Root Diseases: Primary Agents and Secondary Consequences of Disturbance

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Abstract.—The fact that endemic root disease causing pathogens have evolved with forest ecosystems does not necessarily mean they are inconsequential. A pathogen such as the P group of Heterobasidion annosum has become an intractable problem in many Sierra east side pine stands in California because the fungus is adapted to colonization of freshly cut stump surfaces. The S group of Ha is wide spread among true fir forests in California and may be responsible for maintenance of endemic populations of the fir engraver bark beetle and for drought triggered, catastrophic outbreaks of this insect. Other diseases such as black-stain root disease are associated with certain root feeding bark beetles that are attracted to tree roots after site disturbances such as thinning. Fire may also affect various root disease fungi and their pathological behavior in longleaf pine through interactions with various soil factors as a consequence of previous land use.

INTRODUCTION

With the exception of "exotic" or introduced organisms, most forest tree pathogens have co-evolved with forest ecosystems and are normal components of forest stands. Many of these fungi have dual capabilities in that they can kill trees and decay wood. These attributes make such fungi key ecological agents that are responsible for structural diversity in forest stands. Their actions create openings in the canopy, recycle woody debris, and provide wildlife habitat through creation of snags, downed logs, and cavities (Franklin and others, 1989; Schowalter and Filip, 1993).

Root disease fungi can serve as primary agents of disturbance as well as secondary consequences of both invasive and non-invasive management activities. These pathogens respond to a wide range of disturbances, from fire exclusion to intensive timber harvesting and site preparation operations. Understanding how these fungi function and interact with other organisms under differing circumstances and stand management regimes is essential for attainment of sustainable forest productivity. To this end, we present examples of certain root disease causing fungi, their response to disturbance, and their role as disturbance agents.

ANNOSUM ROOT DISEASE

Heterobasidion annosum (Fr.) Bref. is a pathogen affecting temperate coniferous forests throughout the world. In the western United States, root diseases affect approximately 16.8 million acres of commercial forest land and annual volume losses may exceed over 2-1/2 times that due to forest fires (Kliejunas, 1995). In California alone, annual losses of 19.3 million cubic feet are attributed to H. annosum root disease.

Two biological species or intersterility groups (ISG's) of the fungus exist in western North America (designated S and P). Both the S and P ISG's readily colonize freshly cut stump surfaces by means of airborn basidiospore deposition on those surfaces. Stump surfaces may remain susceptible to colonization from 1 to 4 weeks after creation (Cobb and Barber, 1968). The spores germi-
nate, grow down through the stump wood, and colonize the stump and portions of its major lateral roots. Environmental conditions in many parts of the western United States may allow larger colonized stumps to remain infective for up to 50 years after initial infection. Thus, the disease may present itself 50 years after harvest of the original stand, creating mortality centers and gaps throughout the emerging ingrowth. This arises as a consequence of healthy root systems coming into contact with the fungal inoculum in the infected stump wood. The fungus then infects major lateral roots of previously healthy trees, causing root decay and eventual death of infected trees. Mortality can continue as root to root contact is made with adjacent healthy trees, creating ever widening gaps in the canopy. Details of the biology and ecology of this disease are presented in Otrosina and Cobb (1989).

Research has shown the S and P ISG's differ in their ecological, genetic, pathological, and host preference characteristics (Oetrosina and others, 1992, 1993). The P ISG primarily affects pine, incense cedar, and juniper species. One hypothesis inferred from genetic data and field observations is the P ISG was endemic but rare in the western United States until timber harvesting was practiced on a large scale. The P ISG responds to this type of disturbance as a result of its competitive ability to colonize newly created stumps. Thus, increased levels of harvesting can lead to increased *H. annosum* root disease. Fortunately, mitigation of stump infection and colonization is accomplished by application of borax to stump surfaces within a few hours after harvesting. Unfortunately, supplies of borax may not be available in the future for various reasons.

On the other hand, the S ISG of *H. annosum* has different ecological and pathological characteristics. It primarily affects true firs (*Abies* spp.), *Sequoiadendron giganteum* (Lindl.) Buchhloz, and probably Douglas-fir (*Pseudotsuga mensiesii* (Mirb.) Franco). There is strong evidence that this ISG is more widespread among true fir forests than the P group in pine (Garbellotto and others, 1992). One theory contends that *H. annosum* has been a common root disease pathogen in true firs at least since the last ice age (Oetrosina and others, 1993). Recent data indicate that infections in true firs result possibly from natural wounds (fire scars, insects, root breakage) in addition to freshly cut stumps (Oetrosina, unpublished). Thus, *H. annosum* in true firs can act as a primary disturbance agent, causing root and butt rots and increasing susceptibility of affected trees to bark beetle attack by weakening host defenses (Hertert and others, 1975). These infected trees may serve as hosts for endemic populations of bark beetles like the fir engraver (*Scolytus centralis* LeConte). During periods of protracted drought stress, insect outbreaks from these endemic centers can reach catastrophic proportions, causing widespread mortality at the landscape level (Bryerman and Ferrell, 1988).

Fire prevention may be regarded as a disturbance in forest ecosystems that evolved with fire. In this context, *H. annosum* plays a role in ecosystems such as *S. giganteum* whereby exclusion of fire is responsible for decline in health of certain stands of this species in the Sequoia-Kings Canyon National Park. Shade tolerant firs comprising much of the ingrowth in these *S. giganteum* stands may be responsible for transmitting the fungus to the sequoia via root contacts with infected firs. Normally, periodic fires would minimize the true fir component in these stands, ostensibly reducing the risk of transmission of *H. annosum*.

Because the S ISG of this fungus does not normally infect pines, speculations have been made regarding the role of this fungus in the maintenance of the ponderosa pine (*Pinus ponderosa* Doug. ex Laws. component of California mixed conifer stands in the central Sierra Nevada. Some butt rotted true firs in these stands, for example, may fall or blow down, exposing mineral soil for pine seed germination in the root ball area. The emerging pine seedlings growing in the resultant gap do not become infected because the S ISG is present in the fir root mass. Further research is needed relating to this suggested mechanism of gap dynamics in this forest type.

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BLACK-STAIN ROOT DISEASE

Black-stain root disease is caused by 3 host specific varieties of the fungal genus Leptographium Lagerb. and Melin. These varieties, Leptographium wageneri var. wageneri (Kendr.) Wingfield, Leptographium wageneri var. ponderosum (Harrington and Cobb) Harrington and Cobb, and Leptographium wageneri var. pseudotsugae Harrington and Cobb, are host specific to pinyons; ponderosa pines, Jeffrey pines (Pinus jeffreyi Grev. and Balf.), and other western “hard” pines; and Douglas-fir, respectively.

The fungus is spread from tree to tree through infected roots contacting fine roots of uninfected trees. This fungus is also capable of growing a short distance (about 5 cm) through the soil and infecting fine rootlets. Once infected, larger roots eventually become colonized by the fungus, blocking water transport. Trees quickly decline and die as a result of the infection or they become predisposed to bark beetle attack. Losses can range from isolated pockets of infection in affected stands to catastrophic reductions in stock levels characterized by mortality centers that increase in size as long as susceptible trees are present. The reader is referred to Harrington and Cobb (1988) for details regarding these and other aspects of the disease.

Site disturbance is a major factor for initiation of this disease in Douglas-fir stands (Harrington and others, 1983; Hansen, 1978). Overland spread and initiation of infection in stands of Douglas-fir is a result of insect vectors, primarily root feeding bark beetles such as Hylastes nigrinus (Witcosky and others, 1986). In Douglas-fir, the beetles may be attracted to roots via chemical attractants given off by stressed or damaged tree root systems (Witcosky and others, 1987). Thus, disturbance resulting in damage to root systems such as during logging operations may increase risk of disease. Site factors such as soil compaction or poor drainage may also play a role in the disease, particularly in ponderosa pine (Wilks and others, 1985).

There are strong indications that insect vectors similar to those attacking Douglas-fir roots are also involved in overland spread and initiation of new infections in ponderosa pine (Cobb, 1988). Site disturbance may also be a factor in the development of black-stain root disease in ponderosa pine stands, although causal relationships have not yet been established (Cobb, 1988). The root feeding scolytid Hylastes macer has been implicated as a vector of black-stain root disease in ponderosa pine (Goheen and Cobb, 1978). This insect probably responds to chemical signals given off by injured roots or stressed trees.

Site disturbance as a result of timber harvesting in ponderosa pine stands may increase insect vector populations, thus increasing the likelihood of the disease developing in some stands. We recently conducted insect trapping studies in clearcut and thinned stands to monitor populations of potential vectors of black-stain root disease. Our catch data indicates a rapid increase in catch of H. macer through the flight season in sites that were thinned or clearcut compared to adjacent, undisturbed stands (figs. 1 and 2). The thinned stands represented in figure 1 had severe black-stain root disease 3 years after thinning, characterized by continuing mortality and stocking that is below desired levels. Further studies are now underway in ponderosa pine stands to determine effects of levels of site disturbance (thinning by mechanical shearing versus chainsaw felling) and

![Pitfall Trap Catches from Devil’s Garden](image_url)

**Figure 1.** —Weekly pitfall trap catches of Hylastes macer, suspected vector of Leptographium wageneri var. ponderosum, in two ponderosa pine stands that have undergone thinning the previous season in the Devil’s Garden Ranger District, Modoc National Forest, California. Note the higher levels of insects trapped in the thinned stands (cross hatched and diagonal bars) compared to the undisturbed control stand (solid black bar) located within 0.5 to 1.5 kilometers of thinned stands.
timing of thinning (before or after bark beetle flight period) on insect vector populations and subsequent black-stain root disease occurrence in these stands.

EFFECTS OF FIRE

Many forest ecosystems have evolved with fire as a major factor responsible for maintenance of forest tree species and other vegetation. For example, in the southeastern United States coastal plain, periodic fire is essential for establishment and preservation of longleaf pine (Pinus palustris Mill.). However, the 60 to 80 million acres of land historically occupied by longleaf pine is now down to approximately 3 million acres. A large portion of these lands are currently used for other agricultural purposes or are planted to loblolly pine or other forest species.

While no research data is available at this time, past land uses may have a bearing on subsequent restoration of ecosystems such as longleaf pine. For example, the Savannah River Site near New Ellenton, South Carolina, under jurisdiction of the United States Department of Energy, with its forest lands managed by the USDA Forest Service in Region 8, have planted longleaf pine since the mid 1950’s. The purpose for this and other pine species was to mitigate soil erosion on lands previously used for subsistence agriculture. Many of the stands now are about 40 years old and have been subjected to various prescribed fire regimes in addition to thinning and harvesting. A general increase in mortality has been observed in 30+ year old longleaf pine stands at the Savannah River Site. The major cause of mortality in longleaf pine on these sites is H. annosum. Recent preliminary studies on occurrence of root diseases in longleaf pine stands in the above age classes have revealed a relationship between recency of prescribed fire and increased mortality in burned versus unburned plots (Table 1). In addition to H. annosum, a high proportion of mortality trees sampled had various Leptographium species and bark beetle galleries associated with larger (>5 cm diameter) roots of recently dead and dying trees in plots that have undergone prescribed burning within the last 3 years (Ottosina and others, 1995). The role of Leptographium in this ecosystem is unclear, however, some species are known pathogens of pines in the southeastern United States (Nevill and others, 1995) and may be responsible for declining stand health. While the prescribed burning regime was determined to be a “cool” burn, small lateral roots located within 5 cm of the soil surface had signs of damage, as determined by microscopic observations. Such damage was not observed on unburned plots.

It is not known at this time how various factors such as presence of Leptographium, root feeding bark beetles, thinning operations, fire regimes, various edaphic factors, and past land uses affect

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<th>Table 1.—Contrast in mortality and association of certain root infecting fungi in prescribed burned and unburned plots in a 30 year-old longleaf pine stand at the Savannah River Site.</th>
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<td>Mortality (number of trees per hectare)</td>
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<tr>
<td>Percent Heterobasidion annosum recovered from sampled trees and stumps%</td>
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<tr>
<td>Percent Leptographium sp. recovered from sampled trees and stumps</td>
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*Percent H. annosum and percent Leptographium based upon 20 and 8 tree or stump root samples from the burned and unburned plots, respectively.
these longleaf pine stands. However, these associations raise suspicions and provide the impetus for further research. Questions such as: Does certain past land use history have a bearing on current observations of mortality and associated root infecting fungi? Does land use history and these biotic and abiotic factors interact in some way? Although longleaf pine ecosystems have evolved with fire, perhaps changes (as yet unknown) resulting from past land use events are affecting outcomes of stand developmental processes in an unexpected way. Answering these and similar questions may have relevance to "ecosystem restoration" projects in other situations as well.

CONCLUSIONS

Root disease causing fungi can respond to disturbances and changes in forest conditions and can act as primary causal agents of disturbance. In either case, they can be responsible for considerable losses in forest productivity, a consequence that cannot be ignored if we are going to utilize various products, recreational as well as commodities, derived from forests. At the landscape level, mortality due to diseases and insects may appear to be insignificant. However, because the stand is the unit on which we operate, losses and ecological changes brought about by diseases such as we have discussed do impact management plans. Forest stands are necessarily a part of management on a landscape scale and thus disease impacts must be considered when implementing overall large scale forest planning strategies.

There are considerable voids in our knowledge of the biology and interactions of these root disease causing fungi with forests. An understanding of root disease fungi and their interactions with various forest ecosystems must be obtained in order to avoid unacceptable outcomes as management plans are implemented. These organisms and the diseases they cause must be recognized as potent biological forces that can alter forest structure and can negatively impact productivity.

LITERATURE CITED


Ootrosina, W.J.; Chase, T.E.; Cobb, F.W., Jr. 1992. Allozyme differentiation of intersterility groups of Heterobasidion

91