

Fungi and diseases — natural components of healthy forests¹

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Abstract: Forest health is described and perceived in different ways by the general public, land owners, managers, politicians, and scientists, depending on their values and objectives. Native tree pathogens and diseases are often associated with negative impacts even though damage is limited or not widespread. Too often, the concepts of tree health and forest health are used interchangeably and are not related to scale. Similar to fire, occurrences of disease outbreaks focus on the negative effects. However, native pathogens often exist in equilibrium with natural forest communities so their critical ecological roles are not easily discernible. Examined holistically, native fungi and diseases, dead and dying trees, and the many complex ecological interactions among them provide valuable benefits that ultimately contribute to sustainable, healthy forest ecosystems.

Key words: forest succession, wildlife habitat, forest diversity, forest management, forest health, tree health.

Résumé : Le public en général, les propriétaires de boisés, les aménagistes, les politiciens et les scientifiques perçoivent et décrivent la santé de la forêt de façons différentes, selon leurs valeurs et leurs objectifs. On associe souvent les pathogènes et les maladies des arbres à des impacts négatifs, bien que les dommages soient limités et de faible étendue. Trop souvent, les concepts de la santé des arbres et des forêts sont confondus n'étant pas reliés à l'échelle du phénomène. Tout comme pour le feu, on ne note que les effets négatifs des incidences de maladies épidémiques. Cependant, les pathogènes indigènes vivent souvent en équilibre avec les communautés forestières naturelles, de sorte qu'il n'est pas facile de discerner leurs rôles écologiques critiques. Examinés dans leur ensemble, les champignons et les maladies, les arbres morts ou mourants, ainsi que de nombreuses interactions écologiques complexes entre eux, représentent de précieux bénéfices qui contribuent ultimement au maintien durable d'écosystèmes en santé.

Mots-clés : succession forestière, habitat de la faune, diversité forestière, aménagement forestier, santé des forêts, santé des arbres.

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Introduction

Definitions of forest health

Forest health is a subject increasingly discussed among land managers, woodland owners, political leaders, and the general public alike. But exactly what do people mean by forest health, and is there a common vision of what a healthy forest looks like? The Society of American Foresters (SAF) define forest health as "the perceived condition of a forest derived from concerns about such factors as its age, structure, composition, function, vigor, presence of unusual levels of insects or disease, and resilience to disturbance" (Helms 1998).

Two perspectives of forest health, a utilitarian or economic and an ecosystem concept, have been described (Kolb et al. 1994). People who define forest health using the utilitarian concept often consider timber production of primary importance and so dying trees represent an unhealthy con-

dition. Under the ecosystem concept a range of objectives in addition to timber management is desired and health is defined in terms of function and resilience to disturbance.

The issue of forest health is complex, and definitions and descriptions of healthy forests often reflect the varied values of forests to individuals and interested segments of society. However, common to many definitions of forest health are the elements of biological diversity, a balance among vegetation mortality, regeneration and growth, and the capacity to recover from stress factors and disturbance.

Forest health and ecological considerations

Forests are made up of more than just trees; they are ecosystems with extensive tree cover, wildlife, and associated processes as defined by SAF (Helms 1998). Maintaining diverse habitats for all wildlife species across landscapes is an objective of sustaining healthy ecosystems. Although tree

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diseases can cause large economic losses, they also create critical habitat for many species of wildlife we value.

Within forests, naturally occurring pathogens are critical components in many ecosystem processes. The dynamics and diversity of forested landscapes can be shaped by pathogens, and diseases can influence landscape patterns (Holdenrieder et al. 2004). Pathogens and insect pests respond to changing forest conditions and their activities can contribute to the maintenance or recovery of long-term forest function equilibrium (Schowalter 1994; Filip et al. 1996). Native pathogens can contribute to species diversity, alter plant succession, provide unique habitat structure and biological legacies and regulate stand density and nutrient availability.

Leopold (1966) recognized the value of pathogens to wildlife when he wrote "But for diseases and insect pests, there would likely be no food in these trees, and hence no chickadees to add cheer to my woods in winter." Many birds and small mammals prey on forest insect pests. With the exception of periodic large outbreaks, birds and mammals along with other factors maintain insect pest populations below damaging levels (Filip et al. 1996).

In this paper we review recent literature exploring the role of native fungi and diseases in relation to forest health in the broad sense. We provide examples from the literature and our research that suggest sustainable forest ecosystems include many native fungi and diseases that provide critical ecosystem functions in addition to carbon and nutrient cycling and the many critical mycorrhizal associations between fungi and roots of higher plants.

Holistic examination of forest health

Diseases, stand growth, and forest succession

Tree death is a natural but complex ecological process (Franklin et al. 1987) in which one or several pathogens and other microbes are often involved. Many fungi are pathogens of specific tree species causing tree mortality in highly susceptible trees. For example, the facultative fungal parasite *Melanamphora spinifera* (Wall.) Laflamme is killing beech (*Fagus sylvatica* L.) of all ages in Europe, by colonizing the cambium at the root collar of suppressed trees only (Laflamme 1975). This basal canker is also present in North America on *Fagus grandifolia* Ehrh. (Sterner and Davidson 1984). Thus, pathogens can influence tree density and the rate and direction of forest succession (Haack and Byler 1993; Castello et al. 1995). In addition, the activity and impact of fungi are highly influenced by microclimate that can determine spatial patterns of affected trees across the landscape. In the United States, the incidence of blister rust on white pine (*Pinus strobus* L.) caused by *Cronartium ribicola* Fischer is largely determined by microclimatic conditions (Van Arsdel 1965).

The ecological roles of dead trees in forest ecosystems continue long after they die. Falling dead trees and snags injure or kill additional trees, disturb and mix soil, and create suitable microsites as seedbeds. As substrates and resources for tree regeneration, decaying logs are important sites for seedling recruitment (McGee and Birmingham 1997).

Manion and Griffin (2001) provide evidence that in natural stands, a predictable level of tree mortality is essential

for sustaining healthy forests. The loss in health of some species is compensated for by the enhanced development of other species resulting in a balanced forest system. Pathogens can thus serve as thinning agents, regulating stand density and species composition.

In the temperate zone, balsam fir (*Abies balsamea* (L.) Mill) trees growing on dry sites are gradually invaded by a root and butt fungus *Perenniporia subacida* (Peck) Donk. This pathogen does not usually kill trees, but it reduces their mechanical wind firmness. Windthrow in mature stands creates large canopy gaps that help in the regeneration of other conifer species (Boulet 2003). *Inonotus tomentosus* (Fr:Fr) P. Karst. causes a similar phenomenon in mature spruce (*Picea* spp.) growing in maritime climates (Whitney 1988).

Dwarf mistletoes (*Arceuthobium* spp.) and root-rot fungi slowly kill trees in expanding infection centers creating canopy gaps that are often invaded by tree species that are resistant to these diseases, changing the forest composition and dynamics of species succession. Annosus root rot caused by *Heterobasidion annosum* (Fr.) Bref. is typical of a root-rot organism that results in infection centers. On poor sites planted with red pine (*Pinus resinosa* Ait.) in eastern Canada, *H. annosum* invades through fresh stumps after thinning. The disease eventually progresses to neighboring trees, killing them, as well as regenerating conifers. Hardwood species, such as ash (*Fraxinus* spp.) and oak (*Quercus* spp.), are not susceptible to root rot, so they are able to colonize the infection centers. Similar observations are reported from Europe (Korhonen et al. 1998).

The North American race of *Gremmeniella abietina* (Lagerb.), the cause of scleroderris canker, can damage jack (*Pinus banksiana*) Lamb. and red pine. However, study of the disease in natural jack pine regeneration found that epidemic levels of the disease did not result in excessive seedling mortality or negative growth impacts (Laflamme 2005). Instead, the disease served as a natural selection agent, regulating stand density and providing a benefit to the developing stand.

Diseases and forest diversity

The positive role that native pathogens play in forest ecosystems, largely overshadowed in the past by their obvious destructive actions when they interfered with timber management goals, is increasingly being recognized (Ostry and Nicholls 1997; Winder and Shamoun 2006). Pathogens exert selection forces on plant communities and shape the size and structure of plant populations, often leading to changes in species diversity. Pathogens may also influence the occurrence and spatial distribution of disease resistance genes (Burdon 1991). Pathogenic activities cause diversification among species and genera, as well as within species, owing to genotypic differences in disease resistance (Dinoor and Eshed 1984).

Root diseases can create unique habitats within infection centers that may favour plant and animal species not adapted to the dense, unaffected portions of forests, and thereby increase diversity across landscapes (van der Kamp 1991). Similarly, decaying logs provide unique habitats supporting seedling communities of different species from other sites on the forest floor, increasing tree diversity (McGee and Birmingham 1997).

The actions of fungi and disease create spatial and temporal diversity in plant species, age classes, and habitat for wildlife within forest stands and across landscapes. The resulting tree death creates new resources such as light, nutrients, seedbeds, and moisture that contribute to future stand development and stability.

Fungi, diseases, and wildlife interactions

Many species of wildlife derive numerous benefits, including shelter and food, directly and indirectly from the actions of fungi and diseases. Many wildlife species require healthy, dying, and standing or fallen dead trees to complete their life cycle. Tree pathogens change plant communities in ways that can increase species diversity, alter succession, and result in structural changes providing, for instance, snags and down wood that improve bird and mammal habitat and are critical in maintaining and enhancing essential food webs.

Dwarf mistletoes kill several coniferous species throughout the northern hemisphere, and have significant impact on timber production. However, the result of infestation by dwarf mistletoes on trees can be to attract many species of wildlife and provide them with numerous benefits (Bennetts et al. 1996). Mistletoes create openings in canopies that result in sites favorable for the establishment of a diverse array of plant species that in turn provide habitat for wildlife that otherwise would not be attracted to unaffected areas. Mistletoe shoots are a food source and are eaten by some mammal and bird species. Birds are attracted to trees affected by dwarf mistletoe, where they prey on insects associated with the dying and dead trees. Trees with mistletoe brooms are used by wildlife more frequently than unbroomed trees for foraging, caching food, nesting, roosting, and resting (Mathiasen et al. 2004).

White trunk rot caused by *Phellinus tremulae* (Bondartsev) Bondartsev & Borisov results in increasingly large volume losses in stands of trembling aspen (*Populus tremuloides* Michx.) as they age. However, many primary and secondary cavity nesting birds and mammals require infected trees, which are preferentially selected because of the habitat they provide (Kilham 1971; Hart and Hart 2001; Nicholls and Ostry 2003).

Hypoxylon canker caused by *Entoleuca mammata* (Wahlenberg:Fr.) J.D. Rogers & Y.M. Ju is the most damaging disease of aspen in the Lake States of Minnesota, Wisconsin, and Michigan, but various insects associated with infected trees are important prey for species of woodpeckers (Ostry and Anderson 1998). These insects, some of which feed directly on the fungus, are attracted to the cankers and in turn are sought out by woodpeckers, which remove these insects from under the diseased bark.

These interactions among fungi, diseases, and wildlife are only a few examples of the benefits of native pathogens in forest systems. Undoubtedly, with additional studies, numerous other examples of native fungi and diseases providing critical benefits to healthy forest ecosystems will be found.

Implications for forest management

Native pathogens are natural components of forests, and under normal conditions they are in equilibrium within the

ecosystem and provide critical services that often improve forest diversity. In natural plant communities, genetic, ecological and pathological factors are in dynamic equilibrium and the level of disease is usually very low (Dinoor and Eshed 1984).

This dynamic balanced equilibrium in the system can be altered to favour a pathogen when forest management alters one or more interacting components. Often disease outbreaks are indicative of the existence of less-than-optimum underlying forest conditions, and their presence alone is not necessarily the cause of the perceived reduced forest health status.

Dying and dead trees, trees with decay, snags, fungal fruit bodies, and downed wood are essential in providing habitat for many life forms and serve many ecological functions, including supporting populations of natural enemies, parasites, and predators of insect pests (Nebeker 1989; Torgerson et al. 1990; Komonen 2003). Forest managers should consider the size and distribution of dead wood in forests under management today, and be able to estimate future recruitment of deadwood to maintain forest structure following harvest (Shifley et al. 1997). Fungi and diseases, while they are sometimes considered disturbance agents that may interfere with timber management objectives, more often should be viewed holistically as contributing to the maintenance of functions, diversity, and resiliency of forest systems.

Forest managers should learn to recognize the value of these interactions at the landscape scale, and weigh their management decisions in regard to forest health to enhance multiple values and long-term ecosystem sustainability. Enhanced understanding of the long-term influence of diseases on forest systems will enable managers to make informed decisions on what, if any, intervention is needed to avoid or reduce crop loss but at the same time maintain healthy forest functions and services.

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