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Origin and Distribution of *Phytophthora cinnamomi*

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In the 1976-77 Yearbook (3), I presented some information on the possible geographic origin of the cosmopolitan plant pathogen, - *Phytophthora cinnamomi,* well known in California as the cause of avocado root rot. Theories, at least partially justified, on the native origin of this fungus and information on its spread to all of the countries where it is presently distributed provide a fascinating and significant story. This paper updates some of this information and provides data on the distribution of the fungus around the world.

Phytophthora cinnamomi is of course known in California primarily because of the great damage it causes to avocado trees. Since its discovery in Sumatra on cinnamon trees in 1922 by Rands, it has spread to or been found in over 70 countries all over the world, attacking over 1000 plants, ranging from acacia through great numbers of primarily woody plants, including chestnut, pineapple, eucalyptus (over 100 species), several species of pine, many ornamental plants including azalea, camellia, rhododendron, and various conifers; many native plants in Australia and in South Africa; cinnamon, cinchona (quinine tree), oak, sycamore, pear, peach, grape, walnut, larch, spruce, and ceanothus,

P. cinnamomi was first described from avocado roots in southern California in 1942 by Wager. The first description of *P. cinnamomi* in the United States was in 1930, on rhododendron in New Jersey. There had been reports, however, of a severe root disease of chestnut in the 18th century in southern U.S.; what is possibly the same disease was found in the 1930's to be caused by *P. cinnamomi.*

Information on the possible origin of a plant pathogenic fungus such as *P. cinnamomi* is significant for two reasons: (1) If the fungus is not a native soil inhabitant in the area in question (for example, southern California), exclusion of the fungus from new plantings by all possible means; i.e., clean nursery stock, prevention of soil and water movement from infested areas, and other precautions, becomes highly significant; and (2) if a fungus and its host plant are both native to the same area, this would be an ideal place to look for resistance to the fungus. Plants that survive for long periods in the presence of the pathogen are more likely to have developed resistance than plants not co-existing with the fungus. This has proven true with fungi such as the chestnut blight fungus (*Endothia parasitica*); both the tree and the pathogen have centers of origin in China and resistant chestnut trees have developed there.

What kind of a fungus is *P. cinnamomi*? From temperature data, it is a fungus that grows best in mild temperate or subtropical regions. It does not grow or survive at low soil temperatures (below 6°C) or at high soil temperatures (above 34-36°C). Optimum

temperatures are in the range of 21-27°C. The pathogen does not survive well or spread rapidly under low soil moisture conditions, which is evidence against its origin in the drier areas of the world such as southern California where severe disease now occurs under irrigation. Periods of abundant soil moisture promote production of sporangia, release of zoospores, and invasion of host roots. *P. cinnamomi* does not develop, however, under conditions of continuously saturated soil with consequent low oxygen concentrations. It produces disease most rapidly under soil conditions of somewhat acid to neutral pH.

Where in the world do we find areas with such environmental conditions? The moist subtropics seem to provide the best possibilities; this includes many areas in the Americas from Mexico to Peru and Brazil, with possibilities in the higher elevations in the tropical part of that large region. Other likely areas are northeastern Australia and areas with moderate elevation in Papua New Guinea, the Malaysian archipelago, Taiwan, and the southern part of South Africa.

Dr. Rands, who originally isolated and described *P. cinnamomi* from cinnamon trees in Sumatra, mentioned a possible area of origin in that country, stating that "The causal fungus (*P. cinnamomi*) is believed to have come into the plantings along with its natural host (cinnamon) which is indigenous to the region. Further explorations still should be made in that area.

Data available in 1977 (3) indicated the possibility of an origin of *P. cinnamomi* in a large area extending from northeastern Australia through New Guinea, Sumatra, and Malysia. Other references have merely indicated an "Asian" origin.

Shepherd, in Australia, proposed that the fungus entered northern Australia with "Indo-Malaysian floristic elements during Pleistocene-Holicene times (millions of years ago) from a center of origin in the New Guinea-Celebes region." Other researchers in New Zealand and Australia (Newhook and Podger) proposed that *P. cinnamomi* came into Australia probably no earlier than the late 18th century; the evidence does not seem very convincing in this regard. Both mating types of *P. cinnamomi* are found in eastern Australia, another indication that that region may be included in the center of origin of the fungus. There are also indications in eastern and northeastern Australia of native trees and shrubs showing some resistance to the pathogen.

Recent information since 1977 indicates that the origin may include Taiwan. Dr. Ko from Hawaii and coworkers in Taiwan (1) have data pointing to Taiwan as within the center of origin of the fungus. They isolated *P. cinnamomi* from healthy, natural forest in the central region of Taiwan; and also found the two mating types of the fungus in almost equal ratio in samples from that area—typical of the situation in centers of origin.

Recent information also points to another very different region as another possible center of origin. Pathologist, Dr. von Broembsen in South Africa (2), has presented evidence that *P. cinnamomi* may be indigenous to the South Western Cape Province. She isolated the fungus from many native plants in undisturbed locations and also from rivers flowing from remote mountain areas. The fungus was found there on native plants that did not show symptoms — evidence of resistant plants in that region.

We have additional data here at Riverside, from many root and soil samples taken since

the original article in 1977, indicating that *P. cinnamomi* is not an indigenous fungus in the Americas. These samples are from native avocado trees and avocado relatives in Central America, and also from additional samples taken from the United States. These include native forest trees (redwood, pine, Monterey cypress, and Douglas fir) primarily along the California coast and in Oregon and Washington. Efforts were made to collect root and soil samples primarily from moist areas where *P. cinnamomi,* if present, would have the best possibility for survival and chances would be better for isolation. Cultures were made from roots, using media selective for *Phytophthora,* and in some cases samples were trapped with *Persea indica* seedlings (a plant very susceptible to *P. cinnamomi*).

Phytophthora cinnamomi was not recovered from any of the samples from forest trees, native avocados, or avocado relatives mentioned. This confirms the earlier data, reported in 1977, that involved over 300 samples from southern California and nearly 400 samples from 17 countries in Latin America.

These data on occurrence of *P. cinnamomi* in native vegetation (in Taiwan and South Africa, for example) in quite widely spread regions raise the question as to when fungi such as this evolved. Were they in existence at the time of continental drift? According to some plant scientists, the last possible time for direct migration between West Gondwanaland (including Africa and South America) and Australia was approximately 100±10 million years ago. Could some movement of *P. cinnamomi* from Africa to the Australasian area, or the reverse, have occurred while the land bridge was still intact?

Distribution

How can a fungus such as *P. cinnamomi* have been moved from any possible centers of origin to many countries around the world? This pathogen can be moved to new areas by any means by which moist soil is moved, including movement of nursery stock or other types of plant material carrying soil, by soil transported on cultivation equipment, logging equipment, shoes or boots, hooves of animals. Movement can also occur by means of water moving across infested soil, down drainage areas, etc.

In the huge disease area in the forests of Western Australia, there is good evidence of movement of *P. cinnamomi* in various types of nursery stock from eastern Australia into small forest communities in the forest, then spread of the fungus into the forest by water, cultivation or logging equipment, or other means of man's activities. Tremendous devastation has been caused in the Western Australian forests, with several hundred thousand acres now affected, and *P. cinnamomi* not only killing the jarran eucalyptus (*Eucalyptus marginata*), but also attacking over 75 other types of native trees, shrubs, and annual flowers.

In Hawaii, the fungus was isolated from streams carrying run-off water from ohia forests. In California, we have similar evidence of spread of the pathogen along drainage channels within avocado groves and in arroyos where drainage from avocado groves carries the fungus downhill to uninfested areas. The movement of the pathogen in mountain streams in South Africa was already noted above.

It has been proposed by two forest pathologists, Dr. Crandall and Dr. Gravatt, that *P.*

cinnamomi was introduced into southern ports in the United States in the 18th century on plant material carried by ships from Asia. They suggest the fungus was carried with plant material throughout the Pacific Islands on various trade routes and similarly to Africa, Europe, and various ports in the Americas. Two other pathologists (Drs. Campbell and Hendrix) suggested that perhaps the fungus is native to the Southeastern U.S., as they found it in some fairly remote forests in several states (including especially Tennessee, Alabama, and Georgia). They did not present conclusive evidence; and it is definitely possible that the fungus could have been transported to those areas over the past 200 years by the activities of man, or by animals, or water movement. The fungus may have been introduced into Mexico, some of the other Latin American countries, and possibly Hawaii in voyages by early Spanish and other explorers from the southern Asian, South Pacific, and Australian areas.

The fungus could have come to Hawaii with some of the plant materials brought by the early Polynesian explorers and settlers. Some of these early colonizers of the Hawaiian Islands came from the Marquesas Islands from 500 to 700 A.D. They came in huge double-hulled voyaging canoes, carrying people and plants and animals to use in their new home. Seedling plants with soil were carried—bananas, coconuts, yams, taro, sweet potato, breadfruit, for example.

P. cinnamomi was probably imported into California from tropical America, Hawaii, or Australia in the late 19th century, with importations of avocado or other subtropical or tropical plants. In the early days of the avocado industry, avocado seeds (which can carry the fungus if fruit has fallen on infested soil) or seedling plants were readily imported into California, from Mexico, Central America, and also from Hawaii and the Pacific before quarantine regulations were established. *P. cinnamomi* is quite common on cultivated avocado in Mexico, Honduras, El Salvador, Costa Rica, Trinidad, Colombia, Venezuela, Brazil, Peru, Chile, and Argentina, and is also found in Cuba, Haiti, Puerto Rico, and St. Croix. Once established in a planting and especially in a nursery, *P. cinnamomi* could have been spread to new plantings in much of southern California. Thirty or forty years ago, we isolated the fungus from several avocado as well as ornamental nurseries. This still occurs occasionally, unfortunately.

Movement of plants from one part of the world to another, and of wild plants into cultivation, was an ancient practice. There is evidence of voyages across the Pacific that could carry plants beginning as early as 2500 B.C.

In Mexico or other countries in Latin America, for example, could *P. cinnamomi* have been introduced into some nursery or home planting on tropical plants from Southeast Asia or Australia or Hawaii, and then become spread to avocado nurseries and avocado plantings? Could the infestation possibly have come from southern California after the fungus was introduced here from Hawaii or Australia? This seems unlikely with the much longer cultivation of plants in Mexico and Central America as compared to California.

Regardless of how the fungus was dispersed, the fact is that *P. cinnamomi* is found in nearly 70 countries around the world, including the following:

Europe—Azores, Belgium, Canary Islands, France, Germany, Great Britain, Greece, Irish Rep., Italy, Netherlands, Portugal, Spain, Switzerland, USSR, Yugoslavia.

Middle East—Israel.

Africa—Cameroon, Congo (Popular Republic), Guinea, Ivory Coast, Kenya, Malagasy Rep., Morocco, Rhodesia, So. Africa, Uganda, Zaire Rep., Zambia.

Central and South America, West Indies—Argentina, Barbados, Belize, Bolivia, Brazil, Chile, Colombia, Costa Rica, Cuba, Dominican Rep., Guatemala, Guyana, Haiti, Honduras, Jamaica, Panama, Peru, Puerto Rico, St. Croix, St. Lucia, St. Vincent, Salvador, Trinidad, Venezuela.

North America—Canada, Mexico, United States (Alabama, Arizona, Arkansas, California, Delaware, Florida, Georgia, Indiana, Kentucky, Louisiana, Maryland, Mississippi, Missouri, New Jersey, New York, North Carolina, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, Tennessee, Texas, Virginia, Washington).

Asia, Australasia, Oceania—Australia (ACT, New South Wales, Queensland, South Australia, Tasmania, Victoria, Western Australia), Caroline Islands, Cook Islands, Fiji, Hawaii, India, Indonesia (Java, Sumatra), Malaysia (Malaya, Sabah), New Zealand, Okinawa, Papua New Guinea, Philippines, Taiwan, Turkey, Vietnam.

The A_2 mating or compatibility type is the common type around the world, with the A_1 found in only six countries: Australia, Malagasay Republic (Madagascar), Papua New Guinea, South Africa, Taiwan, and the United States.

In conclusion, it is extremely likely that *P. cinnamomi* is another example of a destructive fungus being introduced into the United States from other countries. Other examples include the fungi causing the Dutch elm disease, white pine blister, rust, and chestnut blight. The list of countries invaded by *Phytophthora cinnamomi* is gradually increasing.

Literature Cited

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