RESEARCH SUMMARY

forest sciences
NELSON FOREST REGION

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The Life Cycle and Dynamics of *Armillaria ostoyae*

■ **understanding the life cycle and dynamics of *Armillaria ostoyae* is critical to better forest management**

INTRODUCTION

Armillaria ostoyae is the primary root pathogen of conifers in the southern half of British Columbia. In order to manage sites infected by *A. ostoyae*, the life cycle and dynamics of the fungus must be understood.

DISEASE LIFE CYCLE

Armillaria ostoyae can survive in two distinct phases: as a parasite actively colonizing living trees, or as a saprophyte using a dead host's root system as a food base.

Parasitic Phase:
The most damaging phase of *A. ostoyae* is the parasitic or pathogenic phase. In this phase, the fungus infects a living host plant, colonizes it, and often kills it. The time from infection to death varies considerably and may take anywhere from a few years to several decades.

Armillaria ostoyae uses inoculum to attack and infect new hosts. The inoculum can be either mycelia or rhizomorphs. The mycelia of *A. ostoyae* spread through root-to-root contacts between infected and uninfected trees. They spread on or in woody substrates and cannot spread through soil. Mycelia spread from infected roots into the outer bark of uninfected roots that they come into contact with. From here they spread in a fan-shaped pattern through the bark of the newly infected host. As the infected bark area increases, the fans begin to penetrate into the cambium of the new host. Eventually they spread up the roots, to the cambium at the root collar, girdling the stem and killing the tree (6).

Armillaria ostoyae also initiates new infections via rhizomorphs. Rhizomorphs are root-like structures (1 to 3 mm. in diameter) that originate on a colonized root system and spread from there through the soil. Rhizomorphs of *A. ostoyae* can grow up to a metre from a host tree's root system. When a rhizomorph encounters a suitable host root, it attaches itself to the root and attempts to infect it


Characteristic mycelial fans of *Armillaria ostoyae*

by penetrating its bark (6). Rhizomorphs have only a limited inoculum potential (see below) and this decreases with increasing distance from the host material. Colonization of a potential host is often only successful within 30 cm or so of the original host material, and on the roots of young trees (i.e. less than 10 years old). Rhizomorphs are an important mechanism for the spread of root disease in juvenile stands, and may also play a role in disease intensification within root systems.

Armillaria ostoyae may also be present as inactive lesions on the root system of a living host without spreading significantly or causing disease symptoms. This equilibrium may be disturbed by biotic factors such as bark beetles or blister rust, or by human factors such as partial cutting. Factors such as these appear to upset the balance between the tree and the fungus, and the fungus begins to spread. This shift from an inactive state to an active parasitic state is poorly understood (Morrison, pers. comm.).

Saphrophytic Phase:
The saprophytic phase of *A. ostoyae* occurs following host tree death. This phase allows the fungus to persist in a dead host so it can take full advantage of the food supplies found in the host's tissues. *Armillaria ostoyae* is a weak saprophytic competitor so it must colonize its hosts prior to their death. In this way, it can become established ahead of other more competitive saprophytic fungi. Once established in a host tree or stump, the fungus can persist as a saphrophyte for decades (depending on the size of the host) until the food base becomes depleted.

Armillaria ostoyae may persist on a site indefinitely (i.e. for centuries) because of its ability to act both parasitically and saphrophytically. The parasitic phase of the fungus can infect a continual supply of living, susceptible hosts. As these hosts die, the fungus acts saphrophytically to utilize the food substrates contained in them (6). The fungus decays its host's tissues and uses the cellulose in them as a food base. The fungus in the tissues is a source of inoculum which is capable of attacking and infecting new hosts.

Some sources suggest that mushroom spores may be an additional mechanism responsible for the long distance spread of *A. ostoyae* (Reiche pers. comm.). However, current indications are that disease spread from spores is relatively insignificant for *A. ostoyae* (Morrison, pers. comm.).

DISEASE DYNAMICS

The ability of *A. ostoyae* to spread and colonize new hosts (via mycelial inoculum or rhizomorphs) depends on several factors. These include: the inoculum potential on a site, the presence of susceptible hosts, and the vigour of the fungus. Each is discussed below.

Inoculum Potential
Inoculum potential refers to the energy available to a fungus for infecting potential hosts. Unless an inoculum source has the potential to initiate attacks on living trees, it is of little concern as a disease agent. The predominant inoculum of *Armillaria ostoyae* is mycelial inoculum. Several factors affect the abundance of mycelia and their inoculum potential. These include: the size of the substrate in which the mycelia persist, the nutrient (food) content of the substrate, and the presence of competing organisms.

The effect of substrate size on the amount of inoculum seems fairly straight forward; the larger the substrate, the more inoculum may be present. *A. ostoyae* must infect a host while the host is living. In many cases, the fungus is held at bay by the host tree's defence mechanisms and does not spread significantly until the host dies (this can take decades). In some cases, the fungus will spread throughout the cambium of the roots and lower bole of the host, forming characteristic mycelial fans, and killing the tree within a few years. In both cases, the death of the host allows a very rapid expansion of the fungus in the host tissues.

This rapid colonization of the host provides high levels of inoculum with high inoculum potential. This allows the fungus to attack new hosts through either mycelial or rhizomorph inoculum. In order for the inoculum to remain vigorous, the fungus needs new sources of energy.

The ability of *Armillaria* to utilize woody substrates as food seems to be enhanced by the presence of sugars or starches (2). Evidence indicates that the sugar content in the roots of many tree species may increase when a tree is stressed, and that phenolic compounds which might combat infection may be reduced (2). The decline in phenolic compounds may increase a tree's susceptibility to *Armillaria* attack, and the elevated starch and sugar content presumably increases inoculum vigour. This results in increased inoculum potential.

Over time, sugars and other suitable foods in a host's tissues become depleted, and the inoculum potential of the *Armillaria* fungi using that host drops. Other saprophytic organisms capable of using these poorer substrates more effectively eventually colonize the tissue, and the energy available to *Armillaria* for inoculating new substrates is reduced.

Presence of Susceptible Hosts
The presence of susceptible hosts is critical to the persistence of *Armillaria* on a site. *A. ostoyae* can survive saprophytically in the roots of a large stump for decades, until the food base becomes depleted. However, its long term survival on a site requires an ongoing supply of living, susceptible hosts. These are trees or shrubs that are not resistant to attack and are available for colonization by the fungus.

<u>Species Resistance</u>
Armillaria ostoyae can attack all tree species found in B.C. although conifers are its principal host (12). The fungus may also infect many woody shrubs (i.e. false box, false azalea) and some herbaceous plants.

It appears that conifers less than 15 years old (regardless of species) are quite susceptible to *A. ostoyae* (6) The susceptibility of older trees varies according to host species. The susceptibility of older trees has been ranked by Morrison et. al. (6). However, there is some evidence that this ranking may vary (12) and it is subject to change as new information becomes available. The ranking suggested by Morrison et. al. (from most susceptible to least) is as follows:

> Douglas-fir > Abies spp. > spruce > lodgepole pine > hemlock > cedar > ponderosa pine > birch > larch

Morrison et al (6) do not recommend planting susceptible or moderately susceptible species when trying to regenerate infected sites. Larch and birch are the only species on this list that show sufficient potential (as resistant species) to be planted in infected areas. However, plantations of these species will, in many cases, be limited by silvicultural constraints. Where these species are well suited to a site, even they will be susceptible to the disease initially.

Woods (12) questions the position of larch in the ranking, and suggests that more research is needed prior to making management decisions based upon the species susceptibility ranking. Van der Kamp (UBC, pers. comm.) suggests that the relative susceptibility ranking of older trees may vary depending on factors such as site productivity. Others suggest that site moisture, and the occurrence of heart rot, mistletoe, and other damaging agents may also affect species susceptibility.

Host Condition

The condition, or vigour, of potential hosts also has a significant influence on susceptibility to infection. Potential host trees have mechanisms, such as resinosus or the formation of callus tissues, by which they can fight off *Armillaria* infections. Young trees (up to age 15) generally have poorly developed defence mechanisms and are unable to resist *Armillaria* infection. In healthy older trees however, an *A. ostoyae* attack may be held in check indefinitely if the vigour of the fungus is not too great. The ability of a tree to resist an attack is in part determined by the level of stress it may be under due to various factors.

There are a number of hypotheses to explain why some trees are more susceptible to *A. ostoyae* than others. Morrison (pers. comm) suggests that the incidence and damage of *A. ostoyae* are greater in areas with better site productivity (pers. comm. 1994). Harvey (3) discusses the susceptibility of poorly site-adapted species to infection. Nutrient levels and pH levels low enough to affect seedling vigour result in more infection and more mortality from *Armillaria* root disease (10). Moore et. al. (5) suggest that it may be possible to manipulate a tree's nutritional status (through potassium fertilization) so that the tree's root chemistry is altered to the detriment of *A. ostoyae*. Vigorous seedlings show more resinosus and callus formation (signs that they are fighting the attack) than less vigorous ones. However, vigorous growth caused by fertilization may mask the symptoms of infection rather than reduce the level of infection (9). Suppressed trees appear to be more susceptible to *A. ostoyae* infection (1). Other common stress factors that may increase susceptibility include drought, insect defoliation, and light or nitrogen deficiency (11). Human activities such as site disturbance (4) or pollution can also influence host vigour and may have a significant influence on susceptibility.

Armillaria Vigour

The vigour of *A. ostoyae* is determined primarily by food base characteristics. However, various environmental characteristics may also affect vigor and rate of spread. These include soil conditions such as moisture, temperature, O^2/CO^2 balance, and texture.

Another significant factor affecting the vigour of *Armillaria* appears to be human disturbance. Partial cutting, precommercial thinning, and broad-leaved brush control have the potential to increase inoculum loads on forested sites (6).

Fire can affect *Armillaria* vigor by modifying a number of site variables. Fire alters the vegetation community present on a site and post fire species may have different susceptibility to *Armillaria* root disease than species previously present. Fire also alters soil characteristics such as pH, nutrient status, and organic matter content. This may affect the vigour of various soil fungi, including *A. ostoyae* and fungi that are antagonistic to *A. ostoyae*. For example, populations of *Hypholoma* and *Trichoderma* fungi, both of which are antagonistic to *Armillaria*, may be increased by fire (7, 8).

A better understanding of the lifecycle and dynamics of *Armillaria* fungi is critical to ensuring that forest management activities do not increase the intensity of *Armillaria* root disease in forested areas.

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