DISEASES OF FOREST TREES: CONSEQUENCES OF EXOTIC ECOSYSTEMS?

William J. Otrosina[1]

Abstract—Much attention is now given to risks and impacts of exotic pest introductions in forest ecosystems. This concern is for good reason because, once introduced, an exotic pathogen or insect encounters little resistance in the native plant population and can produce catastrophic losses in relatively short periods of time. Most native fungal pathogens of forest trees have co-evolved for eons with their hosts and have reached a sort of balance between them and populations of susceptible tree species. Recent studies on various forest types have indicated a higher incidence of certain fungal pathogens than were previously thought to occur. These pathogens are either the type not normally thought of as highly virulent or are those that have not been previously reported as a serious problem on a particular host. For example, pathogenic fungi belonging to both the *Leptographium* complex and *Heterobasidion annosum,* are associated with mortality after prescribed burning in certain longleaf pine stands. Yet, this tree species has traditionally been ranked as highly tolerant to these fungi. Could these observations reflect some manifestation of "exotic ecosystems," whereby the conditions under which particular tree species evolved are no longer present or are altered in some way that increases their susceptibility to these fungi? With the current emphasis on ecosystem restoration and alternative silvicultural regimes, it is critical to address such questions in order to avert losses in forest productivity.

INTRODUCTION

Forest tree species and all other living organisms have evolved under various environmental conditions through eons of time. Nearly all species that have ever lived are now extinct (Raup 1986). Adaptations to climatic factors, soils, pests, diseases, and a host of disturbance events, operating at a variety of scales, have forged the characteristics of each tree species we now observe, including their functions in forest ecosystems.

From the perspective of forest pathological processes, individual tree species and ecosystems are in some form of quasi-equilibrium with various pathogens. This is in contrast to situations involving introduced pests or exotic organisms, which generally cause rapid and catastrophic mortality on native tree species. On the other hand, many root disease pathogens that have co-evolved with their hosts often cause excessive mortality and disruption of long-term stand management goals. Why then, in a theoretically stable system from the host-pathogen perspective, are there significant problems with various diseases in coniferous forest stands over a wide range of forest types and ecological conditions? Have presettlement forest conditions changed, through past land uses, to the extent that unstable or "exotic ecosystems" are created by various management activities which have led to undesirable losses due to various forest tree diseases?

For many decades, forest pathologists have studied the effects of various management regimes and their relationships to forest tree disease. As a result, an empirical understanding of relationships between site factors, disturbance, past and present management practices, and silvicultural procedures relative to many forest diseases has been attained. In the light of these discerned relationships, the purpose of this paper is to introduce the concept of exotic ecosystems, defined as unstable ecosystems arising from rapid edaphic and environmental changes brought about by past land use or current management practices. These will be presented in the context of how various silvicultural regimes, disturbances, and past land use practices have interacted to create disease problems.

ROOT DISEASE

Annosus Root Disease

Caused by the fungus *Heterobasidion annosum* Fr.(Bref.), this disease is often devastating on temperate zone conifers worldwide. Two biological species of this fungus occur in western North America. One, called "S," attacks primarily true firs and Sequoia while the other, called "P," attacks mainly pines and juniper. In the Eastern United States, only the P group has been found to date.

The fungus attacks pines (P group) by spores landing on freshly cut stump surfaces. The spores germinate and rapidly colonize portions of stumps, with mycelia growing downward and further colonizing stump roots. Healthy trees whose root systems contact infected stump roots become infected, thus creating ever-widening gaps or disease centers in affected stands (Otrosina and Cobb 1989). Based upon isozyme and DNA studies (Otrosina and others 1992, 1993; Garbelotto and others 1996), the P group in the Western United States was probably rare until presettlement times. It may have occupied niches created by natural wounding events such as blowdowns or possibly fire scars and was a part of Western United States pine ecosystems, creating occasional openings in stands.

By the late 19th century, timber harvesting was conducted on a large scale. Another boom in timber harvesting occurred during the 1950's as a result of post-World War II housing demand (MacCleery 1992). As a result, freshly cut stump surfaces were created in large amounts over 40 to 50 years in old-growth east-side Sierra Nevada pine stands. Many of these stands were subjected to selective harvesting with repeated entries. These partial cutting

[1] Supervisory Research Plant Pathologist, USDA Forest Service, Southern Research Station, Tree Root Biology, 320 Green Street, Athens, GA 30602.

techniques often resulted in stem-damaged residual trees, soil compaction, and root damage. Because fresh stump surfaces are an ideal niche for *H. annosum* colonization, populations of the P group increased dramatically, increasing the likelihood of disease transmission to residuals by root contacts with infected stump roots. The fungus, once in a stand, is intractable and can survive for over 60 years (Otrosina and Cobb 1989). Thus, stand development is affected far into the rotation with the disease perpetuating itself by continued spread in ever-widening mortality centers.

Fire exclusion also has affected annosum root disease incidence in many stands. For example, a general shift in species composition has taken place in the Sierra east-side forest type as a result of fire exclusion. Once park-like stands of predominantly ponderosa pine are now dominated by shade-tolerant, true fir species (Petersen 1989). The S biological species of *H. annosum* is widespread on true firs (Otrosina and Cobb 1989, Otrosina and others 1992) and apparently infects firs more frequently as a result of direct infection through natural wounds or means other than freshly cut stumps (Garbelotto and others 1996). This is in contrast to the P group of *H. annosum* in pine species, which had a more restricted range on pines prior to management activities. The characteristically overstocked stands of firs resulting from fire exclusion have a high incidence of root disease that renders them susceptible to catastrophic insect outbreaks (Hertert and others 1975) and wildfires (Otrosina and Ferrell 1995). Thus, fire exclusion can be thought of as a disturbance resulting in an exotic ecosystem in which current tree species assemblages exist in a pathologically, entomologically, and silviculturally unstable system driven by widespread root disease.

Another example of exotic ecosystems arising from fire exclusion and the presence of root disease is the present decline in health of *Sequoiadendron giganteum* (Lindl.) Buckholz stands in the Sequoia-Kings Canyon National Park. Decades of aggressive fire exclusion have encouraged the ingrowth of shade-tolerant true firs under old growth *S. giganteum*. Because true firs can be infected with the *H. annosum* S group in the absence of harvesting or thinning activities, the resultant presence of firs in sequoia stands may be responsible for transmitting the fungus to the sequoia via root contacts (Piirto and others 1992). Normally, periodic fires would minimize the true fir component in these stands, thereby reducing the risk of transmission of *H. annosum*.

LONGLEAF PINE, FIRE, AND ROOT DISEASE

Leptographium spp. and *Heterobasidion annosum*

Longleaf pine (*Pinus palustris* Mill.) once occupied over 30 million hectares throughout the Southern United States. At present, only about 5 percent of the original longleaf pine sites are occupied by this species. Changes in land use such as agriculture, commercial development, and conversion to other forest species such as loblolly pine (*P. taeda* L.) and slash pine (*P. elliottii* Engelm.) have contributed to the dramatic decrease in the range of longleaf pine.

Fire is an essential component of longleaf pine ecosystems, being necessary for the establishment of reproduction and for maintaining stand health. This tree species co-evolved with fire as an essential component of its life cycle. Over the past several years, increased mortality has been reported to occur in certain stands, and this mortality appears to be associated with prescribed burning (Otrosina and others 1995). A preliminary research study conducted on a 40-year-old longleaf pine stand at the Savannah River Site in New Ellenton, SC, revealed that burned plots had three times greater mortality 1 year post-burning than unburned check plots. Histological observations on fine roots (<2 mm in diameter) of longleaf pine obtained from the upper few centimeters of soil in the relatively cool burns have shown internal tissue damage when compared to roots from unburned check plots (Otrosina and others 1995). Also, twofold to threefold differences in isolation frequency of the root pathogens *H. annosum* and *Leptographium* species were associated with roots of mortality trees (Otrosina and Ferrell 1995). A recent follow-up study on these plots 3 years post-burn revealed a still higher isolation frequency of *Leptographium* species as compared to check plots (fig. 1). *H. annosum* also was isolated in higher frequency in burn plots 3 years post-treatment, although at a lower frequency than 1 year after burning (fig. 1).

The association of *Leptographium* species with fire and mortality is significant because this fungal genus contains many forest tree root pathogenic species which have varying degrees of pathogenicity toward pine species (Harrington and Cobb 1988, Nevill and others 1995). Many

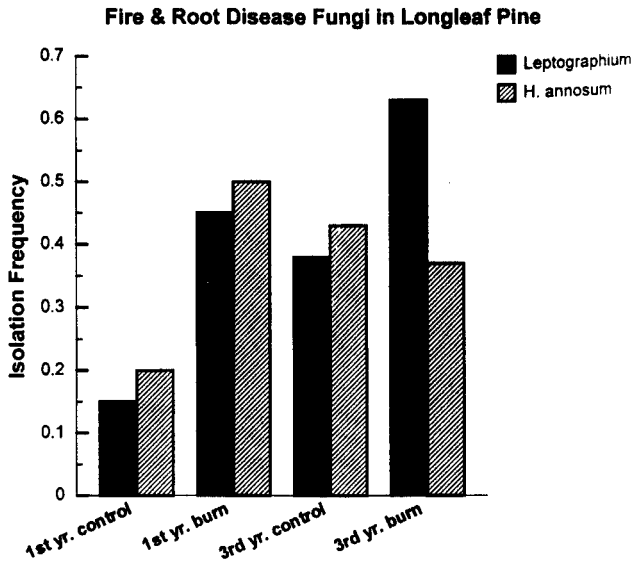

Figure 1—Isolation frequency of *Heterobasidion annosum* and *Leptographium* species in 40-year-old longleaf pine. Data were taken 1 and 3 years after burning in prescribed burned and unburned research plots at the Savannah River Site, New Ellenton, SC.

Leptographium species are also associated with various species of root-feeding bark beetles which can serve as vectors or as wounding agents that allow introduction of root pathogenic fungi (Harrington and Cobb 1988). Observations of insects in larger woody roots of post-fire longleaf pine have been documented (Otrosina and others 1995) but their roles with respect to these fungi and longleaf pine mortality have not been established.

Regarding these associations with fire, fungi, and insects in longleaf pine, obvious questions arise. Why, in a tree species that is adapted to and has evolved with fire, are we observing root pathogens and associated mortality in such high frequency? What are the roles of these various fungal species and insects in relation to the observed longleaf pine mortality? Longleaf pine has been regarded as either tolerant or resistant to root disease (Hodges 1969) and prescribed fire has been reported to decrease incidence of annosum root disease in southern pines (Froelich and others 1978).

Observations based upon windthrown trees suggest that on some sites, severe erosion of up to 2 feet of top soil may have severely restricted longleaf pine root systems to the upper 60 to 70 cm of soil profile (Otrosina unpublished data). Longleaf pine has evolved in deep sands and develops an extensive tap root system in these soils. Thus, although regenerated within physiographically correct sites, longleaf pine on eroded soils are forced into a new ecosystem structure, an exotic ecosystem, with respect to current soil conditions. These conditions, in turn, may produce unstable and unpredictable outcomes when standard management practices are employed. Precisely what relationships exist between fire, mortality, root disease fungi, and soil conditions form the basis for now ongoing research.

IMPLICATIONS

There are many more examples in forest pathology and entomology where man has unknowingly created certain conditions whereby native organisms, both fungal pathogens and insects, have become serious problems threatening forest sustainability (Goheen and Otrosina 1997, Otrosina and Ferrell 1995). The activities of man have rapidly and dramatically changed landscapes and ecosystems over a short period of time. The adaptations developed over eons of evolutionary time in forest tree species may no longer serve these species when forced into sometimes radically "new" ecosystem structures. These new structures are characterized by interactions not experienced by the tree species in an evolutionary sense, resulting in an unpredictable and unstable or chaotic system (Moir and Mowrer 1995) susceptible to various and unexpected disease problems. The exotic ecosystem concept put forth here is a new viewpoint on subjects contemplated by forest pathologists, entomologists, and silviculturists, encompassing well-known abstractions such as predisposing factors, stress, disturbance regimes, and sustainability.

Some viewpoints regarding endemic forest tree root diseases embrace the idea that because these disease causing fungi are endemic to forest ecosystems, they perform beneficial functions among which are creating gaps in forest canopies, decomposing woody debris, or producing cavities for wildlife. These views assert, depending upon management objectives, that root diseases may or may not be detrimental. Such a notion presumes their function and regulatory dynamics are the same at present as they were prior to various management activities. Nevertheless, attention must be granted to the issue that some ecosystems may now be comprised of tree species that are maladapted to current conditions, resulting in varying degrees of instability.

For example, after years of successful wildfire suppression and politically motivated resistance to use of prescribed burning as a silvicultural tool, many forest stands whose natural history involved periodic burning now have large accumulations of litter and fuel. The recent focus on forest health issues acknowledges the importance of fire in many forest ecosystems and are recommending reintroduction of fire to these stands. Forest stands in these situations should be regarded as exotic ecosystems with the appropriate caution exercised. The new set of initial conditions may bring about unexpected forest health problems when fire is reintroduced in many stands. On the other hand, many forest ecosystems are quite resilient and stable under various management regimes; however, it is imperative that we strive to understand disease processes resulting from these new sets of conditions in order to identify the ecosystems and related conditions under which instability and unpredictability develop.

ACKNOWLEDGMENT

The author thanks the Savannah River Forest Station, USDA Forest Service, New Ellenton, SC, and U.S. Department of Energy, Savannah River Site, for their help and financial support of longleaf pine studies reported in this paper.

LITERATURE CITED

Froelich, R.C.; Hodges, C.S.; Sackett, S.S. 1978. Prescribed burning reduces severity of annosus root rot in the South. Forest Science. 24: 93-100.

Garbelotto, M; Ratcliff, A.; Bruns, T.D.; Cobb, F.W., Jr.; Otrosina, W.J. 1996. Use of taxon-specific competitive-priming PCR to study host specificity, hybridization, and intergroup gene flow in intersterility groups of *Heterobasidion annosum*. Phytopathology. 86: 543-551.

Goheen, Donald; Otrosina, W.J. [In press]. Characteristics and consequences of root diseases in western North America. In: Frankel, S.J., ed. Users guide for the Western Root Disease Model, Version 3.0. U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Albany, CA.

Harrington, T.C.; Cobb, F.W., Jr. 1988. *Leptographium* root diseases on conifers. American Phytopathological Society Press, St. Paul, MN. 149 p.

Hertert, H.D.; Miller, D.L.; Partridge, A.D. 1975. Interactions of bark beetles (Coleoptera:Scolytidae) and root pathogens in grand fir in northern Idaho. Can. Ent. 107: 899-904.

Hodges, C.S. 1969. Relative susceptibility of loblolly, longleaf, and slash pine roots to infection. [Abstract]. Phytopathology. 59: 1031.

MacCleery, Douglas W. 1992. American forests: A history of resiliency and recovery. FS-540. Washington, DC: U.S. Department of Agriculture, Forest Service. 58 p.

Moir, W.H.; Mowrer, H. Todd. 1995. Unsustainability. Forest Ecology and Management. 73: 239-248.

Nevill, R.J.; Kelley, W.D.; Hess, N.J.; Perry, T.J. 1995. Pathogenicity to loblolly pines of fungi recovered from trees attacked by southern pine beetles. Southern Journal of Applied Forestry. 19: 78-83.

Otrosina, W.J.; Cobb, F.W., Jr. 1989. Biology, ecology, and epidemiology of *Heterobasidion annosum*. In: Otrosina, W.J.; Scharpf, R.F., tech. coords. Proceedings of the symposium on research and management of annosus root disease (*Heterobasidion annosum*) in Western North America; 1989 April 18-21; Monterey, CA. Gen. Tech. Rep. PSW-116. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 26-33.

Otrosina, W.J.; Chase, T.E.; Cobb, F.W., Jr. 1992. Allozyme differentiation of intersterility groups of *Heterobasidion annosum* isolated from conifers in western North America. Phytopathology. 82: 540-545.

Otrosina, W.J.; Chase, T.E.; Cobb, F.W., Jr.; Korhonen, K. 1993. Population structure of *Heterobasidion annosum* from North America and Europe. Canadian Journal of Botany. 71: 1064-1071.

Otrosina, W.J.; Ferrell, G.T. 1995. Root diseases: primary agents and secondary consequences of disturbance. In: Eskew, Lane G., comp. Forest health through silviculture. Proceedings of the 1995 national silviculture workshop; 1995 May; Mescalero, NM. Gen. Tech. Rep. RM-GTR-267. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 87-92.

Otrosina, W.J.; White, L.W.; Walkingshaw, C.H. 1995. *Heterobasidion annosum* and blue stain fungi in roots of longleaf pine are associated with increased mortality following prescribed burning. [Abstract]. Phytopathology. 85: 1197.

Petersen, G. 1989. Prescribing control in mixed conifer stands affected by annosus root disease. In: Otrosina, W.J.; Scharpf, R.F., tech. coords. Proceedings of the symposium on research and management of annosus root disease (*Heterobasidion annosum*) in Western North America; 1989 April 18-21; Monterey, CA. Gen. Tech. Rep. PSW-116. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 146-149.

Piirto, D.D.; Cobb, F.W., Jr.; Workinger, A.C.; Otrosina, W.J.; Parmeter, J.R., Jr.; Chase, T.E. 1992. Biological and management implications in the giant sequoia ecosystem: Part II—pathogenicity and genetics of *Heterobasidion annosum*. Report submitted to National Park Service, Sequoia-Kings Canyon National Park in fulfillment of Cooperative Agreement No. 8000-8-0005 with California Polytechnic University, San Luis Obispo, CA.

Raup, David M. 1986. Biological extinction in earth history. Science. 231: 1528-1533.