Book – Chapter 13

FOREST PATHOLOGY

From Genes to Landscapes

Edited by

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Front cover: root disease pocket in a mature forest in the Black Hills. (Courtesy of John E. Lundquist)

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CHAPTER 13

Exotic Ecosystems: Where Root Disease Is Not a Beneficial Component of Temperate Conifer Forests

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Introduction

Forest tree species and ecosystems have evolved under climatic, geological, and biological forces over eons of time. The present flora represents the sum of these selective forces that have acted upon ancestral and modern species. Adaptations to climatic factors, soils, insects, 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. Thus, modern flora is adapted to the conditions existing at present. The stochastic and inexorable nature of climatic, geological, and biological selective forces becomes more striking when we consider that possibly 99% of all species that ever existed are now extinct (Raup 1986).

Root disease fungi, particularly root rotting Basidiomycetes, are key drivers of coniferous forest ecosystems. In the primeval forest, these organisms perform functions vital to the ecosystem. Among these functions is creation of openings by causing mortality in overstory trees, thus influencing stand structure and composition. Hansen and Goheen (2000) discuss the influence of root-rotting fungi on coniferous forest ecosystems, drawing on *Phellinus weirii* (Murr.) Gilbertson as a model pathosystem.

From the forest pathological process standpoint, there is a presumption that individual tree species and ecosystems exist in some form of quasi-equilibrium with various pathogens. This contrasts with circumstances involving introduced pests or exotic organisms, which generally cause rapid and catastrophic mortality in indigenous tree species. On the other hand, native root disease pathogens that have co-evolved with their hosts and are presumably in equilibrium with them often cause excessive mortality and disruption of long-term stand management goals. Additionally, such tree mortality caused by root disease is not necessarily limited to low vigor individuals (Hansen and Goheen 2000). Why, then, in a theoretically stable system from the host-pathogen perspective, are there significant problems with various indigenous diseases in coniferous forest stands over a wide range of forest types and ecological conditions?

Ecological events such as diseases, fire, and other disturbances perform important functions in overall forest ecosystem structure, health, and sustainability. The general view that native root disease pathogens are in equilibrium with their hosts and therefore are a natural and beneficial component of temperate coniferous forest ecosystems has crept into much of the forest management philosophy in North American forestry. Along with other ecological events such as fire, tree killing insects and diseases are generally regarded as beneficial disturbances in the forest management policy termed Ecosystem Management (Averill 1997). Nonetheless, there are significant departures from the idyllic notion that native root disease fungi have co-evolved with their hosts and therefore function in the same manner under present conditions as they did prior to anthropogenic influences on the forest landscape. These departures can often have unpredictable effects that result in undesirable economic and ecological impacts.

An exotic ecosystem is defined as a pathologically unstable ecosystem arising from rapid edaphic and environmental changes brought about by past land use or current management practices. The purpose of this paper is to explore the concept of exotic ecosystems, by example of some root disease pathogens such as *Heterobasidion annosum* (Fr.) Bref., to illustrate the hazards of assigning relatively benign ecological roles to such forest tree pathogens.

Heterobasidion annosum and Anthropogenic Influences

Heterobasidion annosum is an economically important pathogen of temperate zone conifers throughout the world. Recently, two new species of this fungus were described from European populations. One species, *H. parviporum* Niemlä & Korhonen, delimited the European S intersterility group and the other, *H. abietinum* Niemlä & Korhonen, delimits the European F group (Niemlä and Korhonen 1998). *Heterobasidion annosum sensu stricto* is retained as representing the European P group. The *H. annosum sensu lato* S and P groups (biological species) in North America are genetically distinct entities but have not yet been assigned species status. Virtually no gene flow occurs between the North American S and P biological species, despite their close proximity and overlapping host niches (Otrosina *et al.* 1992; Otrosina *et al.* 1993). In North America, there is also considerable host specificity between the S and P biological species. Generally, the P biological species attacks mainly pine species and western juniper (*Juniperus occidentalis* Hook.) while the S biological species attacks true firs (*Abies* spp.), giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Recently, an S X P (SP) hybrid genet of *H. annosum* was recovered from an east side Sierra ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) site in the Modoc National Forest in California (Garbelotto *et al.* 1996, 1999). DNA polymerase chain reaction (PCR) and isozyme analyses confirm that the SP heterokaryon is a true hybrid and is heterozygous for S and P alleles at many loci. Field evidence showed that the SP hybrid genet was extensively distributed in the mortality center. It was isolated from one slightly symptomatic ponderosa pine and two slightly symptomatic juniper trees, indicating stability and virulence of the hybrid. An adjacent ponderosa pine stump harbored the hybrid, and may have served as the primary focus of infection for this genet.

The existence of the SP hybrid in *H. annosum* has implications for forest management activities because such actions influence pathogen populations. Prior to about 200 years ago, forests in the western United States were not harvested extensively and were in some quasi-equilibrium with natural processes such as wild fire, insects, and root diseases such as that caused by *H. annosum* (Otrosina *et al.* 1992). How, given compelling evidence that significant gene flow does not occur in nature between the S and P biological species, did the hybrid develop given the known reproductive barriers that exist (Chase and Ullrich 1990)? One scenario that may explain this phenomenon lies in the activities of civilization, namely the relatively recent advent of timber harvesting, beginning within the past 150 years. By the late 19th century, timber was harvested on a large scale. Harvesting surged again during the 1950's as a result of post—World War II housing demand (MacCleery 1992). Freshly cut stump surfaces are well known to be a suitable niche for the process of infection and colonization. Because stumps of ponderosa pine, other pine species, and true firs can be infected by either S or P biological species, and because the fungus can survive over 50 years in stumps under western United States environmental conditions (Otrosina and Cobb 1989; Otrosina *et al.* 1992), large numbers of stump infections initiated over the past century resulted in increased probabilities of S and P hyphae coming into contact. Similar to forced hybridization obtained in laboratory studies (Chase and Ullrich 1990), individual stumps infected by both S and P biological species may provide suitable opportunities for the hybridization process to occur in nature.

From the pathogenic organism perspective, there is little doubt that circumstances similar to that experienced by *H. annosum*, that is, relatively sudden appearance of susceptible tissue, existed in the past. Large-scale events such as storm damage, earthquakes, and wildfires certainly shaped the population structure of the pathogen by altering forest composition and creating exposed tissue for colonization. Recent human activities resulting in creation of stumps, however, are unprecedented in evolutionary history of this pathogen. A large amount of newly susceptible tissue was created over a relatively short time and over a significant portion of the susceptible forested landscape. The existence of the *H. annosum* SP hybrid may be an example and an indicator of anthropogenic influence on evolutionary direction or speciation in this pathogen. Also, recent and rapid environmental changes that have impacted the ponderosa pine ecosystem, including decades of fire exclusion, increased recreational impacts, and atmospheric changes such as increased CO^2, ozone, and other pollutants, may be greater than this ecosystem has previously experienced (Waring and Law 2001). Indeed, there is evidence that photochemical oxidants may increase susceptibility of ponderosa and Jeffrey pines to *H. annosum* attack (James *et al.* 1980, James and Cobb 1982). These circumstances may reduce the applicability of past management experiences as they relate to predicting growth and ecological outcomes of management actions (Waring and Law 2001). The effects of man's activities on forest pathogen population structure and evolution have not been widely studied. Nonetheless, this matter has implications for forest management regarding possible shifts in pathogen host range, transfer of virulence genes, and resultant impacts on forest health.

Fire and *Heterobasidion annosum*

Many forest ecosystems and component tree species have evolved with fire. Some forest types, such as longleaf pine (*Pinus palustris* Mill.) and giant sequoia, depend upon periodic light burns for maintenance of stand vigor and health. The latter tree species was once widely distributed in western North America but is now limited to about 75 groves on the western slope of the Sierra Nevada (Rundel

1972). Until recently, fire suppression over the last 50 or more years in groves of sequoia and mixed conifer forests has resulted in increased fuel loads and an increased component of true firs (*Abies* sp). Because fir stands generally have widespread *H. annosum* infection (Otrosina and Cobb 1989; Otrosina *et al.* 1992, Garbelotto *et al.* 1999), contagion towards sequoia roots via contacts with infected firs may be responsible for increased *H. annosum* infection in sequoia. Evidence validating this hypothesis has recently been advanced (Piirto *et al.* 1998). Also, because of years of fire suppression, excessive fuel loads now present an unacceptably high risk of infection by *H. annosum* via fire scars and various other pathogenic fungi. Normally, periodic fires characteristic of this ecosystem would minimize the true fir component, thereby reducing the transmission of *H. annosum*. Notwithstanding the beneficial role of fire, its re-introduction in fire-dependent ecosystems requires caution and an awareness of risks involved.

Another exotic ecosystem exemplified by fire exclusion in fire-dependent systems is the Sierra east-side ponderosa pine /Jeffrey pine forest type. Across significant portions of the landscape, once park-like stands of predominantly ponderosa or Jeffrey pines are now dominated by shade tolerant true fir species (Petersen 1989). Since the S biological species of *H. annosum* is widespread on true firs in the western United States, and apparently infects firs more frequently through natural wounds or means other than cut stumps (Garbelotto *et al.* 1996, 1999), characteristically overstocked stands resulting from fire exclusion have a high incidence of root disease that render them susceptible to catastrophic insect outbreaks (Hertert *et al.* 1975) and wildfires (Otrosina and Ferrell 1995) In this case, fire exclusion itself 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 root disease.

Fire Induced Decline and Mortality in Longleaf Pine

Fire is an essential component of the longleaf pine ecosystem, being necessary for the establishment of reproduction and for maintaining stand health. Periodic fires prepare seed beds for natural regeneration and function in the control of brown spot foliar disease of grass-stage seedlings caused by *Mycosphaerealla dearnessii* Barr (= *Scirrhia acicola* (Dearn.) Siggers). Although longleaf pine (*Pinus palustris* Mill.) once occupied over 30 million hectares throughout the southern United States, only about 5 % of the original longleaf pine sites are currently occupied by this species. Agriculture, commercial development, and conversion to other forest species such as loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) have contributed to this dramatic decrease. Currently, various agencies are attempting to restore this species to many sites in its former range. The longleaf pine ecosystem also supplies important habitat for the endangered red-cockaded woodpecker (*Picoides borealis*).

Over the past several years, however, increased mortality at age 35-45 has been observed in certain stands, and this mortality appears to be associated with prescribed burning (Otrosina *et al.* 1995). A research study in 40 year-old longleaf pine stands undergoing three different burn intensities, conducted at the Savannah River Site, Savannah River Forest Station, in New Ellenton, South Carolina, revealed that mortality over a three-year period post burning was significantly greater in the plots receiving hot burns (Sullivan *et al.* 2003), and regardless of burn temperature, crown symptom severity, as indicated by reduced foliar density, length, and green color, increased significantly versus those in unburned control plots (Otrosina *et al.* 2002). Histological observations on fine roots (< 3 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 *et al.* 2002). Stereo microscopic observations of fine roots also reveal evidence of damage present in plots having relatively cool burn temperatures (approximately 60 C at organic matter - soil interface). The root pathogens *H. annosum* and *Leptographium* species, primarily *L. terebrantis* Barras & Perry and *L. procerum* (W.B. Kendr.) Syd. & P. Syd. were associated with roots of killed trees but were also widespread throughout the plots, regardless of treatment or presence of crown symptoms (Otrosina *et al.* 2002).

The association of *Leptographium* species with fire and decline in longleaf pine is significant because this fungal genus contains many species with varying degrees of pathogenicity toward pine species (Harrington and Cobb 1988; Nevill *et al.* 1995). Many *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). Presence of *L. terebrantis* and *L. procerum* has been associated with southern pine beetle attack in loblolly pine, and their presence on roots may be indicators of stress (Otrosina *et al.* 1997, Otrosina *et al.* 1999). Insects have been observed in larger woody roots of post-fire longleaf pine (Otrosina *et al.* 1995), but their roles with respect to these fungi and longleaf pine mortality have not been established. Certain non-aggressive root feeding bark beetles such as *Hylastes salebrosus* Eichoff and *H. tenuis* Eichoff, which may vector *Leptographium* species, are attracted in numbers positively correlated with burn severity in longleaf pine study plots (Sullivan *et al.* 2003).

Obvious questions arise about associations among fire, fungi, and insects in longleaf pine. Why are we observing root pathogens and associated mortality in such high frequency in a tree species that has adapted to and evolved with fire? 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 (Froeliche *et al.* 1978).

Observations based upon wind thrown 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 60-70 cm of soil profile (Otrosina *et al.* 1999). Longleaf pine has evolved in deep, sandy soils, and typically has an extensive tap root system in these soils. Thus, although regenerated within physiographically correct sites, longleaf pines 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. On the other hand, longleaf pine mortality cannot always be related to shallow or degraded soils. Decline and mortality in longleaf pine has also been associated with prescribed burning on sites with deep sandy soils (Otrosina *et al.* 2002).

A scenario describing a complex interaction of factors has been advanced to explain the above observations (Otrosina 2002). Because of longer-than-normal prescribed burning intervals, organic matter from needle litter forms a humus layer containing fine roots. When fire is re introduced into the system, indirect but lethal heating kills the fine roots and mycorrhizae. Root-pathogenic fungi such as *H. annosum* and *Leptographium* species are widespread on roots prior to this event, and are adding to overall stress by the cryptic root infections that divert physiological resources in the tree toward defensive compounds. The root pathogens add to stress caused by heat-induced death of fine roots in the organic matter layer and upper mineral soil. Thus, reintroduction of fire after a longer-than-normal hiatus tips the balance toward steady decline and mortality in longleaf pine (Figure 13.1). Under these circumstances, efforts to restore longleaf pine are thwarted, particularly those management goals requiring rotations longer than 75 years, as required for red-cockaded woodpecker habitat. Current research is attempting to clarify interactions among fire, tree mortality, root disease fungi, and soil conditions.

Conclusions

Despite the power of natural phenomena to influence evolutionary pathways, modern man, employing various means in the creation of the infrastructure of civilization, has brought about unprecedented changes in and influence upon edaphic and environmental conditions. There are many more examples in forest pathology and entomology where man has unknowingly created conditions whereby native organisms, both fungal pathogens and insects, have become serious problems threatening forest sustainability (Otrosina and Ferrell 1995, Goheen and Otrosina 1997, Hansen and Goheen 2000). Human activities have rapidly and dramatically changed landscapes and ecosystems over a short period of time. The adaptations developed by forest tree species over eons of evolutionary time 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 (Figure 13.2) addresses subjects contemplated by forest pathologists, entomologists, and silviculturists, encompassing well-known abstractions such as predisposing factors, stress, disturbance regimes, and sustainability. The concept calls further attention to consequences of management decisions: actions (and non-actions) that may be taken in response to biological realities or political expediency. The ideas presented here should not be construed as a condemnation of most or all forest management activities, as advocated by some individuals and organizations, but as a framework employed to make more informed management decisions.

Because of those disease-causing fungi that are endemic to forest ecosystems, forest tree root diseases are sometimes viewed as performing beneficial functions, among which are creating gaps in forest canopies, decomposing woody debris, or producing cavities for wildlife. Depending

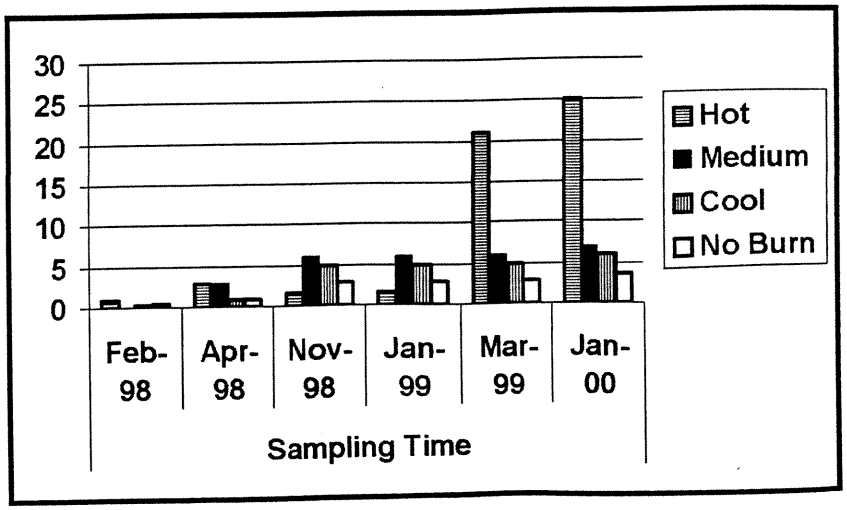

Figure 13.1. Delayed mortality after initiation of prescribed burning treatments in a longleaf pine stand. Mortality was greatest in the hot burn treatment, although temperatures at the soil-organic matter interface averaged < 61° C. Abundant fine roots in the organic matter layer were killed or damaged, although not consumed by the burn treatments. This is hypothesized as an important factor in the decline syndrome after fire reintroduction, an example of an "exotic" longleaf pine ecosystem

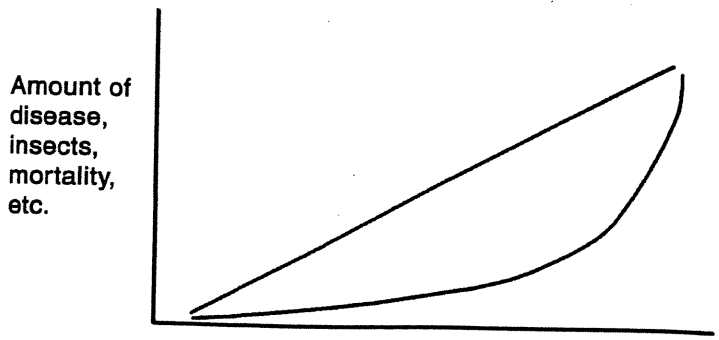

Figure 13.2. Conceptual model of "exotic" or pathologically unstable ecosystem. The curved line represents ecosystems that have a degree of stability or resiliency toward disturbance or management activities. From a forest pathological viewpoint, the land manager's challenge is to determine the "exoticness" of a particular forest ecosystem.

upon management objectives, root diseases thus are not detrimental. Such a notion presumes their function and regulatory dynamics are the same at present as they were prior to application of various management activities and environmental changes. On the other hand, we must consider the idea that some ecosystems are comprised of tree species that are maladapted to current conditions, that is, presently existing outside their evolutionary adaptations, resulting in varying degrees of instability (Moir and Mowrer 1995). Some members of the forest management community articulate an objective to attain "pre-settlement" conditions as a desired future condition in certain forest stands. Even if a precise knowledge of pre-settlement conditions existed, there are formidable obstacles to attaining these goals in some measure because "The affected ecosystems may follow presently unknown rules of ecosystem reorganization and may also be in a period of instability...." (Moir and Mowrer 1995).

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 fuel. The recent focus on forest health issues acknowledges the importance of fire in many forest ecosystems, and recommends reintroduction of fire to these stands. Forest stands in these situations should be regarded as exotic ecosystems (Figure 13.2) requiring appropriate caution. The new set of initial conditions may bring about unexpected root disease or other forest health problems when fire is reintroduced. A "one size fits all" approach to managing ecosystems or a focus on a single issue or species can result in negative outcomes. On the other hand, many forest ecosystems are quite resilient and stable under various management regimes. It is imperative that we strive to identify and understand disease processes resulting from new sets of ecological conditions in order to recognize exotic ecosystems and the circumstances under which pathological instability and unpredictability may develop.

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