Phytophthora was discovered in Europe as the cause of potato late blight and the subsequent Irish potato famine, but that first potato epidemic came from the Americas. Today sudden oak death, with its aerial pathology, has disquieting parallels to late blight. We are reminded once again that the story of Phytophthora in forests of North America, as in other parts of the world, is largely one of devastating introduced pathogens. Phytophthora lateralis, in Oregon and California, exemplifies the dangers. The omnivorous and seemingly ubiquitous Phytophthora cinnamomi transformed the landscape of the southeastern United States about 200 years ago. It hasn't gone away. There is also an unfolding story of indigenous forest Phytophthoras. As we begin to understand bits and pieces of their pathology and their ecology, we can increasingly see that they are important players as well.

Phytophthora ramorum is the headline story, but curiously, the closest relative of P. ramorum, at least based on ITS-DNA sequence, is another exotic forest Phytophthora that is destructive in Oregon and northern California, P. lateralis. Phytophthora lateralis kills Port-Orford-cedar (POC) (Chamaecyparis lawsoniana), through much of the tree's limited native range. POC is a unique forest tree, growing wild only in southwestern Oregon and northwestern California. It has been planted widely as an ornamental, however, and the disease first appeared in the ornamental nurseries in 1923. There is only speculation about the origin of the pathogen, but it seems likely that unregulated international plant movements in the horticultural trade were somehow responsible for the introduction.

By the early 1950s P. lateralis was killing POC in the tree's native range along the southern Oregon coast. It spread quickly into the mountains, following road construction and timber harvest. POC regenerates prolifically in disturbed soil, and it is especially abundant, and vulnerable, immediately adjacent to roads. Today the rate of disease increase has slowed dramatically, largely because most of the most vulnerable stands of cedar are already infected. Federal land agencies have launched a large, expensive, and multifaceted disease management and research effort to halt the further spread of the pathogen, protect the remaining significant uninfected stands of POC, and bring cedar back in the areas already infested. The strategies include road closures, roadside sanitation, silviculture including targeted planting and spacing of POC, and genetic resistance.

Phytophthora cinnamomi arrived unannounced in North America
perhaps 200 or more years ago and spread silently but with lethal effect across the southeastern United States. Nothing is known of the early history, but by 1824 there were clear reports of sudden and unprecedented mortality of American chestnut and related Castanea species in forests and woodlands across the southern Appalachians. Chestnut had already largely disappeared from the southern Appalachian foothills before chestnut blight reached that region. Littleleaf disease of shortleaf pine (Pinus echinata) first attracted attention in the 1930s. Shortleaf pine grows broadly in the Piedmont and Coastal Plain of the southeastern United States, especially on abandoned agricultural lands. Littleleaf disease was most destructive in an area that broadly overlapped the former southern range of chestnut. Exhaustive searches for causal agents led in 1948 to the isolation of P. cinnamomi from symptomatic shortleaf pine trees, but because P. cinnamomi was seemingly everywhere in the South, and because inoculations often did not result in symptoms, it took years more to confirm the etiology. Phytophthora cinnamomi continues to attract attention in forests in the southeastern United States. Littleleaf is still around, and other pines are damaged on poorly drained soils. Oaks are damaged from South Carolina to Texas. There is also continuing work on Phytophthora root rot of Frasier fir- a Christmas tree disease. The pathogen is apparently not present in native stands of Abies fraseri, found on organic soils above 1500 m elevation, but it is present in transplant nurseries at lower elevations in the Christmas tree growing areas. One infected seedling per hectare may trigger an epidemic in downslope areas following heavy rains.

P. cinnamomi was presumably introduced to the Hawaiian Archipelago, perhaps with the first colonizing Pacific Islanders. Today it is implicated in ohia decline, an episodic, locally devastating disease of mature forest ohia (Metrosideros colina). In one disease scenario, water drainage in the dense pahoehoe lava flows progressively deteriorates as organic matter and decomposing rock gradually plug the cracks in the otherwise dense and uniform flow. Trees are progressively stressed by poor drainage, and mature trees, with their greater demands, are unable to replace rootlets killed by P. cinnamomi.

In the forests of the southeastern United States and in Hawaii, where P. cinnamomi has been present for hundreds of years, it is easy to forget that it is an exotic, invasive pathogen with the potential for devastation. The disease is now chronic; there are no longer advancing fronts of infestation marked by dead trees. The pathogen has reached its climatic limits. The dramatic ecological changes are history now, and new, disease-tolerant plant communities have replaced what was lost. Unfortunately, in many cases, we will never know what was lost. P. cinnamomi is not gone from these forests, however, and the Frasier fir Christmas tree story illustrates the pathogen’s potential to rise to new opportunities created by human activity and perhaps changing climates.

The story is apparently replaying now in the state of Colima, Mexico. P. cinnamomi is locally epidemic in an area of several
hundred hectares around a village in that state, killing several native oak species and other susceptible vegetation in the surrounding communal woodlands. The mortality began in 1987. *P. cinnamomi* appears to be spread primarily on the feet of cattle that graze freely. This may be another American ecological tragedy in the making.

Scattered information suggests that indigenous Phytophthoras are widespread but not often abundant in many temperate forest ecosystems, usually in the absence of dramatic disease. *Phytophthora hevea* is occasionally recovered from North American forest soils; however, it is widespread and apparently ecologically significant in Central American rain forests. Davidson demonstrated that it was an important cause of damping off of wild cashew, *Anacardium excelsum*, in a very diverse Panamanian tropical forest. Furthermore, it was most abundant, and caused the most damping off, where cashew seedlings were most abundant. Davidson hypothesized that *P. hevea* was exerting negative density dependent selection on cashew and thus maintaining the diversity of the tropical forest.

*P. gonapodyides* is undoubtedly the most widespread species in temperate forests in North America as well as Europe. It seems to be ubiquitous in forest streams of the western United States, including very remote areas in Alaska and Oregon. What is this abundant organism doing in the forest? Seemingly not much, but we have to wonder. There are many more wild Phytophthoras; in our continuing work in Oregon, we have recovered at least 13 species from forest soils and streams. Only 3 of these, *P. ramorum*, *P. lateralis*, and *P. cambivora*, are associated with recognized diseases in our forests.

We are left then with a very uneven picture of *Phytophthora* in North America. We can conclude that exotic pathogens are extremely dangerous in forest ecosystems and that other *Phytophthora* species are widespread in forests, usually not causing recognizable disease. Most significantly, we must continue to acknowledge how little we know about forest Phytophthoras.

**References**


