is waterlogged (2,3), probably because of a slight shift in balance of antagonists. Depending on the duration of submersion, it may take a month or more to recover suppressiveness. This feature of soil may also be lost by application of excessive masses of inoculum, temporarily destroying the microbial balance. The roots of volunteer avocado seedlings growing underneath completely healthy avocado trees in suppressive soil usually are mostly rotted, but seedlings growing in the tree interspaces will have little or no root decay (7). Although this has not been studied, it is probable that root exudates from shade-grown seedlings are more favorable to P. cinnamomi infection than are those from sun-grown plants. In any case, this provides a good means of fungus survival in suppressive soils.

There are at least two general means by which suppressive soils operate to decrease activity of *P. cinnamomi*. The fungus requires a stimulatory compound produced by soil bacteria to form abundant zoosporangia in soil. These bacteria occur in all soils, but may be repressed by inhibitory microorganisms, or the compound may be destroyed by them. This apparently is the dominant effect in the Ashburner suppressive soil. The inhibitors seem to be inactivated in waterlogged suppressive soil, and infection then occurs. Other antagonists may operate more directly by attacking the mycelium, chlamydospores, vesicles, or zoosporangia of the pathogen (3,4). This is clearly shown by the Ware soil, in which the fungus produces copious zoosporangia. Why then is it suppressive? Probably the germ tubes of the zoospores are attacked, preventing infection. This is shown in Table 1.

It is of interest how Ashburner first devised his system 40 years ago. He felled rainforest for his planting area. Reading that avocado was a rainforest tree in Central America, he tried to maintain rainforest conditions in his grove. He was told that

Table 1. Mechanisms of biocontrol of Phytophthora cinnamomi in avocado soils in Queensland, Australia.

		Pathogen	Sporangial Stimulators	Sporangial Inhibitors	Lytic Micro- organisms	Root Rot
SUPPRESSIVE	Moist	Sporangia sparse (Ashburner)	+	++++	+++	Slight
		Mycelium lysed (Ware)	++++	+	++++	Moderate
	Water- logged	Sporangia and mycelium moderate	+++	+	+++	Moderate to severe
CONDUCIVE		Sporangia and mycelium abundant	++++	+	- +-	Severe

this meant high organic matter on the surface, fairly high calcium, magnesium, phosphate, and nitrogen (mainly in the ammonium form), and a pH near neutrality. The trees he planted were from a nursery that supplied trees to many others who subsequently sustained heavy root-rot losses. Probably the trees were infected, or at least infested, when planted. The rest is history! Ashburner might well be called a precocious organic gardener, and the pertinence of his reasoning was exceptional.

In rainforests, nutrients are brought up from deep soils by roots and are recycled in the surface by fallen leaves. Calcium is locked up in the organic cycle, with almost none lost, but is one of the first cations to be leached from mineral soil. Thus, Queensland rainforests have 3,200-10,400 ppm exchangeable Ca, but the organic matter is lost and Ca is quickly reduced to 180-270 ppm in cultivated pineapple fields. Suppressive avocado soils range from 3,000 to 6,000 ppm (3,7). The highly conducive Western Australia Gosnell sand has only about 160 ppm. Cultivation has, in this sense, been a largely exploitive process. Nitrogen (as NH₄) and Mg are also involved in the organic cycle. With loss of organic matter and Ca, the soil becomes too acid for bacteria. Microorganisms also decline because of loss of Ca and N, and the soil rapidly becomes biologically impoverished (1,3).

It is not surprising that *P. cinnamomi* has not been recovered from "undisturbed" Queensland rainforest soils (7). It may be present in amounts too low to be detected by present methods, but more likely is present only in small pockets of most favorable sites. Several such areas have been observed in which the lowest spot has no *P. cinnamomi* susceptible plants.

Seedlings of susceptible plants start growth in drier years on the margins of the spots, but are killed in moist years. Thus, the size of the area varies directly with rainfall, and the pathogen survives at the fluctuating margins of the spot. In very wet years such sump areas overflow and spread the pathogen more widely, but a series of dry years restrict the pathogen to the original small center. Such areas are difficult to detect in rainforests, and are apt to be attributed to hog wallows or disturbance by man when they are observed. In such situations the fungus is maintained in balance with the vegetation, the environment, and associated microbiota, and disease expression is rare (3). There is no basis in fact for the assumption that absence of root rot means absence of *P. cinnamomi*.

The possible ways this rainforest ecology suppresses activity of P. cinnamomi may be enumerated.

- 1) High organic matter, Ca, and N stimulate antagonistic microorganisms. The soil is biologically very active.
- 2) Soil pH of 6.0-7.0 is favorable for bacteria.
- 3) High organic matter and Ca improve soil structure and drainage.
- 4) High Ca possibly may affect host resistance.
- 5) Healthy plants remove much water from soil and decrease waterlogging.

The ability of suppressive rainforest soil to control P. cinnamomi is impressive. One severely damaged avocado grove was located just above a remnant of rainforest similar to that which had been removed to plant the orchard. Although the fungus has been washed into the rainforest from the grove for many years, it could not be recovered from soil in the rainforest.

PINEAPPLE

Pineapple becomes chlorotic if lime is added to soil, and the Ashburner method, therefore, cannot be used to control P. cinnamomi in this crop. Pegg (7) tried soil acidification in Queensland by applying elemental sulfur to the soil surface and discing it in to a 6-inch depth. In some soils Thiobacillus thiooxidans had to be added with the sulfur. When the pH was lowered to 3.7, P. cinnamomi root and heart rot were controlled. The method is now widely used by Queensland pineapple growers. The low pH of the soil greatly reduces zoospore production and release, increases cation concentration which reduces disease incidence, causes nitrogen to be in the disease-reducing ammonium form, and favors the antagonist, Trichoderma viride, and its antibiotic gliotoxin.

FOREST SOILS, WESTERN AUSTRALIA

The valuable timber tree, jarrah (Eucalyptus marginata), is susceptible to P. cinnamomi; marri (E. calophylla) is more resistant but of less value. In moderately suppressive loam soil both are resistant, but in the prevalent conducive lateritic soil jarrah is quickly killed and marri remains. When suppressive soil is sterilized, both species are susceptible because the suppressive microflora is destroyed, but if a small quantity of nontreated soil is added, suppressiveness is restored. Extracts from the rhizosphere of either species in suppressive soil lyses mycelium and decreases sporangium formation, but in conducive soil lysis and inhibition of sporangia occur only in extract from marri rhizosphere. Rhizosphere microflora from suppressive soil protected both species; that from conducive soil protected marri but not jarrah. Since mycorrhizae are poorer in suppressive than in conducive soil, they are not likely involved in resistance (5,6). Actinomycetes and bacteria are active agents in the rhizosphere. (3,4,5,6)

A shift from the highly susceptible Banksia spp. understory to resistant Acacia spp. gives good control of P. cinnamomi. High-intensity burning brings this about by inducing Acacia seed germination and causing litter accumulation, but low-intensity burning favors Banksia and decreases litter. Phytophthora cinnamomi population is depressed when jarrah is grown in pots with Acacia. Sporangial formation is inhibited in extracts from soil where Acacia is growing, apparently due to antagonistic bacteria in Acacia rhizosphere. There may be injury to eucalyptus from high-intensity burn, so they may have to use low-intensity burn and heat-treated acacia seed. (8)

Eucalyptus dieback occurs in Western Australia, Victoria, and Queensland, always on infertile soil low in humus, and microbiologically poor.

Suppression lies in the organic fraction. Surface litter is conducive at the top but becomes more and more suppressive as it decomposes. The most suppressive area is the zone of interface of mineral soil and organic matter; it declines in both directions from that zone (Broadbent and Baker, unpublished). That generally is the zone of feeder roots. This led to the idea of transferring suppressive microflora to the nursery mixes. Since we could not do it by transferring soil, we tried the organic fraction. Decomposed mushroom compost was tried as recipient, as it is somewhat similar to the organic matter from the Ashburner system. We transferred suppressive microflora from decomposed organic fraction to mushroom compost treated at 140° or 212°F/30 min. Suppressive microflora from organic matter extract was transferred to a *P. cinnamomi* mycelial mat and

then the mat to mushroom soil treated at 212°F/30 min.

The hope is to develop a suppressive nursery mix so that the transplants will carry the suppressive microflora to the field. This must be combined with use of cover crops to supply abundant organic matter, and maintenance of high Ca and NH₄ nitrogen in the field.

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ROOT WEEVILS: FROM CUTTINGS TO LANDSCAPE

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I want to stress the importance of knowing which root weevil is causing problems, because the steps to take to alleviate the situation vary, depending on the species of weevil involved and the stage of development of the plant. Many nurserymen and some trade journal articles discuss the "strawberry root weevil" Otiorynchus ovatus as if that were the problem. In fact, I have never seen it seriously injuring, or even commonly associated with, woody plants.

There are many, perhaps a hundred, "root weevils", larvae