THE DISTRIBUTION OF PHYTOPHTHORA CINNAMOMI

by

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Part II - GEOGRAPHICAL DISTRIBUTION

Early History

Every story must have a beginning, a "once upon a time", and for *Phytophthora cinnamomi* we must make some educated guesses. It has not been reported on any host from China, Korea, Japan, Vietnam, Laos, Cambodia or Thailand. Plants from these areas have been widely introduced to Europe and America. Where data is available they have been found to be mostly resistant or immune, under ordinary conditions, to attack by the cinnamon fungus. Closely related, and in many cases susceptible species of the same genus, are found in these areas, however. So, along with a number of other important parasites of our native plants, we can perhaps be safe in the assumption that it is in Asia that *Phytophihora cinnamomi* had its origin.

Immediately to the south *P. cinnamomi* is found well distributed in Indonesia. From here it takes little imagination to picture the early distribution by the Spanish, Portuguese, French and English from the East Indies to the West Indies and to African, European and American ports as well. Europe, emerging from the "dark ages", was hungry for spices to season the stale and often putrid food available to a world without refrigeration. Cinnamon and camphor were among early introductions from east to west and the avocado, another of the 39 genera in the *Lauraceae*, from west to east. Ships often lay over on both the Ivory Coast and in South Africa. These stops were of comparatively long duration, plant introductions were set out and gardens grown while ships refitted and restocked for the long jump east or west. The introductions to Africa can well come from this source.

It has not been possible to find any accurately reported dates for the African introductions but they were probably early, in either the XV or XVI century. In contrast the introductions to India, Australia, New Zealand, and the Pacific islands appear to be much later and are probably secondary in origin. *P. cinnamomi* must, of necessity, have moved in soil or plant tissue. The role of soil and plants as such a vehicle and the history of plant introductions can be followed in many references (145, 146, 152, 198). The February 1967 issue of Phytopathology (57:100) carries abstracts by McCain and by Mircetich & Zentmyer discussing spore forms of the fungus involved in such spread.

Negative evidence can be of value and in the case of the loss of the chestnut, *Castanea dentata* in America and *C. sativa* in Europe, we have hosts of such economic importance that we can assume their loss would have been noted by competent observers. The chestnut root rot or ink disease was first noted in the late 19th century. A considerable volume of literature was published in Europe long before the causal parasite was known. In America, however, the introduction of chestnut blight (*Endothia parasitica*) at that time caused it to be neglected until 1930. It was apparent that what was being observed was a disease that had first appeared at least 100 years earlier. At this time some support was given the project by agencies of the United States government which came into being during the depression. Among them the Civil Works Administration, Public Works Administration, Works Progress Administration and Civilian Conservation Corps gave assistance in searching the literature for early reports of the loss of the chestnut and other possible hosts. No early references were found. We can, however, bracket the dates of the introductions rather closely.

In North America the Spanish governor of Florida discussed the chestnut in a letter in 1600 without mention of any disease so we can assume the tree was still thriving in the Florida parishes of Alabama and Mississippi at that time (172). As late as 1773 Bartram (35), a trained botanist, made an extensive collecting trip through areas in the southeastern United States. He kept a very detailed record of the trip and made many references to stands of chestnut without mention of any dead or dying stands of trees. He collected the *Gordonia* in Georgia. In 1824 Jones (151) published a note on the loss of trees and shrubs and many years later Hunter (147) discussed the disappearance of the *Gordonia*. A closely related species, *Stewartia*, has been reported to the authors since Part I was released, to be susceptible in North Carolina. The authors published a note on the chestnut root rot in 1945 (74) in which they threorized on the probable dates of the recession of the chestnut. Subsequently, as more information became available on what was described as a "death wave" by various reporters who observed it in its later phases (33, 35, 52, 68, 131, 147, 151, 172, 180, 186, 194, 243, 244, 253) it became apparent that its movement from the coastal plain into the Piedmont plateau had occurred somewhat earlier than the mid 19th century as first thought.

One of the best eye-witness accounts, by a trained observer, is quoted by Rumbold (253). Prof. Eugene Hilgard of Berkely, California stated that while surveying in 1856 in northeastern Mississippi, he found the chestnut trees of that region, both young and old, dead. They had been growing in a mixed forest of pine and oak and as the other trees were in a healthy condition, were very noticable. The dead trees were frequently of large proportions, attaining a height of 80 to 90 feet. When he saw them, these trees were beginning to decay; the bark was dropping off, leaving the trunks bare. The authors saw dead chestnut in 1935 which was known to have died 80 years earlier. This was quite recognizable but had rotted off and fallen to the ground.

The loss of the chestnut would thus seem to have been well under way in the southeastern part of the United States by 1830 and the spread much more rapid than first thought. The introduction of *P. cinnamomi* must then have occurred prior to the 50 year period 1780-1830 in order to have so thoroughly covered an area extending more than 1000 miles in every direction from the probable points of entry at Savannah or Mobile. Eye-witness accounts of dying chestnut are available from southern Mississippi, through the midpart of North and South Carolina into southern Virginia dated around 1850.

Not all chestnut in an area was killed when the disease reached a given point. Isolated valleys, higher and drier sites escaped, often for a half century or longer. The range of chestnut in North America, in the area subject to root rot, extended west to the Mississippi River; south almost to the Gulf of Mexico, and well into southern Alabama, Mississippi, and West Florida; eastward out into the coastal plain; and north to Maryland and Tennessee.

Populations of the closely related and susceptible chinquapins extended the area westward to Texas, Arkansas and Oklahoma; southward to the Gulf and mid-Florida; and eastward to the Atlantic Ocean.

Just why the "recession", well documented as it was, escaped general notice of both the public and agricultural technicians is anyone's guess. A great economic resources was almost gone before the technicians surveying chestnut blight "discovered" it-more than 100 years after the epiphitotic occurred in the chestnut stands along the fall line of the Piedemont from Mississippi to Maryland. The high, dry hills and mountains of the Piedmont slowed but did not stop the Phytophthora. So thoroughly was the earlier loss forgotten that forsters even believed the remnants of chestnut stands seen in Alabama and Mississippi represented a species receding as a result of the Wisconsin glacial recessión (302). A similar recessión was studied in the Ozark chinguapin, where on a miniature scale in Arkansas, Missouri, and Oklahoma, a tree once mistaken for the chestnut, in less than 50 years became known as a species of small bushy stature on the high, dry Ozark ridges. The range of the chestnut overlapped the American chinquapins, many only small bush types, but several such as *C. alabamensis, C. margaretta, C. arcuata, and C. floridana, C. pumila* fine trees in their own right. These passed from the scene along with the chestnut.

In reviewing the literature on the chestnut recession in America and the much more abundant European material, a similarity becomes apparent. Awareness of the problem as a disease showed up in the late 19th and early 20th century. The writers placed most of the earliest outbreaks in the mid 19th century. As these reports are analyzed we find that the limitation is the life span of a man. The disease was remembered on the edge of the Piedmont in America and in the highlands of Europa. We can only guess how long it had actually been there.

The situation in Europe appears to have been similar to that in North America. The basic difference is one of topography. In Europe the spread was up the valleys of the principal rivers from entry points at the great, historic ports at their mouths. The subsequent and later spread was similiar to that in the United States as the fungus moved up the valley sides into higher and drier land. Piccioli (219) made an intensive early study of the chestnut

and concluded that there was no evidence of introductions earlier than 1726 in Spain or 1772 in France. The introductions in Spain were apparently at Cadez and Barcelona and those in France at Marseille (81, 82, 83, 123, 157, 219). The earliest date established for Portugal at Lisboa was around 1838 (122, 206) and for Italy at Genoa in 1842 (25, 48, 49, 122). The disease in England is of such early origin as to be thought endemic (96). In effect, the European introductions occurred at about the same time as those in North America.

The range of chestnut in Europe, in addition to France, Spain, Portugal and Italy included Switzerland, Austria, Netherlands, Germany, the Balkans, Greece, Asia Minor, Armenia, Persia and the Caucas.

Introductions in South and Central America and the Caribbean

No good early record for any of these areas has been found even though an extensive search of the literature, much of it in the areas, has been made. It is probably not just coincidence, however, that areas where the fungus is known today are near the great port cities of Habana, Veracruz, the Gulf of Fonseca, Lima, Valparaiso, and Rio de Janeiro. Bazan (37) believes that there were very early introductions in Peru as there are fragmentary accounts of the loss of large areas of avocados, *Persea americana*. The disease is known to cause sporadic losses wherever avocado is found and both the authors and Bazan witnessed epiphytotics in isolated Peruvian valleys. Probably the avocado was the vehicle for introducing the parasite to the west coast of North America. Ruiz, Pavon and Dombey, the Spanish and French botanists, visited Peru and Chile in 1778 (the diary of the trip was only published in 1931 in Madrid) and collected extensively, especially the *Cinchonas*. These genera of the *Rubiaceae* were subsequently found infected and dying by one of the authors in the very areas where Ruiz and Pavon originally collected them.

Subsequently and more recently, the movement of *Cinchona* and *Persea* spp. and *Ananas comosus* hither and you around the world has resulted in a spread of *P. cinnamomi* to almost everywhere that the climate is favorable or suitable for the organism to grow. In some areas, as in Australia, extensive native populations have been found susceptible. In others, New Zealand for instance, susceptible populations have been introduced.

Taxonomy

The species *Phytophthora cinnamomi* Rands, principal subject of the present publication, was described in 1922 by Dr. Rands as a stripe canker of cinnamon in Sumatra. Dr. Rands believed in not using specific names for fungi but believed in this case that an organism from a tropical host on a mountain top in Sumatra was unlikely to be heard of again. His species is found on all the continents of the world.

The species *Phytophthora cambivora* (Petri) Buisman was described in 1917 by Petri, originally under the generic name *Blepharospora*, from chestnut in Europe and must be considered here because of the confusion between it and the preceeding.

It is no part of the present work to question validity of species. However, to view the activities of *P. cinnamomi* in proper perspective it must be recognized that there is and has been confusion. In fact Petri, who described *P. cambivora* in the first place, seems to have worked with both species without knowing it and in one case actually figured *P. cinnamomi*. We should recognize the possibility that the description of *P. cambivora* is so idealistic for the genus —remember that this is the first of the group described— that some of the later reports from the United States, India and Mauritus may well be members of the genus and group that fit the description but perhaps are not the same thing as Petri's original *P. cambivora*.

Without trying to start a taxonomic argument the authors suggest that since Petri described *P. cambivora* we have a selection that is truly a species and that it has shown up on the other hosts. It fits the original description but by the same reasoning most of the ink disease in Europe is caused by *P. cinnamomi*. Or perhaps, if the original description had been amplified enough it would fit *P. cinnamomi*. But since the species *P. cambivora* can be recognized today as can *P. cinnamomi* it is suggested that the two names both be continued as valid species. It is further suggested that *P. cambivora* be considered as the cause of some of the ink disease of chestnut in Europe, of the maple disease (115, 136, 144, 223, 224), and the live oak disease (181, 182) in America, and probably the disease of Casuarina in Mauritus (197); but that the great bulk of the disease reports of ink disease on chestnut and walnut in Europe and the other reports listed in Part I are caused by *P. cinnamomi*.

In addition to the authors, who received and saw cultures of *P. cinnamomi* under the name of *P. cambivora*, both Petri (214) and Dufrenoy (107, 108) appearance of the *Gordonia*.. A closely related species, *Stewartia*, has been quite evidently worked with both species without realizing it. Faucett (114) and Urquijo (287, 288) both received cultures of *P. cinnamomi* under the name of *P. cambivora*. In the case of Faucett his came direct from Petri. Pimentel (221,222) also appears to have received mis-named isolates. The authors saw the *P. cambivora* isolates from maple and considered them validly that species at a time when the name was often used synonymously with *P. cinnamomi*. Moreau (187) now accepts *P. cinnamomi* as the causal agent of most of the ink disease in France.

Considerable variation in degree of pathogenicity exists within species. Manning & Crossan (169, and in a publication received too late to include in the bibliography —Plant Disease Reporter 50:647-649) reported considerable differences. An intensive survey of forest nursery parasites was made in 1922 (240) without *P. cinnamomi* being recorded but 10 years later it was a major problem of nursery stock. Recent work by Haasis and others indicates that hybridization between *P. cinnamomi* and closely related species can occur. Zentmeyer and his co-workers have shown the compatability that exists between species. Leonian, one of the early students of the genus, felt that there were only a few real species and in discussing the two species here under discussion with the authors wanted to lump them together. This we opposed for several reasons not the least of which was the loss of the name *P. cinnamomi*, by then in world-wide use.

The following general references cover the taxonomic work on the two species. 25, 31, 43, 79, 101, 103, 107, 108, 114, 115, 116, 119, 120, 133, 159, 160, 161, 162, 187, 209, 239, 240, 248, 270, 281, 282, 287, 288, 296.

Reference Distribution by Area

North America 2, 18, 20, 21, 45, 53, 54-62, 67, 71, 72-74, 87-88, 93, 124, 126-127, 129-130, 137, 140, 141, 145, 148, 149, 153, 154, 156, 158, 171, 177, 178, 179, 180, 183-185, 202, 225, 226, 230, 235, 249-251, 252, 254, 259, 266, 267, 271, 275, 276, 277, 278, 279, 283, 294, 297, 298-299, 303-316; and since publication of Part I Roth & Kuhlman, Jour. of Forestry 64:829: for a discussion of soil temperature and moisture.

Central America, Mexico, and Caribbean 23, 28, 50, 66, 91-92, 190-191, 265, 280, 306, 307, 310.

South America 24, 26, 36-39, 75-78, 80, 99, 114, 117-118, 132, 170, 189, 229, 311.

Europe, Near East, and north Africa 1, 3-7, 17, 19, 22, 25, 27, 34, 40-41, 42, 44, 51, 63, 64, 69, 70, 84-85, 89, 94-97, 98, 102-110, 111, 112, 113, 114, 117, 121, 125, 128, 129, 139, 146, 150, 155, 157, 167, 168, 169, 176, 187, 192, 193, 200-201, 203-204, 205, 206, 207-218, 219, 220-222, 227, 231, 232, 233, 234, 244, 246, 247, 255, 256, 257, 260, 268, 270, 284, 285-288, 290, 291, 292-293, 300.

Africa 65, 86, 100, 165-166, 197, 295.

India 136, 236, 237, 238, 289.

Indonesia 239, 258, 269, 272-274, 289.

Hawaii and Tahati 29-31, 135, 142-143, 164, 173-175, 261-263.

Australia and New Zealand 8-16, 46-47, 163, 188, 195-196, 199, 228, 241-242, 264, Additional data on this area and Truk, Panape Saipan and Guam see Zetmyer in the Yearbook of the California Avocado Society 49: 19-25. 1965.

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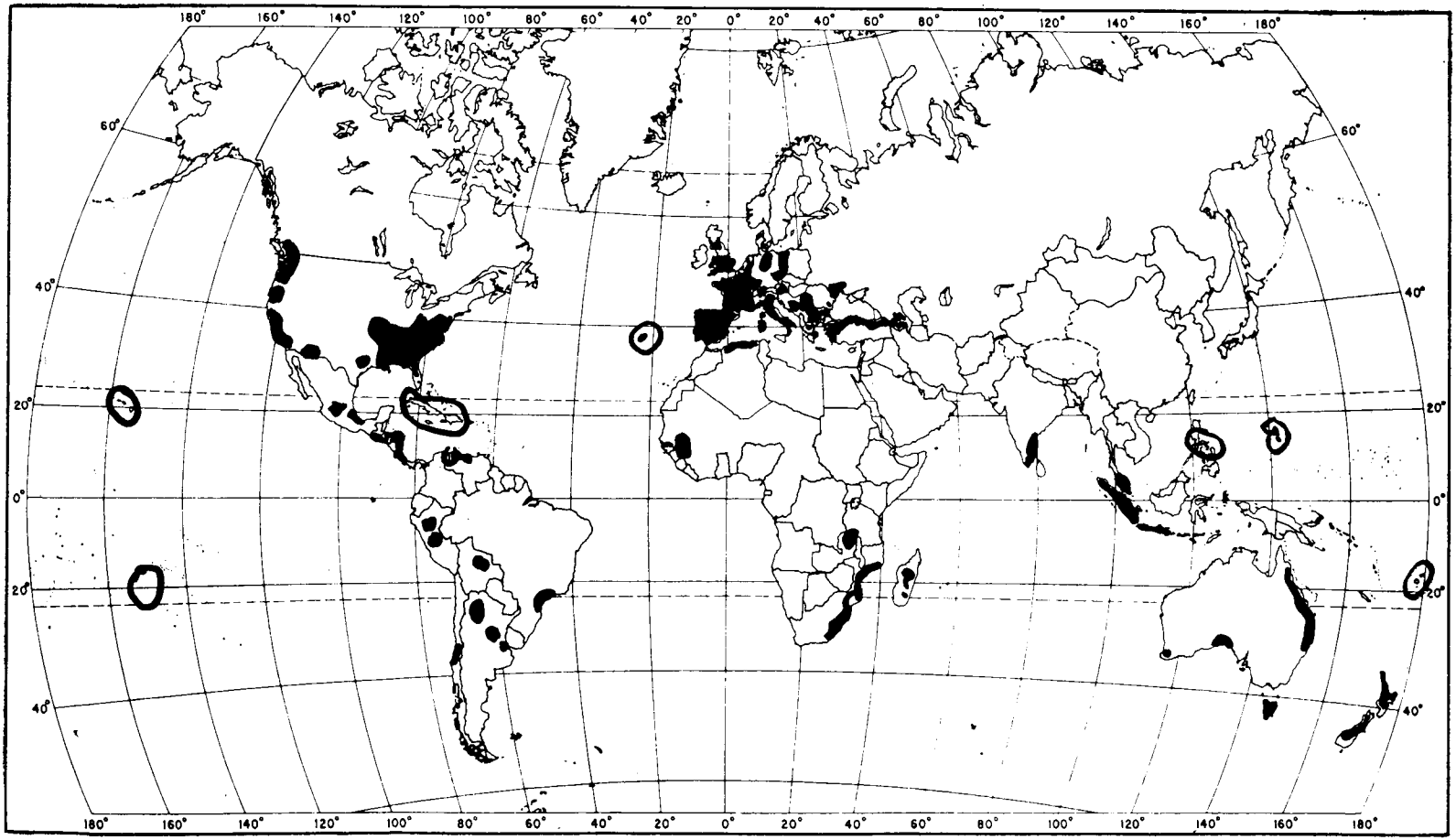

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