THE BEHAVIOUR AND IMPACTS OF *ARMILLARIA OSTOYAE* IN MATURE STANDS AND PLANTATIONS IN THE SHUSWAP REGION OF BRITISH COLUMBIA

by

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ABSTRACT

Armillaria ostoyae causes considerable loss in forest productivity in both immature and mature stands within the Interior Cedar Hemlock (ICH) and the Interior Douglas-fir (IDF) zones of the southern interior of British Columbia. Two studies concerning the impacts of this pathogen where conducted near Salmon Arm, B.C.; one was within four plantations age ten to twenty-five years on Larch Hills, and the other was within mature stands on Hunter's Range and Larch Hills.

In the plantation study the relationship between the levels of *A. ostoyae* infection in mature tree stumps and the regeneration was examined. The evidence of past *A. ostoyae* infection in stumps remains visible on the inner bark for at least thirty years. This evidence may be used to estimate the extent of the disease in the former stand. The relationship between *A. ostoyae* in stumps and *A. ostoyae*-caused mortality in regeneration was significant, though not strongly. Three measures of stump inoculum were compared: the proportion of stumps infected, the number of stumps infected, and the basal area of stumps infected. The number of stumps infected was most closely associated with the proportion of regeneration infected. The relative rates of infection incidence were compared among the eight regeneration species present in the four plantations. A quantitative means of comparing the incidence of infection among species was developed. The number of infected Douglas-fir trees was chosen as a standard measure of disease incidence for each plantation. The incidence of infection in the other seven species were then compared to the Douglas-fir standard. The probability of a young tree becoming infected with *A. ostoyae* did not increase as the distance from an infected stump was reduced. Brushing in one of the twenty-five year old plantations significantly increased the mortality caused by *A. ostoyae*.

The second study was concerned with the impacts of *A. ostoyae* in mature stands approximately 120 years old. The relative rates of incidence of *A. ostoyae* infection were compared between species. The incidence of infection for Western larch (*Larix occidentalis*) was no less than that for Douglas-fir (*Pseudotsuga menziesii*). The ranking of tree species susceptibility may depend more on site than on inherent differences among species. An *A. ostoyae* severity rating system was developed. This system assigned plots a rating based on the proportion of conifer trees infected out of the total number of conifers in the plot. This severity rating was then used in analyses to test the relationship between *A. ostoyae* severity and a variety of site characteristics, including elevation, logging disturbance, site index, and biogeoclimatic site classification. Of these characteristics, past logging disturbance was mostly closely associated with high levels *A. ostoyae* severity. The relationship between the biogeoclimatic ecological classification system and *A. ostoyae* incidence and severity was examined. The ICH zone had significantly more *A. ostoyae* infection than the IDF zone. More detailed analyses using site units within both the ICH and IDF zones did not indicate any significant relationships. The *A. ostoyae* severity rating was also compared to timber volumes. There was a significant relationship between *A. ostoyae* severity and conifer volume in 120 year old stands in the ICH zone. The most severely infected plots had significantly less conifer volume than the less heavily infected areas. There was no significant relationship between *A. ostoyae* severity and conifer volume in the IDF zone. However, there was a clear trend towards lower conifer volumes with increasing *A. ostoyae* severity.

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CHAPTER 1 GENERAL INTRODUCTION

Armillaria ostoyae (Romagn.) Herink, which causes Armillaria root disease, is one of the most serious forest pathogens in southern British Columbia and the Pacific Northwest states (Morrison *et al.* 1985, Wargo and Shaw 1985). *Armillaria ostoyae* reduces timber productivity by reducing tree growth, predisposing trees to attack by insects and other pathogens, and by causing direct mortality.

Armillaria ostoyae has a parasitic phase where the pathogen can aggressively colonize new hosts, and a saprophytic phase where the fungus utilizes the colonized food base for growth (Morrison 1981). In the saprophytic phase, *A. ostoyae* can survive for decades in the large woody portions of its host following host mortality. The persistence of the fungus on site results in long term losses in timber production on sites infested by this pathogen.

Armillaria ostoyae behaves quite differently on the coastal portions of its range compared to the interior. West of the coast mountain range in British Columbia *A. ostoyae* is primarily a disease of young plantations (Morrison 1981). In this area, mortality caused by the disease is normally restricted to trees less than 25 years of age, although trees under severe stress may be killed at any age. *Armillaria ostoyae* impacts are more severe east of the coast mountain range in the southern interior of British Columbia as the pathogen continues to kill trees throughout their rotation (Morrison 1981). In the southern interior, the impacts of *A. ostoyae* are most pronounced in the Interior Cedar Hemlock (ICH) biogeoclimatic zone, but are also felt in the Interior Douglas-Fir (IDF), Montane Spruce (MS), and Sub-Boreal Spruce (SBS) zones (Morrison *et al.* 1991a). The ICH zone has the greatest diversity of tree species of any biogeoclimatic zone in British Columbia. *Armillaria ostoyae* is an integral component of this zone and is at least in part responsible for the species diversity found in these ecosystems. Morrison (1981) suggests *A. ostoyae* accelerates succession in this zone by killing pioneer species such as Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.), allowing the shade tolerant western hemlock (*Tsuga heterophyla* (Rafn.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) to move in.

These species are not distinctly less susceptible to *A. ostoyae*, but appear to be more tolerant (Morrison 1981). *Armillaria ostoyae* may also delay succession in this zone by maintaining heavily infested sites in early seral deciduous species. Deciduous species such as paper birch (*Betula papyrifera* Marsh.), when young, are the most tolerant species to this disease.

Annual losses of timber due to *A. ostoyae* within the ICH zone are estimated to be 105 000 cubic meters (Taylor 1986). The ICH zone is the most productive forest zone in the interior of British Columbia and is second only to the Coastal Western Hemlock (CWH) zone for productivity in all of Canada (Ketcheson *et al.* 1991). Potential gains in productivity from reducing *A. ostoyae* impacts are therefore high in the ICH zone. This research project concentrated on the behavior of *A. ostoyae* within the ICH zone.

The first objective of this study was to develop a better understanding of the development of *A. ostoyae* in plantations established on sites that were previously infested with the disease. A second objective was to determine which factors out of biogeoclimatic site type, site index, disturbance history and elevation have the greatest influence on the distribution and intensity of *A. ostoyae* within the southern interior of British Columbia. The impact of *A. ostoyae* severity on timber volume was also examined.

This thesis consists of four chapters. Chapter 1 is a general introductory chapter which includes a brief literature review of the background biology of *A. ostoyae* as well as a review of literature relevant to Chapters 2 and 3. Chapter 2 covers an examination of the relationship between past levels of *A. ostoyae* infection in mature stands and the subsequent levels of infection in plantations once those mature stands are harvested and regenerated. Chapter 3 covers an examination of the relationship between *A. ostoyae* infection severity and several site factors. These site factors included biogeoclimatic site classification, elevation, prior logging disturbance, and site index. The impact of various levels of *A. ostoyae* infestations on timber volume was also examined. Chapters 2 and 3 both contain four sections: introduction, methods, results and discussion. Chapter 4 consists of the conclusions drawn from the examinations conducted in Chapters 2 and 3.

1.1 The Genus *Armillaria*

Armillaria ostoyae is one of approximately 36 species that belongs to the genus *Armillaria* within the order Agaricales (Watling *et al.* 1991). Several features of the *Armillaria* genus are distinctive from other members of the order. These features include the apparent diploid nuclei in vegetative mycelium, the presence of both parasitic and saprophytic capabilities, and the production of rhizomorphs. Fruiting bodies (basidiomes) are essential for the complete description and naming of species (Watling *et al.* 1991). Two species of *Armillaria* occur throughout the southern interior of British Columbia, *A. sinapina* and *A. ostoyae* (Morrison *et al.* 1985). Species of *Armillaria* occur worldwide. For example *A. borealis* occurs in northern Europe and Russia, *A. luteobubalina* in Australia, and *A. montagnei* in South America (Watling *et al.* 1991). *Armillaria ostoyae* and *A. gallica* are two of the most widely distributed species and are circumpolar within the northern hemisphere (Guillaumin *et al.* 1989).

1.1.1 Parasitic and Saprophytic Phases

Armillaria spp. have both saprophytic and parasitic phases in their life cycle. Within the genus, species differ widely in pathogenicity. Highly pathogenic species such as *A. ostoyae* survive saprophytically in the hosts they have killed during their parasitic phase. *Armillaria ostoyae*, however, appears to be a weak saprophytic competitor. Unless the fungus has colonized host tissue prior to host death, *A. ostoyae* is considered incapable of replacing other fungi in dead stump tissue (Garrett 1970). Thus, stumps that exhibit signs of *A. ostoyae* infection were infected prior to the death of the stump. Stump tissues, although greatly weakened, remain alive for a year or more following cutting which allows *A. ostoyae* to rapidly colonize the entire stump in the absence of competition from obligate saprophytes. Cut stumps, therefore, provide *A. ostoyae* with large sources of inoculum and give the fungus an advantage over competing fungi. Trees killed by *A. ostoyae* also represent large sources of inoculum, however, the fungus has to exert much more energy in order to create that food supply. In this case, *A. ostoyae* not only has to infect the host, but also has to battle with the host's natural resistance mechanisms in order to provide the food supply for the saprophytic stage. Whether the increase in *A. ostoyae* inoculum is the result of logging or from disease-caused mortality, once the inoculum potential is high on a site, the disease may spread rapidly from tree to tree across host root contacts. In mature stands the disease may continue to spread at a high rate until the disease contacts less susceptible hosts or reaches a natural barrier.

Infected stumps are the initial sources of inoculum in plantations. Very young trees growing in contact with infected stumps are quickly killed. These small trees do not contribute to the spread of the disease because of lack of root contacts and their low inoculum potential. The inoculum potential of the colonized stumps decreases with time as *A. ostoyae* and other saprophytic organisms consume the stump tissue. Consequently, in order for the disease to continue to spread in plantations, the young trees must reach a size where root contacts between trees are common and where newly killed trees represent significant amounts of food base for the pathogen.

Weak pathogens such as *A. sinapina* probably exist for the most part as saprophytes (Korhonen 1978, Rishbeth 1985, Wargo and Shaw 1985). Field observations of *A. sinapina* suggests that this species is not capable of attacking healthy conifers (Morrison *et al.* 1991a). Weak pathogenic species do have the ability to act as a facultative parasites on stressed or unhealthy hosts (Kile 1980, Rishbeth 1985, Wargo and Shaw 1985), as do highly pathogenic species such as *A. ostoyae*. The ability of the *Armillaria* genus in general to take on both parasitic and saprophytic roles has undoubtedly contributed to the success of the genus around the world.

1.2 The Disease

1.2.1 Inoculum Potential

All *Armillaria* species survive saprophytically in woody substrates in soil and may exhibit varying degrees of pathogenicity (Redfern and Filip 1991). The survival and vigor of an *Armillaria* clone depends primarily on its inoculum potential. Garrett defined (1960) and then redefined (1970) inoculum potential as "the energy of growth of a parasite available for infection of a host at the surface of the host organ to be infected". Inoculum potential is dependent upon the surface area of fungus in contact with the host, the vigor of the invading hyphae, and environmental effects on the fungus (Redfern and Filip 1991).

Inoculum potential of *Armillaria* spp. is also influenced by the distance between the host and an inoculum source. Inoculum potential is maximized where healthy roots and inoculum are in contact. Where gaps are bridged by rhizomorphs, the inoculum potential diminishes with increasing distance between inoculum source and host (Redfern and Filip 1991).

1.2.2 Inoculum Potential and Disease Dynamics

Inoculum potential of *A. ostoyae* on a site may be greatly increased by forestry operations such as clear-cutting, selective cutting, and thinning. Harvesting, particularly selective logging, has led to inoculum build up on many species of conifer stumps in western North American forests (Byler *et al.* 1990). For the pathogenic species of *Armillaria*, more inoculum typically results in more disease (Redfern and Filip 1991).

The inoculum distribution and potential on sites dictates to a large extent the dynamics of the disease. In natural undisturbed forests where *A. ostoyae* is present, diseased trees occur in groups or as scattered individuals around sources of inoculum (Morrison *et al.* 1991a). The disease may be actively attacking new hosts or be quiescent in lesions on infected tree roots. In these undisturbed forests, the mechanism responsible for *A. ostoyae* switching from a quiescent state to an active state is not well understood. Stresses caused by drought, insect attack or other diseases, such as white pine blister rust may play a role. In managed forests, the transition to the active, aggressive disease state is obvious. Following cutting, the stump is rapidly colonized from active infections or quiescent lesions. *Armillaria ostoyae* then produces a flush of rhizomorphs (Morrison *et al.* 1991a). The inoculum load is then at its maximum because the food base is freshly colonized (Morrison *et al.* 1991a).

In clearcut areas, there is usually a delay of four to five years following planting before significant mortality is observed. This is the length of time required for the fungus to fully colonize the stumps and for *A. ostoyae* rhizomorphs to contact the young tree roots. Mortality initiated by root contacts with an inoculum source does not appear until age ten to fifteen (Morrison *et al.* 1991a). Once there is root closure in a stand, *A. ostoyae* has the potential to spread until a physical or non-host barrier is encountered (Morrison *et al.* 1991a). Hagle and Goheen (1988) refer to a wave pattern of mortality that takes place as stands on infested sites reach pole size. Most of the young trees are killed before they reach a merchantable size and are replaced by abundant regeneration. Mortality then slows until some trees reach pole size and their root systems become large enough to provide the inoculum to fuel another wave of mortality. The primary difference between the wave pattern in undisturbed root disease infected stands and infected clearcut stands is that the cutting sets the time of the wave by creating an immediate food base and stimulating the regeneration that will feed the next wave (Hagle and Goheen 1988).

The conflict between stand management goals and *A. ostoyae* is most clearly demonstrated in partially cut stands. If the pathogen is present in well stocked stands, the impacts can be high. Well stocked and overstocked stands are the most logical candidates for partial harvests. Trees in these stands have a high probability of root contact. As previously mentioned, once an infected tree is harvested its entire root system is colonized. In partial cut operations, "leave" trees are then exposed to large sources of inoculum. Repeated partial harvests every fifteen to twenty years often result in severely infected sites on which few trees reach merchantable size (Morrison *et al.* 1991a). The negative impacts of partial cutting on timber supply in *A. ostoyae* infected stands is even greater when the more *A. ostoyae* tolerant tree species are selectively harvested (Hadfield 1984, Hagle and Goheen 1988). In the Pacific Northwest states, the combined effects of succession, fire control and selective harvesting has resulted in the removal of western white pine (*Pinus monticola* Dougl. ex D. Don), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and western larch (*Larix occidentalis* Nutt.) leaving a predominance of more susceptible species such as Douglas-fir and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl). Similar practices in the southern interior of British Columbia, involving the selective removal of western white pine, and larger Douglas-fir individuals have probably had similar effects on overall timber supply.

Fire also has an influence on the levels of *A. ostoyae* infestation. Fire may directly affect the activity of the pathogen in forests through reduction of inoculum or indirectly through stress effects on the fungal mycelium which leads to natural biocontrol (Reaves *et al.* 1990). On the other hand, fire may lead to a flush of *A. ostoyae* activity similar to that found in cut over areas. By killing infected trees, fire may allow the fungus to rapidly colonize the remaining portions of the tree leading to a build-up of inoculum on the site. Fire also influences the species which regenerate sites, favoring the early seral species such as Douglas-fir and lodgepole pine. These early seral species tend to be more susceptible to *A. ostoyae*. The success of *A. ostoyae* infections depend to a large extent on the inoculum potential. In order to control the disease, therefore, the inoculum potential on a site must be reduced.

1.2.3 Infection

Initial infection of a host occurs either through rhizomorph contact or through host root contact with an inoculum source. Recent work in Europe and North America suggests that rhizomorph production is more important in the less pathogenic species of *Armillaria*. The most pathogenic *Armillaria* species tend to spread primarily through root contacts (Gregory 1985, Morrison 1989).

Penetration of host root bark by rhizomorphs is both a chemical and a mechanical process. The processes vary depending on the host's root surface morphology (Thomas 1934). Root surface morphology typically changes with age, being smooth when the root is young and growing progressively rougher over time. In young roots a rhizomorph becomes attached initially by the hardening of the mucilaginous substance which covers its growing tip. Then, single hyphae developing from the rhizomorph tip penetrate the outer layer of cork cells and anchor the rhizomorph to the root (Morrison *et al.* 1991b). The rhizomorph then penetrates through the cork layer by exerting pressure while at the same time producing secretions which disrupt the cork cells.

In older, scaly roots, rhizomorphs may penetrate the bark scales and develop infection wedges beneath them. In the area surrounding the infection wedge, cell walls turn brown and cell contents are disrupted (Woeste 1956).

Infection may also occur at root contacts between healthy and infected trees. Zeller (1926), based on work on apple trees, suggested that infection of the new host begins when healthy bark contacts toxic substances produced by *A. mellea* in the diseased root. It has been suggested (Morrison *et al.* 1991b) that conifers may become infected in a similar manner. Mycelial fans of *A. ostoyae* first grow in a root's outer bark. As the area of infected bark increases, the mycelial fans penetrate to the inner phloem and cambium.

Mycelial fans act as a unit and continue to kill host tissue in the cambial zone, eventually girdling the root. Once the root is girdled, *A. ostoyae* rapidly colonizes the cambium of the remaining distal portions of the root. The fungus also spreads proximally from the point of infection towards the root collar and onto other primary roots. The location of infections is an important factor in disease development. The closer the initial infection is to the root collar, the more likely that the tree will be girdled and killed (Morrison *et al.* 1991a). Shaw (1980) found that the most lethal attacks on sapling and pole-sized ponderosa pines occurred high on the tap roots or on the root collar. Infections on lateral roots rarely resulted in lethal infections for this species. After a host is killed, its entire root system is rapidly colonized. Thus, the spread of the pathogen through root contacts can occur quite quickly, particularly in fully stocked stands. Shaw and Roth (1976) estimated the rate of spread of *A. mellea* in a ponderosa pine stand to be 1 m/year. Van der Kamp (1992) estimated the rate of *A. ostoyae* spread in a 110 year old interior Douglas-fir stand to be 0.22 m/year. A colonized root system may contain viable *Armillaria* spp. for up to 40 to 70 years after harvest, depending on the size of the stump and other environmental factors (Kile 1980b, Rishbeth 1972b, Shaw 1975).

1.2.4 Hosts

Armillaria species in general have a very broad host range. The factors which determine host preferences in natural stands are not well understood. In the southern interior of British Columbia, *A. ostoyae* attacks all tree species and some shrubs, although conifers are its principle host (Morrison *et al.* 1991a). The forests of the southern interior of B.C. are very species diverse. Conifer species found in this area include Douglas-fir, lodgepole pine, western larch, western redcedar, Engelmann spruce (*Picea engelmanni* Parry ex Engel.), western hemlock, western white pine, ponderosa pine, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), paper birch, and trembling aspen (*Populus tremuloides* Michx.) among others. Morrison *et al.* (1991a) suggested the following ranking of susceptibility among tree species in the southern interior of British Columbia (Table 1).

TABLE 1. Ranking of tree species susceptibility to *Armillaria ostoyae* in the southern interior of British Columbia (from Morrison *et al.* 1991a)

Susceptible:	*Abies* sp. Douglas-fir spruce
Moderately Susceptible:	lodgepole pine hemlock cedar
Tolerant:	ponderosa pine ?birch
Resistant:	larch

No tree species have shown resistance to *A. ostoyae* before the age of fifteen, with the possible exception of paper birch (Merler, B.C. MOF, unpublished data). *Armillaria ostoyae* can have a significant influence on stand composition due to the varying degrees of susceptibility in host species. Within the ICH zone, western redcedar, and paper birch often replace Douglas-fir as the principle species in stands infected with *A. ostoyae*. Although both conifer species exhibit similar susceptibility to initial infections of *A. ostoyae*, western redcedar tends to cope with infection better than Douglas-fir. Western redcedar is often able to surround infections with callus tissue preventing *A. ostoyae* from girdling and killing the tree. Douglas-fir is less successful at combating this pathogen and, once infected, is more rapidly girdled and killed. Western redcedar acts as an inoculum reservoir for *A. ostoyae* on a site, and prevents the disease from disappearing due to lack of inoculum. In the most severely infested areas, even western redcedar cannot survive, leaving paper birch and brush species to dominate the site.

1.2.5 Disease Recognition, Symptoms and Signs

Trees infected by *A. ostoyae* may exhibit some or all of the following symptoms, depending on tree age and location of infection: reduction of shoot growth, changes in foliar characteristics, stress induced reproduction, basal resinosis and death. The most widely accepted hypothesis describing the physiological basis for *A. ostoyae* symptom development involves the physical disruption of the hosts vascular system (Morrison *et al.* 1991b). Infected trees younger than ten years rarely show reduced leader growth prior to death, because mortality occurs within a year of infection (Hintikka 1974). Older, larger trees may show evidence of prolonged infection through reduced leader growth and rounded crowns. However, van der Kamp's (1992) work in a 110 year old Douglas-fir stand indicated that the average time between the first appearance of above ground evidence of infection (mainly basal resinosis) and tree death was only six years. Foliar symptoms in conifers also differ depending on duration of the infections. Trees which are killed quickly have red brown foliage which remains on the tree for approximately a year following death. In trees where the disease progresses more slowly the foliage becomes stunted, chlorotic and sparse throughout the crown (Morrison 1981). In response to advanced infection, usually in the season before death, many conifers produce a crop of cones that are smaller but may be more numerous than normal (Morrison *et al.* 1991a). Conifers which usually have resin canals (*Pseudotsuga, Picea, Larix and Pinus*), or those which form traumatic resin canals (*Tsuga* and *Abies*), may produce resin that exudes through bark fissures at or above the root collar when attacked by *A. ostoyae* (Morrison *et al.* 1991a). Resin exudation does not usually occur above ground until the fungus has reached the root collar. *Armillaria ostoyae* may be well established beneath the bark of a host before any signs of resinosis is visible on the outside of the bark.

Callused lesions are another basal stem indicator which is present in some conifer species, including Douglas-fir, western redcedar, western hemlock, western white pine and western larch. Infections in hosts of these species may be arrested by a strong host response once the trees are more than twenty years old (Morrison *et al.* 1991a). *Armillaria ostoyae* lesions can be surrounded by callusing and the spread of infection held in check. This phenomenon is most common in western redcedar, where the callusing results in flattened portions of the bole and eventual trunk fluting. Beneath the bark of the flattened areas is the characteristic triangular shaped lesion which is formed above the infected root.

Many of these symptoms are not specific to *A. ostoyae* infections and may be induced by several other biotic and abiotic factors. Confirmation of *A. ostoyae* infections requires an examination of the lower bole, root collar and occasionally the larger lateral roots in close proximity to the root collar, for specific signs of the fungus.

The specific signs used to confirm *A. ostoyae* infection include mycelial fans, rhizomorphs, and basidiomes. *Armillaria ostoyae* may also be further confirmed by culturing the pathogen from the host (Morrison *et al.* 1991b).

Mycelial fans beneath the bark are the most useful diagnostic characteristic of *A. ostoyae* in woody species. Mycelial fans may be present early in the infection beneath the bark prior to resinosis and host mortality. Mycelial fans are most abundant in the first few years following host death. They tend to disappear from the above ground portions of dead hosts over time as a result of competition from other fungi, desiccation, and possibly consumption by insects. On conifers, impressions of fans in resin and bark may be present for several years after the fans have gone (Morrison *et al.* 1991a). Under suitable conditions the mycelial fan impression in resin and bark of stumps may remain for over thirty years. These signs of past *A. ostoyae* infections are useful for determining past distribution and incidence of infection in cut over areas. Mycelial fans are also useful for determining the cause of callused basal lesions.

Rhizomorphs of *A. ostoyae* are initiated on a colonized root system and grow into the soil when a mycelial fan reaches the bark-soil interface (Morrison 1972). Rhizomorphs are white within one centimeter of the growing tip, becoming progressively darker shades of brown and eventually black. Rhizomorphs in soil and on the surface of roots are usually 1-3mm in diameter (Morrison 1972). Rhizomorph morphology may be used as a distinguishing feature to differentiate between species of *Armillaria*. Two species of *Armillaria* are widespread in the southern interior of British Columbia. *Armillaria sinapina* forms monopodially branched rhizomorphs which create extensive networks in soil and on root surfaces. *Armillaria ostoyae* forms dichotomously branched rhizomorphs which grow only a few centimeters from the food base (Morrison *et al.* 1991a).

The basidiomes of *A. ostoyae* are found in clusters on the stem of the host or in the soil above diseased roots. Basidiomes often occur on or near hosts lacking other above-ground signs and symptoms (Morrison *et al.* 1991a). In British Columbia, basidiomes typically form in late August through mid-October when favorable temperatures and precipitation occur. Mature basidiomes of *A. ostoyae* are 10-20cm tall, with a cream to brown cap 5-10cm wide with a distinct ring on the stem (Morrison *et al.* 1991a).

In conifers, wood with incipient *A. ostoyae* decay is stained gray to brown, often with a water-soaked appearance (Morrison *et al.* 1991a). Later, as *A. ostoyae* continues to decompose the lignin and cellulose components, the decayed wood becomes yellow brown and stringy, and eventually is reduced to very wet stringy rot, with pale yellow flecks (Williams *et* *al.* 1989). Decayed wood of broadleaved hosts is water soaked and white to yellow, becoming spongy and ultimately distinctly gelatinous (Greig and Strouts 1983).

1.3 Disease Detection and Assessment

1.3.1 Detection

Armillaria ostoyae may be detected in stands based on its signature (*i.e*, its diagnostic symptoms and signs). Stands infested with *A. ostoyae* may differ considerably in appearance. A large disease center may consist of openings of several hectares containing mostly deciduous and brush species with some young conifer regeneration, surrounded by a perimeter of dead and dying mature conifers. In less severely infected areas, western redcedar may survive as the sole conifer component making up the majority of the stocking inside the disease center. Throughout the perimeter of a disease center in older stands, stubs, snags and recently killed trees may be found. Islands of healthy conifers are also often found within disease center perimeters. These islands or "escapes" occupy areas in which viable *A. ostoyae* inoculum was not present at stand renewal. Such islands usually have symptomatic trees along their edges. *Armillaria ostoyae* may also be found in very small disease centers of only one or two infected trees. These small centers are often diffusely distributed throughout mature stands within the ICH zone. The diffuse nature of the infections in some stands makes some forms of surveying for *A. ostoyae* difficult.

1.3.2 Assessment

A variety of methods have been devised to detect *A. ostoyae* and to assess the extent and impacts of the disease. Williams and Leaphart (1978) used large scale colour infrared aerial photographs to estimate the area of root disease centers in northern Idaho. James *et al.* (1984) used a combination of large scale aerial photographs and existing timber inventory data to estimate root disease losses in northern Idaho and northwestern Montana. Similar methods using large scale aerial photography to assess extent of area infected and resulting timber losses in the southern interior of British Columbia have not yet been attempted. There are several potential problems associated with using these methods in this area. First, the infection center boundaries themselves are difficult to delineate in many areas due to the diffuse nature of disease distribution. Second, even in areas with discrete disease centers, the extent of disease outside those centers is impossible to estimate accurately from photographs. Dubreuil (1981) and James (1983) have found that many severely infected trees lack the crown symptoms that are necessary for photo identification. Wallis and Bloomberg (1981) indicated that only one half of root diseased trees within and adjacent to disease centers could be determined from above ground symptoms. Wallis and Bloomberg's work dealt with *Phellinus weirii* (Murr.) Gilbertson, but similar findings are likely for *A. ostoyae*.

Ground survey methods are probably most appropriate for assessing *A. ostoyae* extent and impact. The ground survey method developed for *P. weirii* by Bloomberg *et al.* (1980), along with modifications for multi-disease recording and stratification by disease intensity (Bloomberg 1983), is applicable for surveys of *A. ostoyae* (Morrison *et al.* 1991a). However, this method is difficult to apply in logged, burnt or open stands with diffuse disease distribution due to difficulty in locating boundaries of infection (Morrison *et al.* 1991a). Since many of the stands in the ICH biogeoclimatic zone are logged, burned or contain diffuse *A. ostoyae* infections, the applicability of the Bloomberg method in this zone is questionable.

Another ground survey method, the Pixel survey (Merler and Norris, B.C. Ministry of Forests, unpublished report), uses a series of systematically located transect lines running perpendicular to a base line (Morrison *et al.* 1991a). Pixels are plots that vary in size depending on the age and type of stand to be surveyed. Pixels are contiguous on both sides of the transect lines. Pixels are identified as being either diseased or disease free based on evidence of signs and symptoms of disease within their boundaries. Pixel surveys can provide information on distribution of *A. ostoyae* infected areas. A modification to the pixel survey which involves weighting trees based on dbh and infection status has recently been developed.

The modification renders a better estimate of disease intensity (Merler, B.C. Ministry of Forests, unpub.)

Armillaria ostoyae is known to occur in a large proportion of the ICH zone (Morrison *et al.* 1991a). Based on field observations in two study areas located in the ICH zone around Shuswap Lake, the extent of *A. ostoyae* infections in mature and immature stands within this zone is indeed great. Due to the extremely wide distribution of *A. ostoyae* in the ICH zone, the value of any detection survey made using any of the various methods, is questionable. If the disease is present almost everywhere, why survey to detect where it is? It is clear that the amount of disease detected using any of the survey methods depends on the amount of time and effort spent examining.

1.4 Summary

Armillaria ostoyae is one of the most serious forest pathogens in the southern interior of British Columbia. Several features of the *Armillaria* genus set it apart form other members of the Agaricales, including the production of rhizomorphs, diploid mycelium and the presence of both a parasitic and a saprophytic phase. The ability of *A. ostoyae* to colonize a host as a parasite and then survive in that host saprophytically for extended periods of time poses the greatest challenge for forest managers in their attempts to manage for the disease. The progress of *A. ostoyae* infections depends on the inoculum potential of the pathogen. Inoculum potential is defined as "the energy of growth that is available to the pathogen to infect a new host" (Garrett 1960). Inoculum potential depends on host species, food base size, degree of colonization by the disease, distance from an inoculum source, time since colonization and activity of other fungi and insects. The inoculum potential of a site can be influenced to a large extent by forestry operations and by fire. The amount and distribution of inoculum on a site dictates the spread of the disease. Infection of new hosts takes place either by rhizomorphs penetrating the bark of by root contact with an infected host.

Trees infected by *A. ostoyae* exhibit symptoms and specific signs that may be used to identify the disease. Symptoms include reductions in shoot growth, changes in foliar characteristics, stress induced reproduction, basal resinosis, wood decay and death. Signs of *A. ostoyae* include mycelial fans, rhizomorphs and basidiomes. The symptoms and signs of *A. ostoyae* along with the spatial distribution of infected trees within stands are collectively referred to as the disease's signature. The signature of *A. ostoyae* is used in surveys designed to estimate the extent and impact of the disease.

Most of the research regarding *A. ostoyae* in unmanaged forests in British Columbia has been concerned with the disease at only one point in the life of the stands. There has been very little documentation on the impacts of *A. ostoyae* in the transition from unmanaged mature stands to managed plantations. As a result, it is not known whether the plantations established today, in areas affected by *A. ostoyae*, will be able to produce timber volumes similar to those that were harvested previously. With this information the decision of whether or not to take actions to manage for the disease would be made much clearer.

Armillaria ostoyae is known to occur in a high proportion of the ICH zone in the southern interior of British Columbia. It is not known, however, which areas within this zone are most at risk to the impacts of *A. ostoyae*. With these two pieces of information the decision of whether or not to take actions to control the disease on a specific site would be made much easier.

CHAPTER 2 *ARMILLARIA OSTOYAE* DEVELOPMENT IN PLANTATIONS, FOLLOWING THE HARVEST OF INFECTED STANDS

2.1 Introduction

A considerable amount of the research regarding *A. ostoyae* in western north America has dealt with the disease in natural forests. James *et al.* (1984) estimated the losses in forest productivity in the northern Rocky Mountain National Forests in northern Idaho and northwestern Montana resulting from *A. mellea* and *P. weirii* infections. Their study provided an estimate of current losses to these diseases at one point. They estimated that root diseases accounted for 35% of the annual tree mortality on a three million hectare forest. The volume loss associated with the diseases was 834 000 m^3. There have been several similar studies conducted in the northwest United States (e.g., Filip and Goheen 1982, Stewart *et al.* 1982, Williams and Leaphart 1978, Filip 1977) that were designed to estimate either the area infected by, or the volume losses attributable to *A. ostoyae* in mature stands. Filip and Goheen (1982) estimated that over the past 20 years, 21.6% of the merchantable volume in a severely infected stand in central Oregon was lost to root disease. These loss estimates have helped forest managers select stands for treatment and have aided forest planning (James *et al.* 1984). However, more complete information of productivity losses, is still required.

Growth reduction in trees infected with *A. ostoyae* also contributes to the loss in overall forest productivity. Bloomberg and Morrison (1989) addressed this problem in their study of the relationship of growth reduction in Douglas-fir to infection by *A. ostoyae* in southeastern British Columbia. They found that growth reductions varied among the infected stands. Bloomberg and Morrison (1989) surmised that the differences in growth reduction were probably due to differences in initial disease levels and differences in site and stand conditions. They concluded that individual losses in tree growth were substantial and cumulative over long periods of time, and that growth reductions were due to the destruction of the host root system.

The research in *A. ostoyae* mentioned thus far deals with losses through mortality and growth reduction, in mature natural stands. There is a great need for a better understanding of the behavior of *A. ostoyae* in these mature stands once the areas are harvested and replanted. There is very little information describing how the disease develops in successive crops planted on the same site, except that *A. ostoyae* persists in subsequent rotations in forest plantations (Hood *et al.* 1991). The extent of disease spread and the future losses that will occur in these infected areas is not known. A stump removal trial located near Skimikin, B.C. (Morrison *et al.* 1988) tested the differences in susceptibility between species and the efficacy of stump removal as a means of reducing the inoculum of *A. ostoyae* and *P. weirii*. The trial was originally established to investigate the effectiveness of inoculum control treatments for *P. weirii*. Hence, the amount of *P. weirii* inoculum at the outset of the experiment was determined. At that time, *A. ostoyae* was only considered to be a secondary pathogen of trees attacked by *P. weirii*. This may account for the absence of records of *A. ostoyae* incidence in the original stand (Morrison *et al.* 1988).

The Skimikin trial provides insights into the differences in tree species susceptibility to *A. ostoyae* from plantation establishment up to age 25. The trial provides an example of what happens when a root-disease-infested stand is harvested and replanted with susceptible hosts. It clearly demonstrates the value of removing large sources of inoculum in order to improve plantation survival. However, the question still remains, what was the extent of *A. ostoyae* infection in the previous stand?

With the exception of Morrison and Pellow (1993) very little research has attempted to directly tie the extent of *A. ostoyae* infections in mature stands to the impact of the disease in plantations established on the same sites. Little is known about how individual infection centers behave in older plantations (Hood *et al.* 1991). The reason for this lack of research is due in large part to the length of time required to track the progress of the disease into older plantations. Permanent sample plots established in infected plantations would be ideal; however, they are expensive and they require a long period of time before any meaningful results are available. Preferably, permanent sample plots would be established prior to harvest so that the initial levels of disease in the mature stand could be related to future disease expression in the plantations. Such permanent sample plot installations would require considerable foresight.

One objective of this research was to develop a better understanding of *A. ostoyae* development in plantations following the harvest of infected stands in the ICH biogeoclimatic zone. In order to achieve this objective, without the use of permanent sample plots, a means of estimating infection levels prior to harvest in older plantations was required. The fact that mycelial fans of *A. ostoyae* leave impressions in the resin and bark of conifers for several years after the mycelium itself has disappeared provided that means.

Mycelial fan impressions have been found on stumps that were created over 30 years previously, according to B.C. Ministry of Forests records. Within these areas mycelial fan impressions were also found on snag stumps (*i.e*, stumps that were not a result of logging) that were probably as old as 50 years or more, based on visual comparisons with the logged stumps. The mycelial fan impressions on stumps provide evidence of past *A. ostoyae* infections which may be used to determine the levels of infection in former stands prior to harvest. In order to make this determination, it is clear that the mycelial fan impressions on stumps must provide evidence as to when the fan grew to the root collar. *Armillaria ostoyae* colonizes newly created stumps in three ways: by rapid extension from pre-existing lesions (Kile 1980), by invasion from an epiphytic position on the roots, or by invasion from outside by newly arrived rhizomorphs (Redfern and Filip 1991). In order to determine pre-harvest *A. ostoyae* infection levels, it is essential to differentiate between the mycelial fan impressions left by the fungus post-harvest from those impressions that were visible at the root collar in the stand prior to disturbance.

Based on field observations in stumps cut the previous year, it was discovered that there were subtle differences in *A. ostoyae* mycelial fan morphology. Mycelial fans found beneath resinous bark at or near the root collar were deeply ridged, short (each fan less than 5cm long), contorted and associated with resin. There was an abrupt transition at the edge of these short, contorted fans where the morphology was altered. These new mycelial fans were less deeply ridged, expansive (often longer than 20cm), and free of resin. As the larger mycelial fans were free of resin and appeared to develop from mycelial fans that contained resin, it was believed that the larger mycelial fans had been formed following the cutting of the tree. One principle response of conifer hosts to attack by *A. ostoyae* is the production of resin (Morrison *et al.* 1991b). In order for the host tree to produce resin it must have been alive.

The differences in the size and shape of the mycelial fans could also be explained by the lack of host resistance in the cut stumps. In live hosts, mycelial fans are typically deeply ridged, short, and contorted while those found in dead snags are relatively smooth and long extending over 20cm. In the absence of host resistance the mycelial fans of *A. ostoyae* spread rapidly, creating large sheets of mycelium.

Armillaria ostoyae is rarely capable of infecting dead trees or stumps because it is a poor competitor in relation to strict saprophytes. The stumps with infections classified in this study as post-harvest were in fact infected prior to harvest, but the evidence of infection would not have been visible above ground in the undisturbed stand. The stumps with "post-harvest" infections, in effect, provide an estimate of the number of *A. ostoyae* infections that would be missed in a typical root disease survey. Those infections classified as "pre-harvest" would have shown signs of infection at the root collar. These signs would have been in the form of mycelial fans beneath the bark and perhaps basal resinosis.

Mycelial fan impressions of both forms of *A. ostoyae* mycelium were found in the bark of old stumps within all of the study areas. Thus, it was possible to identify which stumps had shown above ground signs of infection prior to harvest and those which did not exhibit this evidence until after harvest. This evidence allowed for an estimate of the number, proportion and basal area of stumps with root collar lesions caused by past *A. ostoyae* infections in the four plantations used in this study. This evidence was used to determine if future losses in plantations due to this disease could be predicted on the basis of root disease surveys both prior to and following harvest. It was also used to determine which measurement of stump infections, the number, proportion or basal area, was the best for predicting mortality in future plantations. The differing ages of the plantations in this study allowed for an examination of the impacts of *A. ostoyae* in plantations over time. The impacts of *A. ostoyae* included changes in species composition among the stands. Differences in plantation histories allowed for an examination of the effects of brushing treatments on the behavior of *A. ostoyae*. The use of two different plot sizes in the study allowed for an examination of the relationship between infected stumps and the probability of regeneration close to that stump being infected.

2.2 Methods

2.2.1 Study Areas

Four plantations were selected as study areas. All four plantations were located within the Interior Cedar Hemlock biogeoclimatic zone, in the Shuswap moist warm Interior Cedar Hemlock variant (ICHmw2) (Lloyd *et al.* 1990). The study areas lie on the east slopes of Larch Hills, close to Salmon Arm, British Columbia. The plantations chosen were selected using the following criteria: suitable site preparation (broadcast burned rather than mechanical), clearly defined date of establishment, reasonable proximity to each other, and ease of access. The information used to select the four plantations was obtained from a B.C. Ministry of Forests Forest Cover Map (82L.075), scale 1:20 000, produced by the Inventory Branch of the Ministry of Forests. The history of each of the plantations was described on the Forest Cover Map and Forest Service records (Table 2).

Once the four plantations were selected, a preliminary walk through was conducted to determine if *A. ostoyae* was present on the stumps. A test of the proposed sampling methods was also completed.

TABLE 2. Forest management history records for the four plantations

PLANTATION	1969a	1969b	1980	1984
HARVESTED	1968	1965	1974	1979
BURNED	1968	1967?	1976	1980
PLANTED	1969	1969	1980	1984
SPECIES PLANTED	Fdi	Fdi	Pl	Fdi/Pl
TREES/HA	1000	1300	1000	1200
BRUSHING	-	1984/1986	-	1987

2.2.2 Sampling Design

Fifty, 8m-radius-fixed-area plots (0.02ha) were established on a 100 x 100m grid within three of the study areas. The fifty 0.02ha plots resulted in a total area sampled in each plantation of 1ha. The 1980 plantation was sampled with 48 plots as its size and shape did not allow for 50 plots in the grid. The strip lines were laid out on cardinal bearings. Plots were located by tight chaining using a 50m nylon chain and a silva ranger compass.

2.2.3 Sampling Procedure

Once the plot center was established, a 30m Eslon tape was used to locate the circumference of the plot using an 8m radius. The plot perimeter was flagged with florescent tape. The plot was then divided into four sectors. Within each sector, all stumps over 10cm diameter at root collar (DRC) were examined. Stumps species, DRC, origin and disease status was recorded accordingly. Species identification was based on bark and wood characteristics. Due to the age of the stumps, some of which were cut in 1965, species identification was sometimes difficult. Stump origin differentiated snags from cut stumps. Disease status was determined by examining under the bark from the cut surface to the root collar for evidence of mycelial fan impressions. Due to the age of the stumps and the fact that all four plantations were burned for site preparation, many stumps did not have completely intact bark. In such cases, careful examinations under the bark in the crotches of roots at the root collar were performed. Root excavations were not performed in this study. The broadcast burn site preparation method had exposed some roots below the root collar by burning off the duff layer. Much of the below ground portions of these stumps were too badly decomposed to yield any evidence of *A. ostoyae* mycelial fans. Stumps were identified as belonging to one of the following four classes:

CLEAN	-	stumps that still had most of their bark intact and exhibited no signs of *A. ostoyae* mycelial fan impressions;
ARMILLARIA BEFORE	-	stumps where portions of the bark exhibited evidence of mycelial fan impressions that were short, deeply etched, contorted and often associated with resin, and stumps with callused lesions surrounding bark with any mycelial fan impressions;
ARMILLARIA AFTER	-	stumps on which portions of the bark exhibited evidence of mycelial fan impressions that were long, lightly etched and expansive with no evidence of resin and no evidence of *A. ostoyae* before, and stumps with extensive colonization by dichotomously branched rhizomorphs beneath the bark;
NO EVIDENCE	-	stumps which no longer exhibited enough evidence to be clearly placed in any of the other categories.

It is possible that these classification methods were biased. A stump could be positively identified as infected based on a small portion of the inner bark exhibiting mycelial fan impressions or on the presence of rhizomorphs. In order for a stump to be classified as clean, a large proportion of the inner bark yielding no signs of past infection was required. If only a small proportion of the inner bark was intact and exhibited no signs of disease it was not clear that the stump had not been infected. The missing portions of inner bark may have been infected yet there was no way to determine if this was the case. Such stumps were placed in the no-evidence class. Thus, it was less likely for a stump to be classified as clean than to be classified as infected since decay and weathering over time lead to the sloughing of stump bark.

Following stump examinations, the species, height and DRC of all regeneration within each sector was recorded along with any evidence of disease. Height and diameter measurements were visually estimated to the nearest meter and centimeter respectively, and periodically verified. Regeneration infected with *A. ostoyae* was classified as either dead or dying. *Armillaria ostoyae* infections were confirmed by the presence of mycelial fans or mycelial fan impressions beneath the bark at the root collar. Evidence of other disease and insect damage was recorded in comments. In the plantations that had received brushing treatments (1969b and 1984) the brushed stumps were also examined. The DRC and disease status was recorded. Due to excessive stocking levels and resprouting brush competition, some of the brushed stumps could have been missed.

A small survey was also carried out in the mature stands surrounding each of the plantations. The purpose of this survey was to determine whether the pre-harvest levels of infection identified in the stumps was similar to that found in the surrounding mature stands. This survey acted as a check to back up the claim that past *A. ostoyae* infections could be identified as being either pre- or post-harvest based on the morphology of mycelial fan impressions.

Ten fixed area plots of 0.02ha (8m radius) were established in three strips more than 100m outside the cutblock boundaries of three of the plantations. Each tree within the plot was closely examined for any evidence of *A. ostoyae* infection. The humus layer was removed up to 30cm below the root collar in order to simulate the effects of the broadcast burn treatments that were performed on the plantations. As mentioned earlier, the stumps in the plantations often had portions of their roots below the root collar exposed, most likely due to fire. Bark was removed from much of the roots and root collar using an axe. This was necessary since the identification of *A. ostoyae* on the stumps in the plantations often required removal of all the bark in order to positively identify the disease.

2.2.4 Data Analysis

The data was entered into Quatro Pro (Version 3.01. 1991), a spreadsheet program, and then transferred into Systat (Version 5.03. 1991) for analysis. Each plantation was summarized independently. Within plantations, stump data and regeneration data were first summarized independently and later combined. All analyses were conducted using $\alpha=0.05$ unless stated otherwise in the results section.

Stumps

The original stump data consisted of species, DRC, stump origin and disease status. Basal area in square meters per stump was calculated as $(DRC/200)^2 * \pi$.

Stump data were summarized by species, disease status and basal area, such that for each plot the following information was determined:

- total basal area by species (TOTALBA)
- basal area infected pre-harvest (BABEFOR) by species[1]
- basal area infected post-harvest (BAAFTR) by species[2]
- clean basal area/species (CLEANBA)
- no-evidence basal area/species (NOEVBA)
- total number of stumps/species
- number of pre-harvest infected stumps/species (STMPBEFR)
- number of post-harvest infected stumps/species (STMPAFTR)
- number of clean stumps/species (CLEAN)
- number of no-evidence stumps/species (NOEVID)
- proportion of all stumps infected pre-harvest (ARMSEVB)[3]
- proportion of all stumps infected post-harvest (ARMSEVA)[3].

[1] snag stumps showing evidence of past *A. ostoyae* infections were classified as being infected pre-harvest and combined with the other pre-harvest infected stumps.

[2] stumps recorded as infected post-harvest included all stumps exhibiting evidence of *A. ostoyae* infections since stumps infected pre-harvest would remain infected post-harvest.

[3] both of these proportion measures included the no-evidence stumps in the total number of stumps.

Chi-square tests were performed on stump data for the three major species (western redcedar, Douglas-fir and western hemlock) to determine if there were significant differences in their relative frequencies of infection (*i.e*, were the ratios of infected stumps versus clean stumps similar between the three species). This test revealed no significant differences. Based on these results, the basal area, stump frequencies, and infection proportions for all species were combined to arrive at single values for each of these variables for each plot. This was necessary in order to make direct comparisons between the infection status of stumps and regeneration within the same plots. This aspect will be described in detail later.

The stump data were also summarized by species, origin, plantation and diameter class. The following relationships were examined:

- stump frequency by disease category among species
- stump frequency by disease category between mature and immature stands
- stump frequency by disease category among species and between stump origin classes
- stump frequency by origin among plantations
- stump frequency by species and diameter class
- stump frequency by disease category among plantations
- stump frequency by species and plantation
- basal area by disease category among plantations

Stump Frequency Distribution by Species and Disease Status

Due to the very low numbers of stumps for all other species, only western redcedar, Douglas-fir and western hemlock stumps were analyzed for differences in stump distributions between the disease identification classes. Chi-square tests were used to test for differences in the frequency of *A. ostoyae* infection both before and after harvest and for differences in the preservation of evidence among western redcedar, western hemlock, and Douglas-fir. The first Chi-square test included all three species and indicated that there were significant differences among the three species in their relative proportions of stumps in each of the four infection status classes. Further Chi-square tests were performed on the distribution of stumps by species between each infection status class individually. This was accomplished by comparing the proportion of stumps for each species in each of the four infection classes.

Rates of Infection in Stumps Compared to those in the Surrounding Mature Stands

The infection rates found in the stumps of all four plantations combined were compared to those found in the surrounding mature stands. A Chi-square test was used to test for differences between the two areas. All tree and stump species were combined for the analysis.

Stump Species and Disease Status by Stump Origin

The majority of both snag and cut stumps belonged to one of three species: western redcedar, Douglas-fir, and western hemlock. A Chi-square test was used to test for differences among these three species in their relative proportions of snag stumps to cut stumps. All three species were compared in a 3 by 2 contingency table. Further pairwise comparisons using 2 by 2 contingency table tests between the species were used to determine which of the species were significantly different from each other.

Stump Origin by Plantation

A 4 by 2 contingency table Chi-square test was used to test for differences among the four plantations in the proportion of snag stumps out of the total stump count. Pairwise comparisons between the plantations were performed to determine which of the plantations had significantly different proportions of snag stumps.

Stump Frequency Distribution by Species and Diameter Class

The diameter class distributions of the three major species were compared. The overall distribution of stumps among the 10 diameter classes was compared between combinations of species using 10 by 2 contingency tables. Differences among the three species were tested with Chi-square tests at each of the 10 diameter classes using pairwise comparisons between the proportion of stumps in each diameter class for each species in all diameter classes combined.

Stump Frequency Distribution by Disease status and Plantation

The proportions of stumps in each disease class out of the total number of stumps (excluding the no-evidence stumps) were compared among the four plantations. Including the no-evidence stumps would reduce the proportions of infected and clean stumps. The true status of the no-evidence stumps could not be determined. An equal distribution of these stumps between the other three classes, infected pre-harvest, infected post-harvest, and clean, represents a best guess. The lack of evidence in stumps was most often due to ants consuming the inner bark. A series of Chi-square tests were used to test for differences in the proportion of stumps in each of the disease classes among the four plantations. The proportion of stumps that were clean, infected pre-harvest, and infected post-harvest out of the total number of stumps were compared among the four plantations. Plantations were compared using pairwise Chi-square tests (1 degree of freedom).

Stump Frequency Distribution by Species and Plantation

The relative proportions of the three major species were compared among the four plantations using a series of Chi-square tests. The first Chi-square test indicated a significant difference in species composition among the plantations. The proportions of stumps in each of the species out of the total for each plantation were then compared in pair-wise combinations using 2 by 2 contingency tables (1 degree of freedom).

Stump Basal Area Distribution by Disease Status and Plantation

A one-way ANOVA was used to test for differences in the mean plot basal area of stumps infected before and after harvest and those stumps classified as no-evidence between the four plantations. A Tukey multiple range test was then used to determine which of the plantations were significantly different from each other. To express the basal area values as per hectare units the mean basal areas/plot were multiplied by 50. Basal area in this study refers to the cross sectional area of the stump at root collar and not at breast height.

Regeneration

Regeneration data for each plot were summarized by species and disease status such that for each plot the following information was determined:

- total number of trees (TOTREES)
- total number of conifers/ha (CONSTEMS)
- number of conifers infected with *A. ostoyae* (TREINFCT)
- and, proportion of conifers infected (PROINFCT)

The proportion of conifers infected was determined by dividing the total number of conifer trees infected, all species and sizes combined, by the total number of conifers. Planted trees could not always be distinguished from the natural regeneration so the two could not be separated in the analysis.

Regeneration data were also summarized by species and 5cm diameter classes in order to determine relative rates of infection among the species by diameter class. The following relationships concerning the regeneration in the four plantations were examined:

- species composition among plantations
- relative rates *A. ostoyae* incidence among conifer species
- regeneration species distribution by disease status and diameter class
- relative rates of infection among species in smallest diameter class (0-2.5cm)
- diameter class distribution for each plantation
- relative rates of regeneration infection among plantations
- distribution of infected regeneration within plantations by plot

Species Composition Among Plantations

Eight conifer species were present in each of the four plantations. The distributions of these species in relation to plantation, diameter class, and disease status were compared and described. Deciduous species were not included in the analyses although the data were collected. Two of the plantations had received brushing treatments and therefore few deciduous stems remained in these areas.

Comparison of the Relative Rates of *Armillaria ostoyae* Infection Incidence among Conifer Species

The relative rates of *A. ostoyae* infection incidence among conifer species were compared among the eight species found throughout the four plantations. The average rate of infection and the species composition varied among plantations. Thus, averaging the proportion of trees infected by species across all four plantations would confound the rates of infection incidence by possible differences in disease severity among sites. A standard measure of disease severity for each site was required so that comparisons among species could be made given the variability among the plantation sites. The proportion of Douglas-fir infected on a site was chosen as a standard measure of disease incidence, since this species was relatively abundant and generally accepted as susceptible to *A. ostoyae* infection. The rate of infection of each species was then expressed as a ratio to the rate of infection in Douglas-fir for each plantation. These ratios of infection were then tested using a Chi-square test to determine whether or not they were constant across the four plantations. The expected values required for the Chi-square test were calculated using the following formula:

$$\text{Expected value} = SI_i * n_i * K$$

Where:

SI_i = the proportion of Douglas-fir infected in plantation (i)
n_i = the number of species (x) in plantation (i)

$$K = \frac{\text{total number of species (x) trees infected}}{\Sigma(SI_i * n_i)}$$

The K-value was a constant for each species that was used to test the ratios among plantations. A Chi-square test was used to determine if there were significant differences among plantations in the proportion of trees infected for a given species as compared to the proportion of Douglas-fir infected. The null hypothesis for this test was that there was no significant difference between the proportion of species (x) infected and the proportion of Douglas-fir infected over the four plantations. In other words, on those plantations where Douglas-fir was heavily infected, species (x) would be expected to be heavily infected as well. A significant Chi-square result would indicate that the proportion of species (x) infected did not vary in conjunction with that of Douglas-fir. Such a result would indicate that the relative differences in disease incidence among species was perhaps more dependent on site factors than on inherent differences among species. The K-value was a measure of relative disease incidence among species using Douglas-fir as a baseline. A conifer species with an K-value greater than one would, therefore, have a relatively greater proportion of trees infected on a site than Douglas-fir. The reverse could be said for an K-value less than one. The relative rates of infection were compared between lodgepole pine and Douglas-fir (Table 3).

TABLE 3. Relative rates of infection compared between lodgepole pine and Douglas-fir regeneration

Site	Fd SI	Total Pl	Infected Pl	K	Expected	Chi-square
1969a	0.04394	7	0	1.0484	0.3225	-
1969b	0.17995	18	1	1.0484	3.3961	1.987
1980	0.12618	1021	134	1.0484	135.071	0.0085
1984	0.07022	329	28	1.0484	24.213	.593
Total		1375	163		163.0	2.589

If the expected number of a given species was less than one, that expected value was added to the expected value for the plantation with the largest relative difference between expected and actual values. In the example above, the expected number of lodgepole pine trees infected was 0.3225 in the 1969a plantation. This expected value was added to the value for the 1969b plantation since the relative difference between expected and actual values was greatest in this plantation. These methods ensured a most rigorous test of the null hypothesis. Only the greatest differences in the relative proportions of trees infected between the given species and the Douglas-fir standard would be significant among plantations.

Once the K-values had been determined, it was necessary to determine which of the values were significantly different from each other. The proportion of trees infected were compared among all eight conifer species among the four plantations to determine which species were significantly different from each other. Every possible species comparison was made for a total of 28 tests. The proportion of Douglas-fir and lodgepole pine trees that were infected are compared (Table 4).

TABLE 4. Observed and expected numbers of infected lodgepole pine and Douglas-fir regeneration within the four plantations

SITE	Lodgepole Pine			Douglas-Fir			% INFECTED OVERALL
	# TREES	INFECTED		# TREES	INFECTED		
		obs.	exp.		obs.	exp.	
1969a	7	0	0.305	751	33	32.695	0.0435
1969b	18	1	3.188	778	140	137.81	0.1771
1980	1021	134	132.775	317	40	41.224	0.1300
1984	329	28	24.169	1182	83	86.831	0.0735

In this example the null hypothesis was that in each plantation the percent infected of Douglas-fir and lodgepole pine were the same. The resulting Chi-square = 2.260, therefore the null hypothesis cannot be rejected. There is no significant difference in the proportion of trees infected between lodgepole pine and Douglas-fir.

The expected values were determined by calculating the overall percent infected for both species combined for each plantation then multiplying the number of trees in each species by that overall percentage. Each plantation had a separate overall percentage of trees infected. The expected values were then compared to the observed values in a Chi-square test. The degrees of freedom for the Chi-square test was the number of terms compared, minus the number of overall percentages. In the example above, the degrees of freedom was 3 (7 terms minus 4 overall percents infected). If the calculated expected value was less than 1, that value was added to the expected value that differed the most from the observed value for a given plantation and species.

Regeneration Species Distribution by Disease Status and Diameter Class

The frequency distributions of each of the eight species by 5cm diameter class were compared among the regeneration species. The distribution of infected regeneration among the same five, 5cm diameter classes was also examined. The distribution of diseased stems throughout the range of diameter classes were compared among the four major species, western redcedar, Douglas-fir, western hemlock and lodgepole pine.

Spatial Distribution of Infected Regeneration within Plantations

The spatial distribution of infected trees was examined within each of the plantations. The total number plots from each plantation were divided into five classes based on the number of infected trees per plot. The classes ranged from 0 infected trees/plot to greater than 6 infected trees/plot.

Stumps and Regeneration

To analyze the relationship between past and present levels of *A. ostoyae* on a site, it was necessary to determine individual plot values for both stumps and regeneration. The individual stump plot value could then be compared to the individual regeneration plot value for that plot in a correlation analysis. To arrive at a single plot value for stumps, all species of stumps were combined.

For each plot, the following stump measures were determined:

(1) number of stumps infected pre-harvest (STMPBEFR)
(2) number of stumps infected post-harvest (STMPAFTR)
(3) proportion of stumps infected pre-harvest (ARMSEVB)
(4) proportion of stumps infected port-harvest (ARMSEVA)
(5) basal area of stumps infected pre-harvest (BABEFOR)
(6) basal area of stumps infected post-harvest (BAAFTER)

The relationships between the number of conifers infected (TREINFCT), the proportion of conifers infected (PROINFCT), and the number of disease free conifer stems/ha (CONSTEMS), and the variables listed above, were tested using correlation analyses. The correlations were performed on the data from all four plantations combined and from each plantation individually. These tests were designed to determine if the losses due to *A. ostoyae* in plantations were related to infection levels in the previous stand.

Comparison of Measurements of Stump Infection

Correlation analyses were used to determine which measure of stump infection out of the six listed above was most closely related to regeneration mortality if such a relationship did exist. All six measures of stump infection were also compared simultaneously in a stepwise multiple linear regression. This method was used to determine which of the six factors accounted for the greatest degree of variation in the number of conifers infected, the proportion of regeneration infected, and the number of disease free stems/ha.

Effect of Plot Size on the Strength of Relationships Between Infected Stumps and Infected Regeneration

The effect of plot size on the relationships between infected stumps and infected regeneration was analyzed. The correlations between the total number of infected stumps and the number of infected regeneration on full sized plots in all four plantations were determined. This was repeated on a sector (quarter plot) basis in the 1969b and 1984 plantations. The first sector in each of the plots was selected for analysis. A single sector was chosen so that the sample size for both the full size plots and the sectors would be the same (50).

The 1969b plantation was chosen since the relationships between infected stumps and visibly infected regeneration were strongest in this plantation compared to the other three. The 1984 plantation was chosen because it was the youngest of the four. The probability of stumps being closely associated with dead or dying regeneration would be highest in the youngest plantation. As plantations age, the infection of new hosts by *A. ostoyae* depends more on root contacts between infected and healthy trees than on contacts between trees and infected stumps (Morrison pers. comm.).

Analyses were run first with all plots and all number 1 sectors within the 1969b and the 1984 plantations. Following this, the same plantations were analyzed using only those plots and sectors that contained any infected regeneration. An analysis using only those sampling units containing infected trees would conceivably reduce the variation in the relationship. If there was a relationship between infected stumps and infected trees, then removing those sampling units that contained no infected trees from the analysis would place a higher emphasis on those that did contain such trees.

2.3 Results

2.3.1 Stump Results

Stump Frequency Distribution by Species and Disease Status

The vast majority of stumps (94%) throughout all four plantations belonged to one of three species: western redcedar (Cw), Douglas-fir (Fd), or western hemlock (Hw). The remaining 6% of the stumps consisted of sub-alpine fir (Bl), paper birch (Ep), western larch (Lw), lodgepole pine (Pl), western white pine (Pw) and Engelmann spruce (Se). Western white pine actually made up 2.6%, and Engelmann spruce contributed 1.1% of the total stumps. Table 5 describes the distribution of stumps among the infection status classes by species for all four plantations. The percents of stumps infected in Table 5 were calculated by dividing the number of stumps in each infection status class by the total number of stumps. An alternative method involved percent calculations based on only those stumps that could be positively identified as being clean or infected (Table 6).

TABLE 5. Percentage of total stumps by *Armillaria ostoyae* infection status in each species for all four plantations

	Cw	Hw	Fd	Pw	Se	Ep	Lw	Pl	Bl	MEAN
CLEAN	21.0	27.6	25.4	4.9	7.4	26.1	13.3	20.0	20.0	23.6
*Arm.*BEFORE	35.3	32.9	36.6	59.0	37.0	13.0	20.0	40.0	60.0	35.3
*Arm.*AFTER	15.1	30.0	26.9	13.1	37.0	17.4	46.6	0.0	20.0	23.3
NO EVIDENCE	28.6	9.4	11.1	23.0	18.5	43.5	20.0	40.0	0.0	17.7
TOTAL STUMPS	872	735	642	61	27	23	15	5	5	2385

The results (Table 7) demonstrate that there was no significant difference in the proportion of stumps infected prior to harvest among the three major species. Infection classes that did indicate significant differences among species were further tested using pairwise combinations and Chi-square tests to determine which species were significantly different from each other.

TABLE 6. Percentage of total stumps positively identified by infection status in each species for all four plantations

	Cw	Hw	Fd	Pw	Se	Ep	Lw	Pl	Bl	MEAN
CLEAN 29.4	30.5	28.5	6.4	9.1	46.2	16.7	33.3	20.0	28.7	
ARM.BEFORE	49.4	36.3	41.2	76.6	45.5	23.1	25.0	66.7	60.0	42.9
ARM.AFTER	1.2	33.2	30.3	17.0	45.4	30.8	58.3	0.0	20.0	28.3
TOTAL STUMPS (identifiable)	623	666	571	47	22	13	12	3	5	1962

TABLE 7. Comparison of the proportion of stumps infected pre- and post-harvest, clean and no-evidence among the three major species in all four plantations combined (proportions expressed in percent of total in that species)

	Cw	Fd	Hw	TOTAL	CHI-SQUARE
CLEAN	21.0 (1)	25.4 (1)	27.6 (2)	549	10.148
PRE-HARVEST	35.3 (1)	36.6 (1)	32.9 (1)	785	2.256
POST-HARVEST	15.1 (1)	26.9 (2)	30.1 (2)	526	56.025
COMBINED INFECTIONS	50.5 (1)	63.6 (2)	63.0 (2)	1311	36.05
NO EVIDENCE	28.6 (2)	11.1 (1)	9.4 (1)	389	126.101
TOTAL	872	642	735	2249	

Percentages with the same number in brackets below them are not significantly different from the others in that row based on a critical Chi-square value of 3.841 (1 degree of freedom) and pairwise tests. Critical Chi-square value for the entire row comparisons is 5.991 (2 degrees of freedom).

The proportion of stumps infected post-harvest could be viewed as a measure of those stumps that did not exhibit above ground symptoms of infection at the time of harvest. Since *A. ostoyae* can not compete well with other saprophytes, it is very likely that those stumps with infections classified as post-harvest were already infected at the time of harvest. The results (Table 7) indicate that 15.1% (132 out of 872) of western redcedar stumps were infected prior to harvest without showing above ground evidence. The other two major species had significantly more stumps in this category (26.9% and 30.1% of Douglas-fir and western hemlock stumps respectively, had infections prior to harvest without exhibiting any above ground symptoms). These results have important implications for pre-harvest root disease surveys. If the pre-harvest estimates of the extent of root disease infection in a stand may be off by as much as 30%, the value of a survey is questionable.

Rates of Infection in Stumps Compared to those in the Surrounding Mature Stands

The proportion of stumps infected with *A. ostoyae* in the plantations was compared to the proportion of mature trees infected in the stands surrounding the cut-over areas. The results of this test (Table 8) showed that there were no significant differences between the stumps and the mature stands in their respective proportions of infected pre-harvest and clean stumps.

TABLE 8. Comparison of the percent of stumps infected with *Armillaria ostoyae* in all four plantations to that in the surrounding mature trees

	CLEAN	INFECTED PRE-HARVEST	TOTAL
ALL STUMPS (198 plots)	40.7	59.3	1324
MATURE TREES (10 plots)	41.4	58.6	232
TOTAL	635	921	1556

Chi-square critical value=3.841 Chi-square obtained=0.035
There is no significant difference in the proportion infected and clean. ($\alpha=0.05$)

The results of this comparison indicate that the methods used in this study to differentiate between pre- and post-harvest infections were defendable. The proportion of stumps classified as being infected prior to harvest in the plantations was almost identical to the proportion of trees in the mature stands that exhibited signs of *A. ostoyae* infection. Thus, it is likely that the estimates of pre-harvest infections in the plantations were quite representative of the disease conditions in the former stands.

Stump Species and Disease Status by Stump Origin

Of the 2385 stumps examined, 2057 (86%) were cut stumps and 328 (14%) were snag stumps. The majority of stumps belonged to one of three species, western redcedar, Douglas-fir, or western hemlock. The same general species composition was found when only snag stumps were considered. Of the 328 snag stumps tallied, 297 (90.5%) were either western redcedar, Douglas-fir, or western hemlock (Table 9). A Chi-square test indicated that there were significant differences between the species in the proportion of stumps in each origin class (Chi-square critical=5.991, Chi-square obtained=29.62). There was no significant difference between western hemlock and western redcedar (Chi-square obtained=.4177, Chi-square critical=3.841) in the proportional distribution between the two origin classes. There was a significant difference between Douglas-fir and the other two species. A significantly greater proportion of total Douglas-fir stumps were snag stumps compared to western hemlock (Chi-square obtained=22.68) and western redcedar (Chi-square obtained=10.84).

There was a significantly greater proportion of snag stumps infected with *A. ostoyae* than cut stumps. The reason for this seems obvious since a major cause of mortality in natural undisturbed stands would be *A. ostoyae*.

TABLE 9. Percentage of total stumps in each of the three major species in each origin class

	Cw	Fd	Hw	TOTAL
PERCENT CUT	88.8 (1)	80.7 (2)	89.8 (1)	1952
PERCENT SNAG	11.2 (1)	19.3 (2)	10.2 (1)	297
TOTAL	872	642	735	2249

Those percents with the same number in brackets below them are not significantly different from the others in that row (α=0.05).

Stump Origin by Plantation

A Chi-square test indicated that there were significant differences among the four plantations in the proportion of snag stumps out of the total stump count (Chi-square critical=7.815, Chi-square obtained=19.552). There were significantly fewer snag stumps in the 1984 plantation compared to the other three. The proportion of snag stumps in the 1969a, 1969b and 1980 plantations were not significantly different from each other with 18.3, 16.0 and 13.9% respectively. Only 10.0% of the 1984 plantation stumps were snag stumps.

Stump Frequency Distribution by Species and Diameter Class

Western redcedar and western hemlock stumps did not differ significantly in their relative proportions in each of the ten 10cm diameter classes. The critical Chi-square value was 16.919 while the Chi-square obtained was 14.22. Douglas-fir had a significantly different overall distribution of stumps among the 10 classes compared to the other two species, western redcedar (Chi-square 120.97) and western hemlock (Chi-square 116.94). Douglas-fir tended to have fewer small stumps (10-20cm) and relatively more large stumps in the 50-60cm diameter classes (Table 10).

TABLE 10. Percentage of total stumps of the three major species in each of ten 10cm-diameter classes all plantations combined

CLASS	Cw	Fd	Hw	TOTAL
10 cm	9.6 (1)	1.6 (2)	9.7 (1)	164
20 cm	24.4 (1)	12.3 (2)	23.5 (1)	463
30 cm	24.5 (1)	21.5 (1)	24.0 (1)	526
40 cm	17.4 (1)	21.4 (1)	18.6 (1)	425
50 cm	9.7 (1)	18.7 (2)	13.3 (1)	302
60 cm	7.4 (1)	15.4 (2)	5.9 (1)	206
70 cm	3.8 (1)	5.0 (1)	3.5 (1)	91
80 cm	2.0 (1)	1.9 (1)	1.2 (1)	38
90 cm	0.6 (1)	1.7 (2)	0.3 (1)	18
100 cm+	0.7 (1)	0.5 (1)	0.0 (1)	9
TOTAL	866	641	735	2242

Those percentages with the same number in brackets below them are not significantly different from the others in that row ($\alpha=0.05$)

Stump Frequency Distribution by Disease status and Plantation

The frequency distribution of stumps for the four plantations is shown in Figure 1. There were large differences in the number of stumps/ha among the four plantations. The lowest level was found in the 1969a plantation with 420 stumps/ha. The highest level was found in the 1984 plantation with 860 stumps/ha. There were also differences in the amount of disease evidence in stumps among the four plantations. The greatest number of infected stumps occurred in the 1984 plantation with 515/ha compared to only 216/ha in the 1969a plantation.

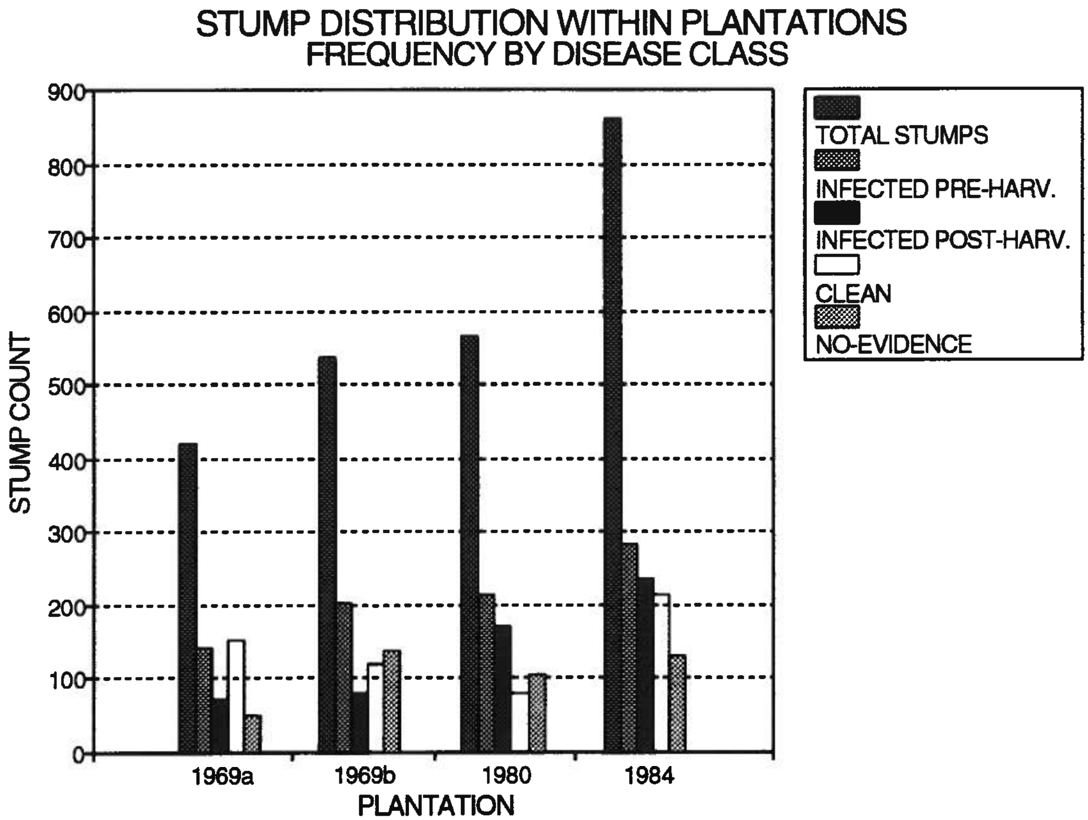

FIGURE 1. Stump distribution among plantations by disease status

The proportion of stumps identified as belonging to one of the three disease classes (*i.e*, clean, infected pre-harvest and infected post-harvest) were compared among the four plantations (Table 11). In this table the proportion of stumps infected post-harvest was not a measure of the total number of stumps infected. Post-harvest infected stumps in this analysis included only those stumps which exhibited signs of being infected post-harvest and did not include the pre-harvest infected stumps.

TABLE 11. Percentage of stumps infected with *Armillaria ostoyae* out of the total identified stumps (excluding no-evidence stumps) for each plantation in percent

	PLANTATION				
DISEASE STATUS	1969a	1969b	1980	1984	TOTAL
CLEAN	41.3 (3)	29.6 (2)	16.9 (1)	29.5 (2)	564
PRE-HARVEST	38.9 (1)	50.5 (2)	46.5 (2)	38.5 (1)	842
POST-HARVEST	19.8 (1)	19.9 (1)	36.6 (2)	32.1 (2)	556
TOTAL	368	402	462	730	1962

Percentages with the same number in brackets below them are not significantly different from the others in that row ($\alpha=0.05$)

The 1969a plantation contained a significantly greater proportion of clean stumps than the other three sites. The high proportion of clean stumps in this plantation probably in part reflects a difference in measurement system. This plantation was the first of the four to be examined. In the early stages of data collection those stumps which lacked enough evidence to make positive identifications were classified as clean. This different measurement system would also account for the low proportion of no-evidence stumps in the 1969a plantation (Fig. 1).

There was a significantly greater proportion of stumps infected pre-harvest in the 1969b plantation compared to the 1969a plantation. The measurement error described above could be partially responsible for this difference since the proportion of clean stumps in the 1969a plantation is possibly over-estimated. The two youngest plantations contained significantly more post-harvest infected stumps than the two older plantations. The mycelial fan impressions left by post-harvest infections are more subtle than those left by pre-harvest infections. It is quite possible that the post-harvest *A. ostoyae* evidence on the older stumps was too weathered to be identified. The 1980 plantation was the most heavily infected of the four plantations when pre- and post-harvest infections were combined.

Stump Frequency Distribution by Species and Plantation

The relative proportions of the three major species of stumps were compared among the four plantations (Table 12).

TABLE 12. Species composition of the stumps in each of the four plantations in percent

PLANTATION	SPECIES Cw	Fd	Hw	TOTAL
1969a	42.0 (1)	21.9 (2)	36.1 (2)	393
1969b	40.5 (1)	20.4 (2)	39.1 (2)	511
1980	37.3 (1)	4.7 (1)	58.1 (3)	558
1984	37.1 (1)	54.1 (3)	8.8 (1)	787
TOTAL	872	642	735	2249

Those percentages with the same number in brackets below them are not significantly different from others in that column (α=0.05 Chi-square critical 3.841)

The two oldest plantations, 1969a and 1969b, had very similar species compositions based on stump evidence. The 1980 and 1984 plantations had very different species compositions from each other and from the two older plantations. The proportion of total stumps made up by western redcedar was not significantly different among the four plantations. The major differences in species composition between the 1980 and 1984 plantations were due to the relative proportions of western hemlock and Douglas-fir. The 1980 plantation contained many more hemlock than Douglas-fir stumps while the reverse was true for the 1984 plantation. These differences in species composition are not clearly related to any differences in the number of stumps within the four disease status categories of each plantation. The low proportion of western hemlock in the 1984 plantation could help to explain the relatively high number of no-evidence stumps within this plantation. One would expect the youngest plantation to contain stumps with the clearest evidence. The 1980 plantation had the greatest number of western hemlock stumps per hectare (337) and it also had the lowest number of clean stumps per hectare (78). All three species had higher proportions of infected stumps in the 1980 plantation.

Stump Basal Area Distribution by Disease Status and Plantation

As previously mentioned, the greatest number of stumps/ha was found in the 1984 plantation. However, the greatest stump basal area was found in the 1980 plantation (Table 13). The stump basal area in the 1980 plantation was 90.0m^2/ha. Of that, 46.83m^2/ha or 52% was infected pre-harvest. The mean plot basal area of stumps infected pre-harvest in the 1980 plantation was significantly greater than the plot means found in the other three plantations. As a consequence, the average clean basal area/plot in the 1980 plantation was significantly less than that found in the other three plantations. The mean clean stump basal area/plot and the mean pre-harvest infected stump basal area/plot did not differ significantly among the 1969a, 1969b and 1984 plantations. The mean post-harvest infected stump basal area/plot was not significantly different among the four plantations. The mean no-evidence stump basal area/plot was similar in all but the 1969a plantation.

TABLE 13. Mean stump basal area for each plantation by disease status (m^2/ha)

	PLANTATION				
DISEASE STATUS	1969a	1969b	1980	1984	TOTAL
CLEAN	26.13 (2)	12.61 (1)	5.93 (1)	16.67 (1)	61.34
INFECTED PRE-HARVEST	27.66 (1)	25.91 (1)	46.83 (2)	31.03 (1)	131.43
INFECTED POST-HARVEST	16.70 (1)	12.04 (1)	24.10 (2)	25.79 (2)	78.63
NO-EVIDENCE	7.32 (1)	15.29 (2)	13.15 (2)	11.79 (2)	47.55
TOTAL	76.17	65.95	90.00	85.30	317.42

Those percentages with the same number in brackets below them do not have significantly different mean basal areas from the others in that row ($\alpha=0.05$). (Tukey test)

Stump Results Summary

The majority of the stumps in all four plantations were either western redcedar, Douglas-fir or western hemlock. The proportion of no-evidence western redcedar stumps was greater than that of Douglas-fir or western hemlock. There were also significantly fewer post-harvest infected western redcedar stumps.

The proportion of snag stumps for each plantation also differed among plantations. The 1984 plantation had the lowest proportion of snag stumps. The other three plantations were not significantly different in this respect. Douglas-fir accounted for 41.8% of all snag stumps, while western hemlock and western redcedar accounted for 25.3 and 33.0% respectively.

There were differences in the number of stumps/ha among the four plantations. The lowest number was found in the 1969a plantation with 420 stumps/ha total. The highest was in the 1984 plantation with 860 stumps/ha. However, total basal area did not vary considerably among plantations.

There were also differences in the amount of disease evidence in stumps among the four plantations. The greatest number of infected stumps occurred in the 1984 plantation with 515/ha compared to only 216/ha in the 1969a plantation. The highest proportion of stumps infected pre-harvest occurred in the 1969b plantation (50.5%). The lowest proportion of stumps infected pre-harvest (38.5%) occurred in the 1984 plantation.

2.3.2 Regeneration

Species Composition Among Plantations

Eight conifer species were present in varying proportions in each of the four plantations (Fig. 2). Three species, Douglas-fir, western redcedar and lodgepole pine, constituted over 80% of the conifer regeneration.

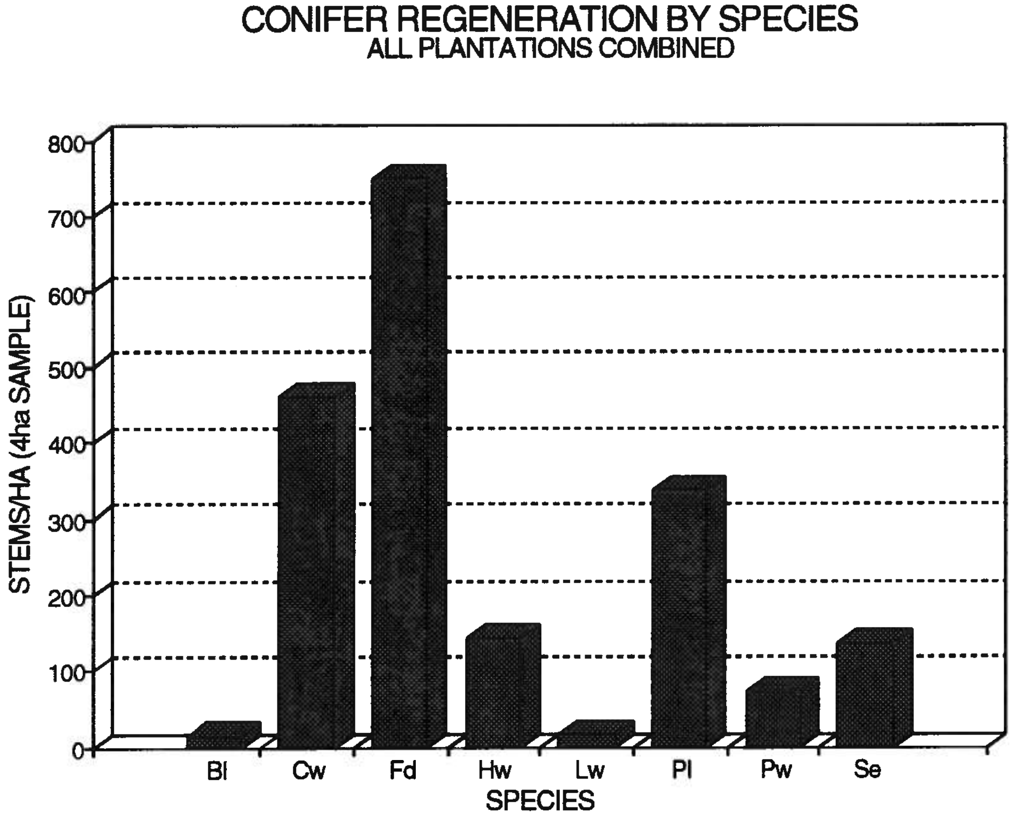

FIGURE 2. Distribution of conifer regeneration by species in all four plantations

While all four plantations had the same eight species present, the relative proportions of the total conifer stocking made up by each species varied significantly (Table 14). The most obvious difference in species composition among the plantations was due to the original species planted on each site. The 1980 plantation was planted to lodgepole pine while the other three were all primarily Douglas-fir plantations with the exception of two areas within the 1984 plantation which were also lodgepole pine. A second difference in species composition in the plantations is found between the two age groups (1980/84 versus 1969). The two older plantations have a fairly even distribution of stems among the species while the trees in the two younger plantations are primarily Douglas-fir or lodgepole pine depending on which species was planted.

TABLE 14. Number of conifer trees by species tallied/ha in each of the four plantations

SPECIES	1969a	1969b	1980	1984	TOTAL
		PLANTATION			
Bl	45	8	1	1	55
Cw	513	937	92	296	1838
Fd	751	778	317	1182	3028
Hw	220	209	77	63	569
Lw	27	4	8	28	67
Pl	7	18	1021	329	1375
Pw	250	67	82	20	419
Se	390	78	11	66	545
TOTAL	2203	2098	1610	1985	7897

Very few deciduous trees exhibited signs of *A. ostoyae* infection. Out of a total of 1304 paper birch trees examined only 6 or 0.46% exhibited signs of *A. ostoyae* infection. Similar rates of infection were found for trembling aspen trees with only 3 out of 506 or 0.59% infected. In relation to most of the conifer regeneration, these rates were miniscule and thus were not believed to be very helpful in determining infection patterns. However, it is important to note that the proportion of western redcedar that was infected was only slightly higher than that of the two major deciduous species.

Comparison of the Relative Rates of *Armillaria ostoyae* Infection Incidence among Conifer Species to a Douglas-fir Standard

There was a significant difference in the proportion of Douglas-fir trees infected among the four plantations (Chi-square=94.69, Chi-square critical=7.815). The highest proportion of stems infected occurred in the 1969b plantation (18.0%) followed by the 1980 (12.6%), 1984 (7.0%) and 1969a plantation (4.4%). The proportion of the other seven conifer species that were infected were then compared to determine if they varied in accordance with Douglas-fir.

The relative rates of *A. ostoyae* infection incidence were compared among the eight species found throughout the four plantations. The proportion of Douglas-fir infected was used as a standard measure of visible infection incidence for each plantation. The proportions of trees infected for the other species were compared to the Douglas-fir standard (Table 15).

TABLE 15. Ranking of conifer species compared to a Douglas-fir standard on the basis of the incidence of *Armillaria ostoyae* infection in plantations age 10-25 years

SPECIES	#TREES	#INFECTED	K-VALUE	CHI-SQUARE	CRITICAL CHI-SQUARE
Fd	3028	296	1.0000	-	-
Cw	1838	12	0.0537	0.450	5.991
Pw	419	9	0.2587	4.514	5.991
Se	545	11	0.2957	2.900	5.991
Hw	569	23	0.3745	8.643	7.815
Lw	67	3	0.6146	1.922	3.841
Pl	1375	167	1.0484	2.589	5.991
Bl	55	3	1.3840	0.055	3.841

Western hemlock was the only conifer species for which the proportion of trees infected differed significantly from the Douglas-fir standard measure of disease incidence among the four plantations. There was no significant difference in the relative rates of infection among the four plantations for the other six species compared to the Douglas-fir standard. This lack of significant differences among the plantations meant that a single K-value could be used for each of the six species over the four sites. The K-value quantified the relative frequency of infection for a species. Western redcedar trees, for example, were infected only 0.054 times as often as Douglas-fir. Since the Chi-square was significant for western hemlock, a single K-value was not used for this species. It appears that the ratio of infected western hemlock to infected Douglas-fir differed significantly from site to site. The 1969a plantation was primarily responsible this difference. None of the 220 western hemlock trees tallied in the 1969a plantation were infected, based on above ground evidence. As stated earlier 4.4% of the Douglas-fir trees were infected in this plantation.

The differences among species K-values were compared (Table 16). The proportion of western larch trees infected by *A. ostoyae* was not significantly different from any of the other species. This lack of differences was due primarily to the low number of larch trees in the four plantations. The proportion of western redcedar trees that were infected was significantly less than that of all other species except western larch.

TABLE 16. Chi-square values from the comparison of the proportions of trees infected with *Armillaria ostoyae* among eight conifer species in four plantations aged 10 to 25 years

	Fd	Cw	Hw	Lw	Pl	Pw	Se	Bl
Fd	-							
Cw	189.482*	-						
Hw	25.873*	34.96*	-					
Lw	3.440	0.0023	2.814	-				
Pl	2.260	38.59*	6.373	1.38	-			
Pw	20.00*	17.455*	10.188*	2.825	12.71*	-		
Se	18.367*	26.72*	2.416	4.923	7.308	0.042	-	
Bl	0.566	16.95*	13.568*	2.692	1.607	6.947	8.567*	-

Chi-square values followed by * are significant

There was no significant difference in the proportion of trees infected between lodgepole pine and Douglas-fir. Western hemlock was included in Table 16 despite the significant Chi-square from Table 15. As described earlier, the reason for the significant Chi-square for western hemlock was due primarily to one plantation. In general the proportion of western hemlock that was infected tended to follow the proportion of Douglas-fir infected.

Regeneration Species and Disease Status Distribution by Diameter Class

The species composition and size of each species was naturally dependent on the age of the plantation and the species originally planted. Western redcedar and western hemlock regeneration were concentrated in diameter classes less than 7.5cm, with 82.8% and 80.5% of each species respectively below that diameter (Table 17). Douglas-fir and lodgepole pine were concentrated in larger diameter classes with 53.4% and 74.3% of their stems respectively in diameter classes greater than 7.5cm. These differences in species size were probably due more to differences in growth rates than differences in age. The western redcedar and western hemlock regeneration, although smaller than the planted species, would probably have been established shortly after the sites had been burned. Observations in mature stands studied on Hunter's Range (Chapter 3) indicated that suppressed understory western redcedar and western hemlock trees were approximately the same age as the overstory Douglas-fir.

TABLE 17. Conifer regeneration species distribution in percent by diameter class (all plantations)

			DIAMETER CLASS(cm)			
SPECIES	1-2.5	2.5-7.5	7.5-12.5	12.5-17.5	17.5-22.5	TOTAL
Bl	10.9	45.5	32.7	7.3	3.6	55
Cw	36.3	46.5	14.4	2.0	0.8	1826
Fd	7.1	39.5	30.1	14.7	8.6	2950
Hw	24.8	55.6	15.9	3.0	0.7	568
Lw	14.5	33.9	21.0	21.0	9.7	62
Pl	0.7	25.0	53.8	19.9	0.7	1375
Pw	11.0	41.3	32.1	11.8	3.8	417
Se	11.0	55.2	25.9	5.9	2.0	545
TOTAL	1141	3180	2276	852	314	7798

The greatest proportion (58.9%) of regeneration mortality due to *A. ostoyae* occurred in the 2.5-7.5cm diameter class (Table 18). The second greatest, 26.5%, occurred in the 7.5-12.5cm diameter class. These two diameter classes together contained 85.4% of all regeneration mortality due to *A. ostoyae*. These two classes also contained 70.3% of all trees, so it is not surprising that the greatest losses to *A. ostoyae* are found in these diameter classes.

TABLE 18. *Armillaria ostoyae* severity distribution by diameter class and plantation (% of total in D-class)

			DIAMETER CLASS(cm)				
PLANTATION	1.0-2.5	2.5-7.5	7.5-12.5	12.5-17.5	17.5-22.5	22.5-27.5	PLANT TOTAL
1984 dying	0.0	0.9	0.4	0.0	0.0	0.0	12
1984 dead	4.9	7.3	0.7	0.0	0.0	0.0	102
1980 dying	0.0	1.4	1.1	1.8	0.0	0.0	20
1980 dead	8.7	24.4	6.5	0.6	0.0	0.0	162
1969b dying	0.2	0.5	2.0	4.7	3.0	2.2	29
1969b dead	1.5	6.4	11.3	8.6	1.2	0.0	118
1969a dying	0.0	0.2	0.3	1.1	0.0	0.0	7
1969a dead	0.0	1.9	2.2	1.4	0.8	0.0	37
TOTAL DYING	1	21	20	20	5	1	68
TOTAL DEAD	32	247	111	26	3	0	419

The distribution of diseased stems throughout the range of diameter classes was compared among the four major species (Table 19).

TABLE 19. Percentage of stems infected with *Armillaria ostoyae* out of the total number of stems in each diameter class for the four major regeneration species

	INFECTED DEAD	INFECTED DYING	DEAD,OTHER CAUSES	TOTAL TREES
Western redcedar				
0-2.5cm	0.3	0.0	0.0	663
2.5-7.5cm	0.5	0.0	0.1	849
7.5-12.5cm	0.8	0.8	0.0	263
12.5-17.5cm	0.0	2.8	0.0	36
17.5cm+	0.0	3.7	0.0	27
Total	8	4	1	1838
Douglas-fir				
0-2.5cm	10.7	0.0	0.5	207
2.5-7.5cm	10.0	1.2	0.2	1165
7.5-12.5cm	7.6	1.4	0.1	894
12.5-17.5cm	6.3	3.5	0.0	432
17.5cm	1.2	1.5	0.0	330
Total	249	47	4	3028
Western hemlock				
0-2.5cm	3.5	0.7	0.0	141
2.5-7.5cm	3.5	0.3	0.6	316
7.5-12.5cm	4.4	1.1	0.0	90
12.5-17.5cm	0.0	0.0	0.0	17
17.5cm+	0.0	0.0	0.0	5
Total	20	3	2	569
Lodgepole pine				
0-2.5cm	10.0	0.0	0.0	10
2.5-7.5cm	31.2	1.2	0.6	327
7.5-12.5cm	6.5	0.4	0.3	724
12.5-17.5cm	0.7	1.5	0.0	272
17.5cm	0.0	0.0	0.0	9
Total	152	11	4	1348

Western redcedar had the lowest proportion of stems infected with only 0.65% of the total stem count. There was very little difference in the number of western redcedar stems killed among the three smallest diameter classes. Only 8 stems out of 1775 were killed in those diameter classes (0.45%). Douglas-fir was second only to lodgepole pine in the proportion of stems infected and killed by *A. ostoyae*. For Douglas-fir, the smallest diameter class was the most severely affected, with 10.7% mortality. The percent mortality decreased with increasing diameter for this species. For western hemlock, the percent mortality was fairly constant over the three smallest diameter classes. Very few large diameter western hemlock were tallied. Those that were recorded, were all healthy. Lodgepole pine was the species most severely affected by *A. ostoyae*. In this species, the losses were greatest in the 2.5-7.5cm diameter class where 31.2% of the trees were killed. The majority of these losses occurred in the 1980 plantation, which was planted solely with lodgepole pine. The cause of the severe losses in lodgepole pine in this study may not be assigned simply to the species. The results in Table 16 indicated that there was no significant difference in the proportion of trees infected between lodgepole pine and Douglas-fir. There are confounding reasons for the high losses in lodgepole pine. The 1980 plantation had the highest stump inoculum load of the four plantations, and as pointed out later, had the highest mortality rate from other causes of the four plantations.

<u>Diameter Class Distribution for each Plantation</u>

The diameter class distribution for each plantation is summarized in Table 20. Naturally, there were no large diameter trees in the two youngest plantations. There was a considerable amount of small diameter regeneration in the two oldest plantations. In both of the 1969 plantations the 2.5-7.5cm diameter class made up the largest proportion of conifer stocking.

TABLE 20. Percentage of total stems in each diameter class by plantation

	PLANTATION			
DIAMETER CLASS (cm)	1969a	1969b	1980	1984
1.0-2.5	8.4	26.1	5.7	16.4
2.5-7.5	44.7	31.7	26.5	56.3
7.5-12.5	26.8	19.7	46.1	27.1
12.5-17.5	12.6	11.3	20.9	0.2
17.5-22.5	6.0	8.1	0.8	0.1
22.5-27.5	1.3	2.2	0.0	0.0
27.5-32.5	0.2	0.9	0.0	0.0
TOTAL TREES	2203	2098	1610	1985

Comparison of *Armillaria ostoyae* Severity Among Plantations

There were significant differences in the incidence of mortality caused by *A. ostoyae* among the four plantations (Table 21).

TABLE 21. Percentage of total conifer trees in each plantation killed by or dying from *Armillaria ostoyae* or killed by other causes

PLANTATION	DEAD	DYING	OTHER CAUSES	TOTAL
1969a	1.7	0.3	3.4	2203
1969b	7.3	1.4	1.1	2098
1980	10.1	1.2	4.2	1610
1984	5.1	0.6	0.5	1985
TOTAL	453	68	174	7896

The 1980 plantation suffered the greatest losses overall with 10.1% mortality due to *A. ostoyae*. Mortality from other causes described below was also the highest in this plantation with 4.2%. The 1969b plantation also had a high rate of mortality with 7.2%. The 1969a plantation had the lowest rate of mortality overall with only 1.7%. The 1969b plantation had significantly more *A. ostoyae* infection than the unbrushed 1969a plantation. These differences in mortality rates are perhaps misleading. The 1969a plantation had the lowest rate of mortality based on the evidence visible. It is quite possible that some trees killed by *A.*

ostoyae in the first 10 years following establishment of the two oldest plantations would no longer be visible. Evidence of *A. ostoyae* caused mortality in the two younger plantations over the same 10 year period would be more obvious.

The 1969b plantation did contain evidence that allowed for an estimate of *A. ostoyae* caused mortality at age 15. This plantation was brushed in 1984. At the time of brushing, all dead Douglas-fir stems were cut down (Jim Wright, Salmon Arm Forest District, pers. com.). The stumps of these Douglas-fir exhibited signs of *A. ostoyae* infection in the form of mycelial fan impressions. The number of these Douglas-fir stumps provided an estimate of the amount of *A. ostoyae* caused mortality in this plantation at age 15. Of the 153 (7.3%) trees killed in the 1969b plantation, 35 (1.7%) were Douglas-fir, killed prior to brushing. It is interesting to note that the percent mortality in the 1969b plantation prior to brushing was identical to the present percent mortality in the 1969a unbrushed plantation.

Armillaria ostoyae was not the only cause of death identified in the four plantations. Western white pine was infected to varying degrees by white pine blister rust (*Cronartium ribicola* J.C. Fisch ex. Rab.) throughout all four plantations. Lodgepole pine was occasionally infected with lethal stem galls caused by western gall rust (*Endocronartium harknessii* [J.P. Moore] Y. Hirat.), Warrens root collar weevil (*Hylobius warreni* Wood) and a needle blight probably caused by *Lophodermella concolor* (Dearn.) Darker. The needle blight was very common throughout all of the lodgepole pine, although it was rarely observed as the primary pathogen responsible for tree death. There was a total of 13 dead trees in the four plantations in the 'other causes' category for which the cause of death could not be identified.

Spatial Distribution of Infected Regeneration within Plantations

The distribution of infected trees within each of the plantations was also examined on a per plot basis (Table 22). The 1969a plantation was clearly the least infected in terms of area, with only 34.0% of the plots containing infected trees. In the 1969b plantation, 74.0% of the plots contained trees showing signs of infection by *A. ostoyae*. The 1980 plantation was most severely affected by *A. ostoyae*. In this plantation 85.4% of the plots showed signs of infection in the regeneration.

TABLE 22. Distribution of plots by increasing frequency of infection for all four plantations

PLANTATION	NUMBER OF PLOTS WITH NUMBER OF INFECTED TREES/PLOT 0	1-2	3-4	5-6	>6	TOTAL PLOTS
1969a	33	10	6	0	1	50
1969b	14	10	9	11	6	50
1980	7	12	11	11	7	48
1984	13	19	11	3	4	50
TOTAL PLOTS	67	51	37	25	18	198

2.3.3 The Relationship Between Past Levels of *Armillaria ostoyae* in Mature Stands and Present Levels of the Disease in Plantations Established on the Same Sites

Correlation analysis was used to analyze the relationship among 18 combinations of variables for all four plantations combined and for each plantation individually (Table 23). In these analyses, post-harvest measures of *A. ostoyae* in stumps included both pre- and post-harvest infections together and so were a measure of the total amount of *A. ostoyae* on the site. For each individual plantation, the sample size was 50 (48 in the 1980 plantation). The sample size for the combined plantation analyses was 198. Since the sample size was virtually the same throughout the four plantations, each of the correlation coefficients in Table 23 can be compared to a single critical correlation coefficient (0.273 for α=0.05, 0.354 for α=0.01). For the analyses involving the four plantations combined, the critical correlation value was 0.138 for α=0.05 and 0.181 for α=0.01.

TABLE 23. Correlation coefficients resulting from the correlation of stump and regeneration variables for each plantation individually and for all four plantations combined compared to critical values (α=0.05 and 0.01)

	1969a	1969b	1980	1984	ALL SITES
TREINFCT vs STMPBEFR	0.117	0.447	0.338	0.088	0.295
TREINFCT vs STMPAFTR	0.210	0.365	0.357	0.224	0.282
TREINFCT vs ARMSEVB	0.021	0.421	0.049	-0.133	0.225
TREINFCT vs ARMSEVA	0.140	0.304	0.095	0.017	0.265
TREINFCT vs BABEFOR	0.044	0.166	0.163	-0.014	0.157
TREINFCT vs BAAFTER	0.044	0.104	0.184	0.148	0.159
PROINFCT vs STMPBEFR	0.280	0.531	0.362	0.371	0.402
PROINFCT vs STMPAFTR	0.340	0.498	0.385	0.438	0.403
PROINFCT vs ARMSEVB	0.113	0.424	0.028	0.077	0.238
PROINFCT vs ARMSEVA	0.200	0.344	0.063	0.138	0.310
PROINFCT vs BABEFOR	0.142	0.246	0.184	0.192	0.267
PROINFCT vs BAAFTER	0.165	0.214	0.219	0.335	0.294
CONSTEMS vs STMPBEFR	-0.302	-0.262	-0.269	-0.473	-0.336
CONSTEMS vs STMPAFTR	-0.372	-0.274	-0.303	-0.357	-0.313
CONSTEMS vs ARMSEVB	-0.170	-0.126	-0.055	-0.279	-0.187
CONSTEMS vs ARMSEVA	-0.290	-0.110	-0.095	-0.105	-0.241
CONSTEMS vs BABEFOR	-0.390	-0.134	-0.158	-0.445	-0.339
CONSTEMS vs BAAFTER	-0.503	-0.170	-0.192	-0.390	-0.387
CRITICAL VALUE α=0.05	±0.273	±0.273	±0.273	±0.273	±0.138
α=0.01	±0.354	±0.354	±0.354	±0.354	±0.181

Comparison of Measurements of Stump Infection

The numbers of stumps infected both pre- and post-harvest were the stump variables most closely correlated with both the number of conifers infected and the proportion of conifers infected. The correlation r-values were higher for the proportion of conifers infected than for the actual number of conifers infected for all four plantations individually and combined. The relationships between infected stumps and infected regeneration were strongest in the 1969b plantation (Fig. 3).

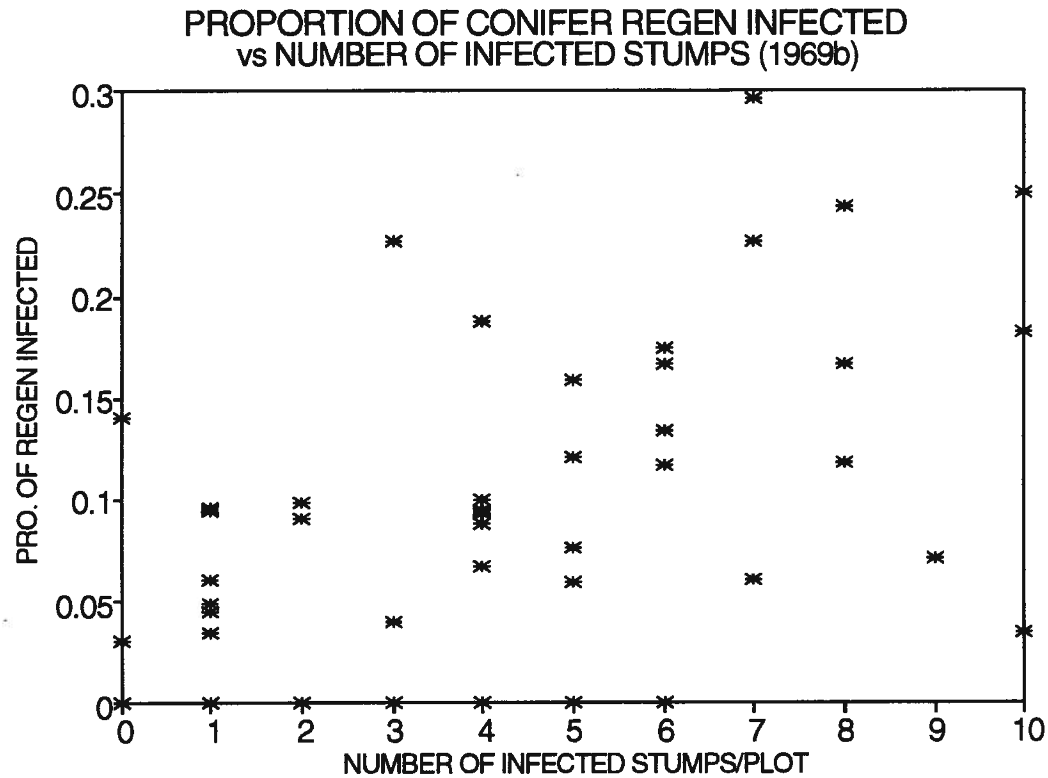

FIGURE 3. **The relationship between the number of stumps infected pre-harvest and the proportion of conifer regeneration infected in the 1969b plantation**

The number of healthy conifer stems/ha was most closely correlated with the basal area of infected stumps over all four plantations combined. It is not clear why the most highly correlated variables for a given plantation are not the most highly correlated over all of the plantations. In the two most severely affected plantations, 1969b and 1980, the number of infected stumps was most closely correlated with the number of disease free stems/ha. In the other two less severely affected plantations, the basal area of infected stumps was more strongly correlated with the number of disease free stems/ha.

The proportion of stumps infected either pre- or post-harvest was not strongly correlated with the number of conifer regeneration infected, the proportion of conifer regeneration infected or the number of healthy stems/ha. Both the number of infected stumps and the basal area of infected stumps were more closely correlated with the regeneration variables than the proportion of stumps infected.

Post-harvest infections were first considered as separate from pre-harvest infections. This was done to determine if there was a difference between the two measures of *A. ostoyae* inoculum in their ability to be used as predictors of future regeneration mortality. This division of inoculum sources was later removed since, logically, those stumps infected pre-harvest would also have to be considered as being infected post-harvest. The addition of post-harvest infected stumps had very little affect on the correlations (Table 23).

Multiple regression, using forward stepwise elimination, confirmed the earlier results in that the total number of infected stumps per plot was most closely related to the proportion of regeneration infected with *A. ostoyae*. All six stump variables were compared simultaneously to each of the regeneration variables in each of the plantations. The total number of infected stumps was the stump variable most closely associated with each of the regeneration variables in all but the 1969a plantation. In this plantation, the basal area of infected stumps was most closely correlated with the number of disease free stems/ha.

Effect of Plot Size on the Strength of Relationships Between Infected Stumps and Infected Regeneration

The effect of plot size on the relationships between the number of infected stumps, both pre- and post-harvest, and the number of regeneration infected was examined. This was done by comparing the correlation r-values of STMPBEFR and STMPAFTR regressed on TREINFCT on the full 8m radius plots and those obtained from quarter plot or sector analyses. In order to compare the r-values for both plots and sectors, an equal sample size was required. Only the first sector in each plot was used in the analyses. The results of these analyses are shown in Table 24.

TABLE 24. Effects of plot size on relationships between the number of infected stumps and the number of infected regeneration

PLANTATION	CORRELATION COEFFICIENT	n	p
1969b	0.365	50	0.012
1969b only infected*	0.473	36	0.004
1969b sector 1	0.022	50	0.878
1969b only infected sector 1's	-0.230	19	0.343
1984	0.224	50	0.097
1984 only infected	0.150	37	0.376
1984 sector 1	0.333	50	0.018
1984 only infected sector 1's	0.277	23	0.201

*"only infected" refers to using only plots or sectors with infected regeneration in the analysis.

In the 1984 plantation, using sectors rather than full sized plots appeared to improve the relationships between the number of infected stumps and the number of infected regeneration. The r-value for the relationship increased from 0.224 to 0.333 by using sectors. In the 1969 brushed plantation it was quite clear that the use of smaller plots did not improve the relationships between infected stumps and infected regeneration. The r-value using full sized plots was 0.365 while the r-value for sectors was 0.022. As mentioned earlier (Table 23), the relationship between the total number of infected stumps and the number infected trees was more closely correlated in the 1969b plantation (r=0.365) than the 1984 plantation (r=0.224).

Similar comparisons were made between plots and sectors using only those sampling units that contained infected trees. The rationale behind this method was that if there was a relationship between proximity of infected trees to infected stumps, it would be clearer if only those sampling units containing infected trees were analyzed. Including only the sampling units containing infected trees in the analysis increased the r-value for the 1969b plantation plot analysis only. The r-value of the sector analysis in the 1969b plantation was decreased by removing the sectors with no infected trees. In the 1984 plantation, removing sampling units with no infected trees reduced the r-values of the relationships for both plots and sectors.

2.4 Discussion

2.4.1 Comparison of the Relative Rates of *Armillaria ostoyae* Infection Incidence among Conifer Species to a Douglas-fir Standard

The ranking of conifer species based on incidence of infection (Table 15) differed considerably from the ranking that Morrison (1981) suggested. Morrison's (1981) species rankings were based on trees that exhibited signs of being challenged by the disease. Whether a species was ranked as more or less susceptible than another, depended on the reaction of the species to the disease. Susceptible species were more likely to succumb to the disease and die when challenged than the more tolerant species. The species rankings reported in Table 15 were based on the proportion of trees infected of a given species out of the total number of that species. It was not known how many of the apparently disease free trees had been challenged by *A. ostoyae*. Therefore, it is not valid to compare directly the ranking of species susceptibility suggested by Morrison (1981) with that reported in Table 15.

Despite the differences in the methods used to rank the species, it appears from this study that the ranking of conifer species susceptibility to *A. ostoyae* deserves more attention in future studies. To say that Douglas-fir is more susceptible to *A. ostoyae* than lodgepole pine (Morrison 1981) is questionable. There was no significant difference in the proportion of trees infected between lodgepole pine and Douglas-fir (Table 16). There is little reason to believe that one of these species would have been challenged by *A. ostoyae* more than the other over the four plantations. Both species would have been exposed to the same inoculum loads because both species were present on all four plantations. A similar argument could be made for including western redcedar in the same susceptibility class as lodgepole pine. It is possible that the plantations were not old enough to express the differences in species susceptibility to *A. ostoyae*. Morrison *et al*. (1991a) stated that there was little difference in susceptibility to *A. ostoyae* among conifer species less than 15 years old. Once again, it is clear that more research is needed into the question of species susceptibility to *A. ostoyae*.

The Chi-square test results (Table 15) for each of the species, except western hemlock, indicated that the proportion of trees infected for a species did not vary significantly from the proportion of Douglas-fir infected. In other words, in those plantations where the proportion of Douglas-fir infected was high, the proportions of the other species infected were also high. Thus, the differences in site among the four plantations did not affect the relative ranking of disease incidence among the conifer species. It was therefore possible to assign a single value (K-value) for each species as a ratio, that described the incidence of disease for that species in relation to a Douglas-fir standard. It was then possible to test for differences among the K-values. These tests (Table 16) indicated whether or not the proportion of trees infected were significantly different between two species. Attaching a statistical significance to the K-values allows for a statistically sound, quantitative ranking of conifer species based on the incidence of *A. ostoyae* infection.

The quantitative ranking of species based on disease incidence has advantages over the qualitative ranking of species susceptibility to *A. ostoyae*. A quantitative ranking of species based on the incidence of disease could provide forest managers with a tool that they may use in cost-benefit analyses of various management options. If it was known that in a given area, western redcedar was infected 0.0537 times as often as Douglas-fir, that number could be used, along with growth rate information for the two species, in calculations of future yields for a site. It is likely that the K-values reported in Table 15 would change as the stand aged. For example, young western redcedar in the plantations rarely exhibited evidence of infection, while the stump evidence indicated that western redcedar was infected just as often as Douglas-fir and western hemlock. Therefore, a series of K-values over the length of the rotation would probably be required for the calculations of future yields described above. A qualitative ranking such as Morrison's (1981) aids in decisions involving species choices, but does not provide the forest manager with values required for more detailed cost-benefit analyses of root disease control options.

The validity of an overall ranking of tree species susceptibility to *A. ostoyae* depends on those species having constant relative proportions of trees infected among species throughout all sites and ages. If the ranking of species suceptibility changes significantly from site to site and with age of the stands, it is not possible to determine an overall ranking of any value.

2.4.2 The Impacts of *Armillaria ostoyae* on Species Composition and Succession within the ICH zone

Armillaria ostoyae influences the species composition of stands within the Interior Cedar Hemlock zone to a considerable degree. The disease's influence has been described as increasing the rate of natural succession in this zone (Morrison 1981). The effects of this influence became quite clear when the differences in species composition between the two youngest and the two oldest plantations were examined. The species composition changed over time from being primarily a single species stand at the time of establishment to a much more diverse stand by age 25. The two 1969 plantations probably looked quite similar to the 1984 plantation about 15 years ago. One interpretation of the data suggests that over time, *A. ostoyae* has selectively removed the more susceptible Douglas-fir leaving openings for the more tolerant western redcedar, western hemlock and deciduous species. Douglas-fir and lodgepole pine were the two most frequently infected tree species. Western redcedar was the least frequently infected conifer species in the regeneration and was infected only slightly more often than paper birch and trembling aspen.

A second interpretation of the data includes the influence of time. The proportion of stems infected with *A. ostoyae* was highest in Douglas-fir and lodgepole pine. These species would appear to be more susceptible to the disease than western hemlock or western redcedar. The former two species were, however, the species planted and so have been on the sites, exposed to the *A. ostoyae* inoculum for the longest time. Although the ages of the trees were not determined, it is likely that the majority of the western redcedar and western hemlock have established in the two oldest plantations sometime after the sites were planted. Differences in species composition between the two oldest and the two youngest plantations (Table 14) indicate that there were few western redcedar and western hemlock in the two youngest stands.

Since all of the plantations were on similar sites surrounded by similar mature stands, it follows that western hemlock and western redcedar would likely ingress into the younger plantations over time. Thus, the western redcedar and western hemlock on the oldest plantations were probably younger than the Douglas-fir. It is possible, given the same length of time on the site as the planted species, that the rates of infection in western hemlock and western redcedar could be just as high. The stump data revealed no significant difference among these three species in the proportion of stumps infected prior to harvest.

The data in Table 19, however, substantiate the claim that Douglas-fir and lodgepole pine are more frequently infected and killed and thus more susceptible than western hemlock and western redcedar. Douglas-fir and lodgepole pine trees in the three smallest diameter classes, 0-2.5cm, 2.5-7.5 and 7.5-12.5, were significantly more heavily infected than western redcedar and western hemlock in the same diameter classes. *Armillaria ostoyae* appears to be affecting succession in this area of the ICH by selectively removing the early seral species and favouring the later seral species.

The impact of *A. ostoyae* on stands could also be characterized as slowing or even reversing succession in stands within the ICH zone. Following major disturbances, such as forest fires, paper birch is often one of the first species to dominate the site. Paper birch also tends to dominate those site which are most severely infected with *A. ostoyae*. The brief examination of deciduous species regeneration, although not nearly as complete as that of the coniferous species in this study, revealed that the proportion of trees infected was significantly less than that of most conifer species.

As mentioned earlier, the majority of stumps within the four plantations examined were either western redcedar, Douglas-fir or western hemlock. Deciduous species stumps decompose very rapidly in relation to the coniferous species stumps. Thus, very little evidence of prior deciduous stocking existed in any of the study areas. The loss of deciduous stump evidence results in an incomplete picture of the past stand's species composition and possibly a loss of important disease evidence. None the less, it appears that the relative proportions of tree species on the sites were strongly influenced by *A. ostoyae*. If the species composition of the original stand was strongly influenced by *A. ostoyae*, it may be possible to predict the level of infection in future stands based on the relative proportions of these three conifer species along with the proportion of deciduous trees.

The 1980 plantation provides a case in point. The 1980 plantation had the greatest *A. ostoyae* inoculum load of all of the plantations in terms of infected basal area. The species composition of the original stand on this site was quite different from that of the other three plantations. There were significantly fewer Douglas-fir stumps and significantly more western hemlock stumps on this site than on the other three sites. These differences in stump species composition between the four plantations could be due to succession alone. Perhaps the former stand on the 1980 site was the oldest of the four sites. The Douglas-fir component of stands in the ICH decreases over time as the species is replaced by the climax species, western hemlock and western redcedar. Douglas-fir is shade intolerant in the ICH zone thus it does not replace itself in an undisturbed stand. Western hemlock and western redcedar are shade tolerant species and are quite capable of growing underneath a Douglas-fir canopy eventually replacing the original stand. Conversely, the low Douglas-fir stump component on this site could have been due to lower resistance of this species to the high *A. ostoyae* inoculum load as compared to western hemlock and western redcedar.

By the time the stands reached maturity (approx 120 years), there was no significant difference among western redcedar and Douglas-fir in the proportion of trees that were infected among all four plantations (Table 7). However, the infected western redcedar stumps would have probably continued to survive with the disease had the area not been harvested since the species has the ability to wall off the basal lesions caused by *A. ostoyae* with callus tissue. The Douglas-fir on the other hand would probably not have fared so well. Douglas-fir also has the ability to grow callus tissue around *A. ostoyae* infections, but western redcedar appears to be more successful at controlling the disease. As the stump origin data points out, very few of the snag stumps were western redcedar. The majority of them were Douglas-fir.

It is likely that western redcedar continues to be more tolerant of *A. ostoyae* as stands mature than the other conifer species. Western redcedar and *A. ostoyae* appear to have reached a relatively stable equilibrium in the ICH zone. The equilibrium between *A. ostoyae* and the early seral species such as Douglas-fir and lodgepole pine, is much more unstable. Western redcedar is more tolerant of infections throughout the rotation and is killed much less frequently than the early seral species. The differential mortality rates among conifer species in response to *A. ostoyae* infections, allow western redcedar to maintain its position in stands while other species are killed. The equilibrium between *A. ostoyae* and the early seral species tends to shift in favor of the disease with ease. The disease may be triggered by factors such as logging, insect attack or other diseases. The insect and disease factors in the ICH tend to affect the early seral species more than western redcedar, putting them at a further disadvantage in this zone. Early seral species in the ICH zone may be killed by spruce budworm (*Choristoneura occidentalis* Freeman), Douglas-fir bark beetle (*Dendroctonus pseudotsugae*), spruce beetle (*Dendroctonus rufipenis* Kirby), mountain pine beetle (*Dendroctonus ponderosae* Hopk.), and white pine blister rust (*Cronartium ribicola* Fisch.) among others. Any one of these insects or diseases could possibly be responsible for shifting the equilibrium in favor of the disease triggering *A. ostoyae* to become aggressive in stands already infected with the pathogen (Kulhavy *et al.* 1984, Cobb 1989, Filip 1989b). Western redcedar was rarely killed by any disease or insect other than *A. ostoyae*, based on observations from the Hunter's Range study area (Chapter 3). The effects of *A. ostoyae* in stands within the ICH favor the survival of western redcedar over other conifer species and, therefore, influence the path of succession in this zone.

2.4.3 The Relationship Between Past and Present Levels of *Armillaria ostoyae* on a Site

There are inherent difficulties associated with analyzing data sets that contain a large number of zeros, particularly when the zeros are associated with the dependent variable. A large number of zero values for the dependent variable creates a situation where part of the data belong to only two classes. In such cases, the dependent variable is referred to as being dichotomous. Without a normal distribution throughout, the data fails to meet the basic requirements of simple linear regression. Many of the trees in the four plantations were healthy and occasionally entire plots exhibited no visible signs of *A. ostoyae* infection. Therefore, these plots would have a proportion of visibly infected regeneration of zero. At the same time, these plots often contained stumps which showed signs of infection. Very few plots were completely disease free in terms of infected stumps. The result is that the relationship between the various measures of stump infection and the proportion of regeneration infected was weak (Fig. 3). The weakness of these relationships was due in large part to the number of zeros in the infected regeneration data. With the zero values removed, the relationship between the proportion of regeneration infected and either the basal area infected or the number of stumps infected was stronger.

Aldrich and Nelson (1985) reviewed the use of LOGIT and PROBIT models for dealing with dichotomous dependent variables. The use of such models for improving the strength of the relationships between *A. ostoyae* infections in stumps and regeneration was considered. The result of using these models would be, at best, a more accurate prediction of the amount of regeneration mortality in a plantation given that some mortality had already occurred. These models would not increase the probability of accurately predicting the amount of regeneration mortality based on the inoculum load in the previous stand alone. The value of such models was not considered to be great in this case. One of the primary objectives of this study was to develop methods for predicting the degree of loss to *A. ostoyae* in a plantation based on the amount of infection in the mature stand prior to harvest. A prediction of expected future regeneration mortality at the time of harvest would aid forest managers in deciding what to prescribe for the site in order to improve productivity of the future stand. If an accurate prediction of regeneration mortality cannot be made until there is already some mortality occurring in the plantation there is little point in making such a prediction. It is too late at that stage in plantation development to do much to improve the situation. Steps must be taken much earlier, at the pre-harvest stage, in order to deal effectively with the disease.

It is important to keep in mind that the conclusions drawn from a plot analysis may not be directly applied on a plantation basis. If, for example, a plot contained no infected stumps, it is still quite possible that trees growing on that plot may become infected. The area surrounding the "clean" plot could easily contain infected stumps. However, if an entire plantation was free of infected stumps, the probability of a tree becoming infected on that plantation would be almost nil. In order to predict the average mortality for a given plantation based on pre-harvest infection levels, a large number of plantations would have to be sampled. Such a study would require a pre-harvest survey of root disease in each plantation, with follow-up surveys of regeneration survival and root disease activity. The results of such a study would provide forest managers with the information they need to plan more effective root disease control programs.

The relationship between the basal area and number of infected stumps, and the proportion of regeneration infected was not strong on an individual plot basis. The relationship was similarly not clear on a plantation wide basis. Regeneration mortality attributable to *A. ostoyae* was greatest in the 1980 plantation where 10.1% of the stems were killed by the disease. The disease was quite evenly distributed over the plantation. Only 14% of the plots in the 1980 plantation exhibited no evidence of infection in the regeneration. The remaining 86% of plots contained at least one infected tree each. The highest number of infected trees in a plot in the 1980 plantation was 15. The majority (83.1%) of the stumps in the 1980 plantation were infected with *A. ostoyae* either before or after harvest. The species composition of the regeneration may have contributed to the high levels of mortality in the 1980 plantation. However, the results reported in Table 16 indicated that there were no significant differences between lodgepole pine and Douglas-fir in the relative proportion of trees infected. Regardless of possible confounding species effects, this plantation had the highest cross sectional area of stumps infected with *A. ostoyae* prior to harvest and suffered the highest losses following plantation establishment.

The relationship was not so clear in the other plantations. The two 1969 plantations had different treatment histories and therefore the proportions of regeneration infected could not be legitimately compared between the two. The differences in the number of infected stumps between the two were not great. Furthermore, any effects on regeneration survival due to differences in initial inoculum loads would have been confounded by the effects of the brushing treatment in the 1969b plantation. The effects of the brushing treatment in the 1969b plantation are discussed later. The 1984 plantation had the highest number of infected stumps of the four sites. This plantation also had one of the highest proportions of stumps infected with *A. ostoyae* (70.6%). However, the proportion of regeneration infected on this plantation was only 5.7%, second only to the 1969a plantation for low incidence of infection. Perhaps the inconsistency of the relationship between infected stumps and infected regeneration demonstrated by this plantation was due primarily to the age of the plantation. It is possible that with another 5 years the relationship between infected stumps and infected regeneration would be clearer, as in the 1980 plantation. Whether or not more time would accentuate the relationship is not known. The results from this plantation illustrate the high variability associated with the relationship between infected stumps and infected regeneration. The ability to predict future plantation losses based on the amount of infection in mature stands remains questionable.

2.4.4 The Proximity of Infected Regeneration to Infected Stumps

It is apparent that the proximity of regeneration to infected stumps does not increase their likelihood of being infected by age 25. Conceivably, if the spatial distribution of infected stumps did have a large influence on the distribution of infected regeneration, examining the plots on a more detailed scale should have improved the correlations between the two measures. Smaller plots would tie together more closely the infected stumps with infected regeneration, if in fact they were closely associated with each other. The correlations between the number of infected stumps/sector and the number of infected regeneration/sector would then be expected to increase. The strength of the correlations did not improve over those found using the full sized plots in the 1969b plantation (Table 24). This suggested that the tree's proximity to infected stumps no longer had a large influence in determining the probability of that tree becoming infected. Morrison (Forestry Canada, unpublished data) stated that new infections originated from contacts with diseased trees rather than infected stumps in stands older than 20 years. The results from this study support that claim.

It appeared that stumps were still functioning as the primary source of inoculum responsible for infecting the regeneration at age 10. Examining the 1984 plantation on a sector by sector basis improved the correlations between the number of infected stumps and the number of infected regeneration. The correlation r-values were higher in the sector analysis than in the plot analysis in this plantation. These results suggest that reducing the maximum distance of a tree from an infected stump increased the probability that that tree would be infected.

Why the sector relationship was more significant in the 1984 plantation than the 1969b plantation is, at first, not clear. The differences in age would be the most obvious reason. Up to age 10, infected stumps were still acting as the primary inoculum source, thus infected trees in the 1984 plantation were still associated with the infected stumps. The sector analysis suggested that in the 1969b plantation the stumps were no longer the primary inoculum sources. If infected trees in the 1969b plantation were at one time associated with infected stumps, this no longer seemed to be the case. It would appear that the evidence of tree mortality that was closely associated with the infected stumps in the past was no longer visible in this plantation. The fact that the 1969b plantation was brushed in 1984 provides some important information regarding the question of proximity to infected stumps. Douglas-fir trees that had been killed by disease up to 1984 were cut down during the brushing treatment. The evidence of these dead trees was still present on the 25 year old 1969b plantation. Since the evidence of past mortality for the 1969b plantation up to age 15 was still quite visible, it is likely that much of the evidence of past *A. ostoyae* caused mortality was still present on the 1969b plantation. Why then was there not enough evidence of infected trees surrounding the infected stumps in the 1969b plantation to make the sector analysis more significant on this site? The answer most likely lies with the brushing treatment. Following brushing, *A. ostoyae* was re-activated and spread rapidly through the freshly cut stumps of the western hemlock, western redcedar and birch regeneration. Any of the Douglas-fir crop tree root systems that were in close association with the infected brushed stems were then exposed to a much greater inoculum potential. An increasing proportion of the Douglas-fir trees have died since brushing. These killed trees were not infected through contact with *A. ostoyae* colonized stumps from the original stand, but most likely by contact with colonized-brushed stumps. It is not surprising, therefore, that the relationship between infected stumps and infected regeneration in this plantation was not improved by sector analysis.

These results have important implications for guidelines concerning silvicultural surveys in the ICH zone. The current guidelines state that any tree within 3 meters of an infected stump can not be considered as free to grow. The results from this study indicate that, in 25 year old plantations, trees within 4m from an infected stump are no more likely to be infected than those trees within 8m if the site has been brushed. In 10 year old plantations there was a stronger relationship between infected trees and infected stumps. Thus, the validity of the 3m rule depends on the age of the plantation and the treatments that have been conducted on the site. A blanket treatment over all plantations within the ICH zone is not appropriate.

2.4.5 The Impacts of Brushing Stands Infected with *Armillaria ostoyae*

The negative impacts of brushing and spacing on the survival of crop trees in areas infected with *A. ostoyae* were quite clear after comparing the two oldest plantations. These two plantations were similar in many respects. They both had similar initial inoculum loads as measured by the basal area of stumps colonized by the fungus, both prior to and following logging. The unbrushed plantation had 44.36m^2/ha of infected stump basal area compared to 37.95m^2/ha in the brushed plantation. The species composition of the regeneration was very similar between the two. The location, slope and aspect of both plantations was also very similar. There were two major differences between the plantations that may have influenced the development of *A. ostoyae* development on these two sites. The first difference was the date of harvest. Although both plantations were established in 1969, the original harvest dates were not the same. The 1969 brushed plantation was logged in 1965 while the unbrushed plantation was logged in 1968. The delay in planting the 1969b plantation probably created the need to brush that stand. The delay in replanting would also be expected to decrease the inoculum potential of *A. ostoyae* on the site. The planting lag would leave the disease with few suitable new hosts for the 5 year period between logging and planting. The second difference, obviously, was the fact that one of the plantations was brushed while the other was not. A summary of the similarities and differences between these two plantations is found in Table 25.

TABLE 25. A comparison of the two 1969 plantations

	1969a	1969b
YEAR LOGGED	1968	1965
YEAR PLANTED	1969	1969
YEAR BRUSHED	-	1986
BASAL AREA INFECTED	$44.4m^2/ha$	$38.0m^2/ha$
DEAD & INFECTED STEMS/HA		
> 12.5cm DIAMETER	8/443 (1.8%)	40/472 (8.5%)
% OF PLOTS INFECTED	34	72

The greatest losses have obviously occurred in the brushed plantation. The Douglas-fir trees that had been killed up to the time of brushing were cut down during the brushing treatment (Jim Wright, Salmon Arm Forest District, pers. com.). The stumps from these trees were still visible on the site. Based on this stump evidence, 35 Douglas-fir stems/ha had been killed by *A. ostoyae* up to 1984. Two of these dead Douglas-fir trees were over 12.5cm in diameter. Twenty-one stems/ha of Douglas-fir over 12.5cm diameter have been killed by *A. ostoyae* since the time of brushing in the 1969b plantation. At the end of the 1993 growing season, 17 stems/ha of Douglas-fir over 12.5cm diameter were infected and dying. Judging by the reduced internodal length of some of the trees, it was likely that these infected trees had been suffering from the effects of *A. ostoyae* infection for several years. Other infected trees showed no signs of reduced growth in the past year. Overall, it appeared that the majority of infected and dying trees had probably been influenced by A. ostoyae over approximately the past 4 years. Thus the rate of mortality in the brushed stand appears to be increasing. In 9 years, 21 stems/ha over 12.5cm DRC were killed, while in the past 4 years, 17 stems/ha over 12.5cm DRC were infected and dying. Conversely, the rate of mortality in the unbrushed plantation was much lower. Only 5 stems/ha over 12.5cm DRC had been killed. The time period over which these trees were killed was difficult to estimate, but it was probably quite similar to the 1969b plantation (approx. 10 years). Only 3 stems/ha over 12.5cm DRC were infected and dying over the same 4 year period described for the 1969b plantation.

There were also large differences between the two plantations in the number of plots that contained infected trees. As shown in Table 23, 34% of the plots in the 1969a plantation contained infected trees. In the 1969b plantation 72% of the plots contained infected regeneration. In this same plantation, 34% of the plots contained 5 or more infected trees compared to only 2% in the unbrushed plantation.

It appears that the disease-host equilibrium discussed in the previous section has been reached in the unbrushed plantation. Brushing the 1969b plantation has seriously disrupted the path to equilibrium in this plantation. It appears possible that the disease-host equilibrium may not be reached in time to salvage a productive stand by the end of the rotation period. As Morrison (1981) suggested, brushing and spacing should not be carried out in Douglas-fir stands infected with *A. ostoyae*. The results of this study strongly supports that suggestion.

The low rate of mortality in the unbrushed, 1969a plantation suggests that perhaps the disease is reaching an equilibrium with the host by age 25. It is also possible, that this plantation has always had a low rate of infection in the regeneration and the rate is not slowing. Ideally, a comparison between the 1969a plantation and the 1984 plantation could provide more definitive answers as to whether or not the impacts of the disease decline by age 25. However, it is more difficult to compare the 1984 plantation to the 1969a plantation than it was to compare the two 1969 plantations. The ten-year-old 1984 plantation had many site factors in common with the 1969a plantation, but there were some important differences. For example, the 1984 plantation had considerably more infected stumps/ha than the 1969a plantation. These differences in initial inoculum load made it difficult to compare rates of infection in the regeneration.

Even if the rate of infection has always been low in the 1969a plantation, this information in itself is reason for some optimism. The 1969a plantation contained 216 infected stumps/ha which represented an infected stump basal area of $44.4m^2$/ha, yet the conifer stocking on that site now is generally quite healthy. There is some mortality still occurring due to *A. ostoyae* and it will most likely continue. There are still 435 healthy Douglas-fir stems/ha over 12.5cm diameter and considerable western hemlock and western redcedar ingress to fill in the gaps. The probability of this stand reaching maturity appears quite high despite the former levels of *A. ostoyae* infection on the site. The prognosis for the stand that was re-entered is obviously not so optimistic.

CHAPTER 3 *ARMILLARIA OSTOYAE* DISTRIBUTION AND SEVERITY IN THE ICH AND IDF BIOGEOCLIMATIC ZONES

3.1 Introduction

Armillaria ostoyae causes significant damage to forests throughout the southern interior of B.C. The ICH biogeoclimatic zone is one of the most severely affected ecological zones in the province. The IDF zone is also affected, but generally to a lesser degree. The areas infected with *A. ostoyae* in these two zones are generally believed to be quite large.

McDonald *et al.* (1987) suggested that disease incidence is greatest in host populations in the transition zones between climax species. They hypothesized that the species in these zones are less adapted to the sites and therefore less resistant to disease. If this is the case, intraspecific variations in host resistance would be most visible in these transition zones. The differences in site conditions would conceivably place extra stress on those species least adapted to the specific conditions on that site. In their review of *Armillaria* spp. research, Kile *et al.* (1991) stated that intraspecific variation in host resistance to *A. ostoyae* has not been investigated. Interspecific variation in host resistance has similarly received little attention. Morrison (1981) reported a qualitative ranking of tree species susceptibility to *A. ostoyae* for the southern interior of B.C. As discussed in the previous chapter, more research is required concerning the ranking of susceptibility to A. ostoyae among the species present in the ICH and IDF zones.

The interaction between *A. ostoyae* and other abiotic and biotic factors within the southern interior of B.C. has not been studied thoroughly. Several of the following factors could have an influence on the expression of this disease: the biogeoclimatic site classification, site index, elevation and disturbance history of the sites. *Armillaria ostoyae* distribution has been associated with particular forest habitat types using the Daubenmire forest vegetation classification system in the Northwest United States (Byler *et al.* 1987 and 1990, McDonald 1990, Williams and Marsden 1982). These studies emphasize the dynamic nature of the interaction between *Armillaria* species and natural forest ecosystems (Kile *et al.* 1991). To date, there has been little work undertaken to link the incidence and severity of *A. ostoyae* to the biogeoclimatic ecosystem classification (BEC) system used in B.C. The BEC system, developed by Dr. V.J. Krajina and his students, incorporates primarily soil, climate, and vegetation data (Meidinger and Pojar 1991). This system of ecological classification is used by the majority of forest managers in B.C. If the probability of a stand being infected with *A. ostoyae* could be linked to this classification system, it would aid forest managers by providing a simple planning tool for dealing with this forest pathogen.

The BEC system uses a fairly wide range of factors to describe the conditions on a site. Other factors, such as elevation and site index, may also influence the behavior of *A. ostoyae* on sites within the same BEC site identification. Hobbs and Partridge (1979) found no relationship between elevation and the incidence and severity of *A. ostoyae* in northern Idaho. Williams and Marsden (1982) found the opposite in the same area of northern Idaho.

Forest management practices have a large influence on the expression of *A. ostoyae*. Partial cutting practices, in particular, have been blamed for increases in *A. ostoyae* activity in numerous studies carried out in the Northwest United States (Filip and Goheen 1982, Byler *et al.* 1987, Shaw *et al.* 1976). Much of the available information is observational, however, and little experimental work has been done on the effect of management practices on disease level (Kile *et al.* 1991). The effects of selective harvests in *A. ostoyae* infested areas in the southern interior of B.C. has received very little attention. Much of the southern interior has been selectively harvested over the past century either for poles or railroad ties. The impact of this disturbance on the behavior of *A. ostoyae* in these stands has not been studied.

The relationship between *A. ostoyae* and *P. weirii*, the two most serious root disease pathogens in the southern interior of B.C., is also not well understood. *Armillaria ostoyae* is believed to cause damage in conjunction with other root rot pathogens of mixed coniferous forests, particularly with *P. weirii* (Filip and Goheen 1984, James *et al.* 1984, Williams and Leaphart 1978). The existence of the relationship between these two diseases is not accepted by all workers in this field of forest pathology. Hansen and Goheen (1989) attributed the associations between these two diseases to chance and to primary secondary relationships. Whether or not there is a relationship between these two disease in the southern interior is not known.

The abiotic and biotic factors described above may or may not influence the activity of *A. ostoyae* in the southern interior. If there is an impact on *A. ostoyae* from any one of the factors, knowledge of the corresponding impact of *A. ostoyae* activity on timber volume would be very beneficial. With the exception of Bloomberg and Morrison's 1989 study, the impacts in terms of forest productivity loss have likewise not been well addressed in the southern interior. No empirical studies to date have attempted to correlate *A. ostoyae* severity in a mature stand with the corresponding loss in coniferous timber volume.

One of the objectives of this study was to gain a better understanding of the ecology of *A. ostoyae* in the ICH and IDF biogeoclimatic zones. This study provides an estimate of the distribution of *A. ostoyae* within both zones and in the transition between the two. Differences in site characteristics within the study locations provided an opportunity to examine intraspecific variation among several conifer species to *A. ostoyae*. The variety of species present in the study area allowed for an examination of interspecific differences in incidence of *A. ostoyae* infection among eight conifer species. This research also examined the possibility of using the BEC system for predicting the probability of stands in the IDF and ICH zone being infected with *A. ostoyae*. The relationship between *A. ostoyae* severity and site was viewed at two levels of classification within the BEC system.

In addition to studying the impacts of site, as defined by the BEC system, the possibility of elevation and site index affecting root disease in the ICH and IDF zones of southern B.C. was also examined.

Another objective of this research was to examine the relationship between prior disturbance and *A. ostoyae* activity in the ICH and IDF biogeoclimatic zones.

After the effects of the various factors on *A. ostoyae* severity were examined, the relationship between *A. ostoyae* severity and both paper birch and conifer volume were analyzed.

3.2 Methods

3.2.1 Study Area

Two separate areas were sampled in this study. The first was located on the west slopes of Hunter's Range, directly to the east of Mara Lake, close to Sicamous, B.C. This area straddles the transition between the Interior Cedar Hemlock (ICH), and the Interior Douglas-fir (IDF) biogeoclimatic zones. Within this study area, the predominant variants of each of these zones were the Shuswap moist warm ICH (ICHmw2) and the Shuswap moist warm IDF variant (IDFmw1) respectively (Lloyd *et al.* 1990). The Hunter's Range site consisted of approximately 4000ha of "relatively" undisturbed forests (*i.e*, few recent cutblocks). A second site was chosen on the northwest slopes of the Larch Hills between Sicamous and Canoe, B.C. This study area was similar in many respects to the Hunter's Range area including the aspect, elevation, disturbance history, and biogeoclimatic site types. The two study areas are less than 12km apart.

The majority of the area on both study sites was burned in the late 1800's as a result of railroad construction. Thus, the age of most of the stands was approximately 120 years. Stands throughout the Shuswap region have also been selectively logged for poles or railroad ties since the early 1900's. Evidence of past logging disturbance was present throughout much of the two study areas. More precise dates for the history of these disturbances were not available. The predominant forest cover type was Douglas-fir at or near 120 years of age.

3.2.2 Sampling Design

The sampling design for the Hunter's Range site consisted of 202 - 8m radius plots (0.02ha) laid out in strip pairs forming a grid. The strip pairs were laid out 400m apart along the contour. The plots were located at 200m intervals along the strips which ran east-west against the contour. This orientation captured the greatest elevational variation to test if elevation had any influence on disease expression. Plots were located by tight chaining from known tie points found on 1:15000 scale Forest Cover Maps (82LO75, 82LO76, 82LO65 and 82LO66) produced by the Inventory Branch of the Ministry of Forests. Since the site identifications for the plots could not be made until they were located, there was an uneven number of plots in each of the biogeoclimatic zones and among the site types.

Thirty-two 8m-radius plot were located using similar methods to those used in the Hunter's Range study for the Larch Hills site.

3.2.3 Sampling Procedure

Once the plot center was located, a 30m Eslon tape was used to establish the perimeter of the 8m radius plots. The perimeter of the plots were flagged with florescent ribbon. Within each plot, the species, diameter at breast height, height and disease code for each living tree and dead standing tree were recorded.

The disease code was determined by examining each tree for the presence of disease signs and symptoms. Evidence of *A. ostoyae* infections included basal resinosis, mycelial fans beneath the bark, healed over basal lesions and thinning crowns. Any trees exhibiting crown symptoms were closely examined to determine if *A. ostoyae* was the causal agent. Root excavations were conducted only on those trees exhibiting crown symptoms. Trees with basal resinosis visible above the ground at the base or on exposed roots were examined for the presence of mycelial fans beneath the bark. These examinations were conducted with an axe and involved chopping into and prying off the resin soaked bark. Healed over basal lesions were identified by their appearance and by the hollow sound they made when hit. Healed over basal lesions typically form flattened portions on the bole directly above an infected root. Each tree was also tapped around the circumference of the root collar with the back of the axe. Those trees with flattened portions on the bole, and those that sounded hollow when hit were examined further by removing the bark at the area in question. If there was no above ground evidence of *A. ostoyae* infection present on a tree, the tree was classified as clean. Trees were assigned a disease code as follows:

0 - no sign of infection
2 - healed over basal *A. ostoyae* lesion
3 - active mycelium, or recent *A. ostoyae* mortality.

Based on the individual tree examinations within each plot, a preliminary disease severity rating was recorded for each plot. The plot disease severity rating was based on the following scheme:

0 - no evidence of disease in plot
1 - evidence of disease on trees < 10cm dbh or dead and down trees only
2 - presence of disease code 2 trees > 10cm dbh within plot
3 - presence of disease code 3 trees > 10cm dbh within plot.

Trees exhibiting crown symptoms and trees within disease centers were also examined for the presence of *P. weirii*. Evidence of *P. weirii* consisted of ectotrophic mycelium on roots, reddish-brown staining of the heartwood, and thinning rounded crowns. Data on this root pathogen were collected in order to describe relationships between this disease and *A. ostoyae*.

A representative tree height was measured for each species present in each plot. This height was used to visually estimate the remaining tree heights within the plot. The height and diameter data were then used to determine the volume for each tree using whole stem cubic meter volume equations for each species (British Columbia Forest Service Inventory Division 1976).

The plot site index was determined by first measuring the height and age of a dominant Douglas-fir within each plot. This information was then used in conjunction with Thrower and Goudie's (1992) site index tables for interior Douglas-fir to find the site index value for each plot. If no suitable Douglas-fir was present within the plot, a sample was chosen from nearby.

Evidence of prior logging disturbance was recorded using the following classification:

0 - no disturbance
1 - disturbance present outside plot radius (*i.e*, stumps or skid trails)
2 - stumps present within plot.

The species and diameter at root collar was recorded for any stumps within plots.

Each plot was classified by biogeoclimatic site types using the field guide for the Kamloops Region (Lloyd *et al.* 1990). Site type classifications were based on the major tree species forming the forest canopy, as well as plant indicator species present in the understory.

The elevation of each plot was determined by transcribing the plot locations from the 1:15000 scale Forest Cover Map to 1:20000 scale contour maps provided by the Ministry of Forests District Office in Salmon Arm B.C. These maps allowed for elevation estimations to the nearest 5m.

The last step in data collection involved determining a final *A. ostoyae* severity rating for each plot. The basic logic of the disease severity rating was as follows:

if no evidence of *A. ostoyae* was present within the plot,
then *A. ostoyae* rating = 0;

if there was evidence of *A. ostoyae* on standing trees within
the plot, then determine the proportion of class 2 and class 3 infected trees out of total number of conifer trees and assign severity rating based on the following ratings:

Proportion of total conifers/plot with class 2 or 3 infections	Class 2	Class 3
0.00 - 0.10	+1	+3
0.11 - 0.20	+2	+6
0.21 - 0.30	+3	+9
0.31 - 0.40	+4	+12
0.41 - 0.50	+5	+15
0.51 - 0.60	+6	+18
0.61 - 0.70	+7	+21
0.71 - 0.80	+8	+24
0.81 - 0.90	+9	+27
0.91 - 1.00	+10	+30

Class 3 infections represented more active and aggressive *A. ostoyae* activity and thus were given a higher severity rating than those trees with class 2 infections. Class 2 infections, as mentioned earlier, were those infections that had been actively resisted by the host tree with no signs of active mycelium. The plot severity rating was the sum of the values for class 2 and 3 infections.

This root disease severity rating formed the basis for comparisons among the plots from differing site types, elevations, disturbance histories, site indices and volume classes. The plot severity ratings formed the dependent variable in this study. A similar disease rating was determined for *P. weirii*.

Any root disease survey involves a compromise between the accuracy of the estimated number of infections and the time available for surveying. The most accurate estimates of the number of *A. ostoyae* infected trees in a stand would require complete excavation of each tree. Such estimates would be impossible on anything but the smallest scale due to the effort and cost involved in excavating the trees. In order to accurately estimate the extent of *A. ostoyae* over a large area, more time must be allotted to covering the ground rather than digging it up. The objectives of this study dealt primarily with the relationships between site and *A. ostoyae*; thus, the emphasis was placed on covering a large area with a large number of plots.

A follow-up study was conducted on the Larch Hills in order to determine more accurately the number of infected trees in mature stands within the ICHmw2. A subsample of 10 plots was taken within an area with similar site characteristics to that of the other study areas mentioned earlier in Chapter 3. The results from the subsample demonstrate more clearly the relationship between the amount of *A. ostoyae* found and the effort required to find it. The subsample consisted of plots located in the mature stands surrounding the plantations sampled in Chapter 2. Data from the same 10 plots were used in Chapter 2 to ensure that the methods used in the plantation study were not over-estimating the number of stumps infected pre-harvest. In Chapter 3 these data are used to demonstrate how more time and effort spent in excavating roots can reveal more *A. ostoyae* infections.

Plot locations were established using the same methods as those described earlier (3.2.2 Sampling Design). Within the plot perimeter, the diameter at breast height and species of every tree was recorded. The roots of each tree were then excavated to a distance of 30cm from the root collar and a depth of approximately 10cm into the mineral soil. The bark of the exposed roots was then removed using an axe to determine whether or not mycelial fans of *A. ostoyae* were present. It was decided at the time of data collection whether or not a given infection would have been tallied using the methods from the Hunter's Range study. This decision was based on the amount of excavation required to find the infection. Those trees with above ground symptoms would have been recorded in the 1992 field season. Those trees with infections below ground but within 30cm of the root collar would have only been recorded in the 1993 field season. The result was a comparison of the ability of the two methods to detect *A. ostoyae* infections in a stand.

3.2.4 Data Analysis

The data was first entered in Quatro-Pro (Version 3.01. 1991) and later transferred to SYSTAT (Version 5.03. 1991) for statistical analysis. The data analysis was divided into two sections; the first section dealt with individual trees and the second with plots. The significance level was set at $\alpha=0.05$ for all tests in Chapter 3.

<u>Individual trees</u>

Differences among tree species in terms of relative proportions infected with *A. ostoyae* were examined first using the Hunter's Range data. The Chi-squared statistic was used with contingency tables, to test the significance of differences in tree species distributions between zones and the frequency of infections among species within zones. For both of these comparisons, a Chi-square test was first performed on all conifer species combined. If the test indicated significant differences among the species, further tests were performed for pairwise comparisons between the species. Those species with similar proportions were tested using 2 by 2 contingency tables to determine if two species had significantly different proportions of infected trees. This method of comparing species was continued until all possible species comparisons had been tested. Differences within species in the proportion of trees infected between zones were also tested using 2 by 2 contingency tables (Chi-square critical=3.841, one degree of freedom). A similar procedure was used to determine if the frequency of infections within a species was significantly different among site units within a zone.

The same methods were then used on the Larch Hills data (32 plots) to determine if the differences among species in the proportion of trees infected, were consistent between the two areas. In particular these data were collected to further examine the incidence of infection for western larch compared to the other conifer species in the IDF and ICH zones.

The data from both the Hunter's Range site and the Larch Hills sites were then combined to examine the differences in disease incidence within species, between the ICH and IDF zones in both sites. The proportion of trees infected for five major species were compared between the Hunter's Range and Larch Hills sites. The comparisons were tested with 2 by 2 contingency tables and the Chi-square statistic.

The species composition was also compared between the Larch Hills and Hunter's Range. The proportion of the total trees comprised of each of the five major species were compared with a Chi-square test. This comparison was made in order to determine if the differences in *A. ostoyae* infection incidence between the two study areas were due to differences in species composition.

The incidence of infection among three of the species (western redcedar, western larch and lodgepole pine) were compared to the incidence of infection for Douglas-fir. The methods used for this analysis were the same as those used to test for differences among the conifer regeneration species in Chapter 2 (pages 30-31). Douglas-fir was chosen as a standard measure of disease incidence for four areas; Hunter's Range ICH, Hunter's Range IDF, Larch Hills ICH, Larch Hills IDF. These methods were designed to determine a quantitative ranking of conifer species based on incidence of *A. ostoyae* infection in mature stands. There were not enough of the other species (western hemlock, Engelmann spruce, western white pine and sub-alpine fir) to be included in this analysis.

The incidence of *A. ostoyae* infections in conifer species were also compared among the biogeoclimatic site units within each of the zones. The proportions of infected trees out of the total for each species were compared among site units using a Chi-square test. If the proportion of trees infected differed significantly among site units, further pairwise comparison Chi-square tests were used to determine which site units had significantly different proportions.

Plots

Plot data were summarized by biogeoclimatic zone and site unit, site index, elevation, disturbance history and disease severity. Plot data combined the information for all species present in the plot into single values for conifer volume, conifer basal area, deciduous volume and basal area and *A. ostoyae* severity. Tree volumes were calculated for each plot (m^3/ha) by species using whole stem cubic meter volume equations (Ministry of Forests, Inventory Branch, 1976). Volumes for each plot were separated into the following categories: conifer volume, birch volume and total volume in cubic meters. Basal area (m^2/ha) was also summarized for each species.

The relationships between *A. ostoyae* severity and disturbance, elevation, site index, and Phellinus severity were compared using correlation analysis to determine which factors were most closely related to the disease. The influence of each of these factors were also examined individually.

Armillaria ostoyae severity and disturbance

The relationship between logging disturbance levels and *A. ostoyae* severity was tested with a one-way analysis of variance (ANOVA). Disturbance histories were divided into three categories (page 80) to determine if there were differences in the mean plot *A. ostoyae* severity depending on the degree of disturbance.

<u>Root disease severity and elevation</u>

The relationship between disease severity and elevation was tested for both *A. ostoyae* and *P. weirii*. Correlation analyses were used to determine if there was a significant relationship between the two root diseases and elevation.

<u>*Armillaria ostoyae* severity vs Biogeoclimatic site unit</u>

The relationship between *A. ostoyae* severity and biogeoclimatic site unit was tested with a one-way analysis of variance (ANOVA). This test determined if there were significant differences among site units in the mean plot severity rating within each zone. The same test was used to determine if there were significant differences between the two zones.

<u>*Armillaria ostoyae* severity vs timber volume</u>

The impact of *A. ostoyae* severity on plot volumes was examined using three different volume measures (conifer volume, birch volume, and total volume). These relationships were analyzed using a one-way ANOVA in each of the zones individually and both zones combined. *Armillaria ostoyae* severity ratings were grouped into 4 classes. The first class, Class 0 included only disease free plots. Severity ratings from 2.0-7.99 were in Class 5, ratings from 8.00-13.99 were in Class 10, and ratings from 14.00-21.00 were in Class 15. The mean volumes were then compared between the 4 classes in both the ICH and IDF zones. Tukey tests were used to identify which of the severity classes had significantly different volumes for each of the three volume measures.

<u>The relationship between *Armillaria ostoyae* and *Phellinus weirii*</u>

The relationship between *A. ostoyae* and *P. weirii* was examined using a Chi-square test for dependency. Correlation analysis was also used to compare the severity ratings for both diseases in the ICH and IDF zones.

3.3 Results

3.3.1 Individual Tree Results

<u>Hunter's Range</u>

A total of 3473 trees within 202 plots were examined. Of these trees, 2580 were in the ICH zone, while 893 were in the IDF zone. Table 26 summarizes the species distribution within each zone by disease status and stocking level. Western redcedar was the only species that had many class 2 infections. Sixteen of the 17, class 2 infected trees examined in the IDF, were western redcedar; while 196 of the 215 class-2-infected trees examined in the ICH were western redcedar. Class 2 infections were those that appeared to be held in check by the host tree, as evidenced by callus margins surrounding the basal lesions. The other species had few, if any, class 2 infections. For this reason class 2 and 3 infections were combined in Table 26, which contains the results of the comparisons of the proportion of trees infected among species.

Stocking levels were considerably different between the two zones. The ICH zone contained 921 trees/ha while the IDF zone contained 720 trees/ha. The predominance of many small western redcedar understory trees in the ICH zone is probably the single most important factor responsible for this difference.

TABLE 26. Percentage of total trees infected with *Armillaria ostoyae* in percent by species by zone (Hunter's Range)

	At	Cw	Ep	Fd	Hw	Lw	Pl	Pw	Se	Bl	TOTAL
IDF ZONE											
CLASS 2&3	0	15.2*	1.0	3.9*	0	12.5	20.3*	0	0	0	9.4
	(1)	(2)	(1)	(1)	(1)	(2)	(2)	(1,2)	(1,2)	(1,2)	
TOTAL TREES	3	138	98	407	4	40	202	0	1	0	893
TREES/HA	2.4	111.3	79.0	328.1	3.2	32.2	162.9	0.0	0.8	0.0	720
ICH ZONE											
CLASS 2&3	0	26.3*	1.7	12.1*	14.2	5.4	33.8*	33.3	8.6	27.8	17.8
	(1)	(4)	(1)	(3)	(3)	(2)	(4)	(4)	(2,3)	(4)	
TOTAL TREES	11	1107	234	588	239	203	71	21	70	36	2580
TREES/HA	3.9	395.4	83.6	210.0	85.4	72.5	25.4	7.5	25	12.9	921
Chi-square	-	6.013	0.238	18.265	0.569	2.645	4.031	0.000	0.082	0.000	29.807

* indicates significant differences (Chi-square critical=3.841) in susceptibility within species between zones. Tree species infection percentages with the same number in brackets beneath them are not significantly different within zones ($\alpha=0.05$).

Larch Hills

A total of 760 trees in 32 plots were examined in mature stands within the Larch Hills. Of these, 453 trees were in the IDF zone and 307 were in the ICH zone (Table 27).

Phellinus pini was included in the results because the fungus was associated with a considerable amount of damage in western larch in both the ICH and IDF. Western larch trees were often killed (19 of 32 infected) as a result of stems failing due to decay caused by *P. pini*. Complete records of *P. pini* were not kept for Hunter's Range; however, the fungus was often associated with western larch in this area as well.

TABLE 27. Percentage of total trees infected with *Armillaria ostoyae* compared among five major species along with the percent of trees infected with other diseases in percent by species by zone (Larch Hills)

		Cw	Pl	Lw	Fd	Ep
IDF:	*A. ostoyae*	30.4	15.3	23.1	10.0	7.0
		(3)	(2)(1)	(3)(2)	(1)	(1)
	P. weirii	0	11.9	7.7	14.6	0
	P. pini	0	0	23.1	0	0
	Dead Symptomless	1.0	8.5	13.5	0.8	1.8
	TOTAL TREES	102	59	104	130	57
ICH:	*A. ostoyae*	69.4	44.4	23.6	12.6	14.7
		(3)	(2)	(2)(1)	(1)	(1)
	P. weirii	0	0	18.2	26.4	0
	P. pini	0	0	14.5	0	0
	Dead Symptomless	0	16.7	9.1	5.7	5.9
	TOTAL TREES	108	18	55	87	34

Armillaria ostoyae infection percentages with the same number in brackets beneath them are not significantly different within zones (Chi-square critical=3.841 α=0.05).

Hunter's Range and Larch Hills combined

The proportion of western larch infected did not differ significantly between the two zones in either study area. There was, however, a considerably greater proportion of western larch infected in the two zones combined in the Larch Hills (23.3%) than in the Hunter's Range (6.6%). In the Larch Hills plots, the proportion of western larch infected in the IDF zone was significantly greater than that of Douglas-fir. This result was consistent with that found in the Hunter's Range plots. In the ICH zone, western larch continued to be significantly more heavily infected than Douglas-fir. The opposite had been found the year before in Hunter's Range. Another difference between the two areas concerning differences in relative incidence of *A. ostoyae* infections existed between lodgepole pine and western larch. The proportion of western larch infected in Hunter's Range was significantly less than that for lodgepole pine in both the ICH and IDF zones. In the Larch Hills, however, the opposite was found with western larch being significantly more heavily infected.

One of the more important differences between the two study areas was in the proportion of trees infected with *A. ostoyae*. The Larch Hills had a significantly greater proportion of trees infected (25.6%) than the Hunter's Range study area (15.9%). The result from the Chi-square test was 40.00 versus a critical value of 3.841 (α=0.05). This difference was examined further by comparing the two study areas based on the proportion of trees infected in each of the species individually (Table 28).

TABLE 28. Comparison of the percentage of total trees infected with *Armillaria ostoyae* in each of the major species between the Larch Hills and Hunter's Range study areas

	Cw	Fd	Lw	Pl	Ep
Larch Hills	50.5	11.1	23.3	22.1	9.9
Hunter's Range	25.1	8.7	6.6	23.8	1.5
Chi-square	57.68	1.075	23.30	0.094	15.79

Critical Chi-square α=0.05 is 3.841, α=0.01 is 6.635

Not all species were more heavily infected in the Larch Hills than in Hunter's Range. Those species that did differ significantly in their proportion of trees infected between the two study areas had significantly more infection in the Larch Hills than in Hunter's Range. It is interesting to note that Douglas-fir, which was one of the three most prevalent species, did not differ significantly in the proportion of trees infected between the two areas.

Differences in species composition were also compared between the two study areas (Table 29). This comparison was made in order to examine the possibility that the differences in the proportion of trees infected between the two areas were due to differences in species composition.

Some of the minor species from the Hunter's Range site were not represented in the Larch Hills site, possibly due to the small number of plots on the latter site. The total number of trees for the Hunter's range site in Table 29 did include these species, thus, the percentages found in this table do not add up to 100. The results in Table 29 indicate that there were significant differences in the species composition between the two study areas. The most significant difference between the two was due to the high proportion of western larch in the Larch Hills study area.

TABLE 29. Comparison of the proportions of the five major species in percent between the Larch Hills and Hunter's Range

	Cw	Fd	Lw	Pl	Ep	TOTAL
Larch Hills	27.9	28.8	21.1	10.2	12.1	754
Hunter's Range	35.8	28.6	7.0	7.9	9.6	3473
Chi-square	17.86	0.008	141.6	4.81	4.61	

Critical Chi-square $\alpha=0.05$ is 3.841, $\alpha=0.01$ is 6.635

The incidences of infection were also compared in four of the species among the four different areas simultaneously. The proportion infected of three species (western redcedar, western larch and lodgepole pine) were compared to the Douglas-fir standard among four areas; Hunter's Range ICH, Hunter's Range ICH, Larch Hills ICH, Larch Hills IDF (Table 30). The methods used in this analysis were the same as those used in Chapter 2 to rank the species of conifer regeneration.

TABLE 30. Ranking of conifer species compared to a Douglas-fir standard on the basis of the incidence of *Armillaria ostoyae* infection in mature stands (approx. 120 years) within the ICH and IDF zones of Hunter's Range and Larch Hills

SPECIES	#TREES	#INFECTED	K-VALUE	CHI-SQUARE	CRITICAL CHI-SQUARE
Fd	1212	111	1.0000	-	-
Cw	1455	418	2.5662	57.950	5.991
Lw	402	53	1.2200	29.377	5.991
Pl	350	82	3.3221	14.578	5.991

The highly significant Chi-square values confirm the differences eluded to earlier. The proportion of trees infected with *A. ostoyae* for a given species differ depending on the site in which the species are found. Due to the large differences in the proportion of trees infected among the different sites for the three species above, it is not possible to state a single K-value for each species. Thus, unlike the regeneration results in Chapter 2, a quantitative ranking of species based on the incidence of infection can not be made with the mature tree data. Despite the significant differences in disease incidence among sites, the K-values in Table 30 indicate some important results. All three of the species that were compared to Douglas-fir had K-values higher than 1.000. Thus, over the four areas (ICH and IDF in both Hunter's Range and Larch Hills) western redcedar, lodgepole pine and western larch were generally more often infected than Douglas-fir.

Incidence of Disease among Site Units (Hunter's Range)

Differences in the incidence of *A. ostoyae* infections within each species among site units within each zone were examined (Table 31). Three of the species (western white pine, Engelmann spruce, and subalpine fir) were combined due to the low numbers of trees in these species in the ICH zone. Only those species that were present in sufficient numbers to test with a Chi-square test were included in the analyses.

TABLE 31A. Percentage of trees infected in percent for each species in each site unit in the ICH zone

SITE UNIT	Fd		Cw		Hw		Lw		(Pw,Se,Bl)	
	%	total	%	total	%	total	%	total	%	total
ICHmk101	11.4	35	15.4	91	0.0	5	0.0	19	17.5	57
ICHmw201	31.6	19	34.3	102	21.7	60	0.0	3	50.0	8
ICHmw201ys	11.9	227	28.0	436	3.6	55	10.8	74	8.3	12
ICHmw202	12.0	83	0.0	19	-	-	0.0	13	-	-
ICHmw203	9.3	182	28.6	360	13.2	38	3.4	89	42.9	7
ICHmw205	16.7	42	17.2	99	17.3	81	0.0	5	11.6	43
Chi-square	7.866		18.125		6.420		4.345		23.56	
Critical	11.070		11.070		7.815		5.991		9.488	

TABLE 31B. Percentage of trees infected in percent for each species in each site unit in the IDF zone

SITE UNIT	Fd %	Fd total	Cw %	Cw total	Lw %	Lw total	Pl %	Pl total
IDFmw101	4.5	247	16.4	128	15.4	130	26.2	26
IDFmw104	3.9	128	0.0	6	0.0	6	11.5	61
IDFmw201	0.0	32	0.0	4	12.5	8	0.0	11
Chi-square	1.429		1.641		0.588		4.815	
Critical	5.991		3.841		3.841		5.991	

Western redcedar was the only individual species that had significantly different incidence of infection among biogeoclimatic site units within either zone. Subalpine fir, western white pine and Engelmann spruce combined also had significantly different proportions among the site units in the ICH. The proportion of western redcedar infected in the ICHmw202, ICHmw205 and ICHmk101 site units was significantly lower than that in the ICHmw201, ICHmw201ys and ICHmw203 site units. There were not enough western redcedar present in the IDF zone to make comparisons between site units.

There were no significant differences among site units for Douglas-fir or western larch in either the IDF or the ICH zones. Western hemlock did not appear in the IDF. Within the ICH zone, there were no significant differences between site units in the proportion of western hemlock trees infected with *A. ostoyae*.

Comparison of Methods of Data Collection

A follow-up study was conducted on the Larch Hills in order to determine more accurately the number of infected trees in mature stands within the ICHmw2 (Table 32). This study compared two methods of root disease data collection and the number of *A. ostoyae* infections found with each method. The 1992 method was used on the Hunter's Range site (202 plots) and the northwest Larch Hills site (32 plots). The 1993 method was used in the plantation study (Chapter 2). The 1993 method involved the removal of the litter layer from the base of the tree. The data from these plots were also used to verify the amounts of infection found in the stump examinations performed in Chapter 2.

TABLE 32. Comparison of the 1992 and 1993 methods of data collection regarding the number of infections found, and the percent of total trees missed using the 1992 method

PLOT	TOTAL CONIFERS	NO. INFECTED 1992	NO. INFECTED 1993	PERCENT MISSED
1	29	10	16	20.7
2	25	14	18	16.0
3	22	10	14	18.2
4	28	13	18	17.9
5	24	8	10	8.3
6	22	5	7	9.1
7	21	14	18	19.0
8	19	11	14	15.8
9	21	10	11	4.8
10	19	4	10	31.6
TOTAL	230	99	136	16.1

Of the 37 trees with "missed" infections, 20 were Douglas-fir, 10 western hemlock, 4 Engelmann spruce, 2 western redcedar, and 1 western larch. Four of the missed Douglas-fir infections were callused-over lesions.

Although the more intensive methods detected 16.1% more infected trees, the majority of these trees were infected with class 2 infections. Thus, the average plot severity rating increased only slightly from 11.1 to 11.5. Using the 1992 methods, the Larch Hills study area had far more infections than the study area on Hunter's Range with 43.0% of the trees infected, compared to only 15.6%. The reasons for this difference are not clear. It is possible that this area in the Larch Hills area was simply more heavily infected than Hunter's Range.

3.3.2 Plot Results (Hunter's Range)

A summary of the plot results including the number of plots/site unit, number of disturbed plots and the number of diseased plots is found in Table 33. There was an unequal number of plots between the two zones. Within the ICH zone 140 plots were examined while 62 plots were examined within the IDF zone. The proportion of plots in each zone may be used as a rough approximation of the distribution of zones within the study area. Using this approximation 140/202 or 69.3% of the area was in the ICH biogeoclimatic zone while 62/202 or 30.7% was in the IDF.

The majority of the 202 plots (86.1%) were diseased with either *A. ostoyae* or *P. weirii* or both. *Armillaria ostoyae* was the most prominent forest pathogen, with over 76.7% of the plots exhibiting evidence of infection. *Phellinus weirii* was present on 18.8% of the plots. Disturbance was also quite widespread throughout the study area with 46.5% of the plots having evidence of logging either in or just outside the plot perimeter. Most of the disturbed plots (86.2%) exhibited evidence of root disease. Similarly, 85.2% of the undisturbed plots also contained evidence of root disease.

TABLE 33. Plot distribution by site unit, disease status, and disturbance history

	ICH						IDF			
SITE UNIT	mw201	mw201ys	mw202	mw203	mw205	mk101	mw101	mw104	mw201	TOTAL
# of PLOTS	14	41	10	44	16	15	41	13	8	202
% DISTURBED	78.6	48.8	20.0	50.0	75.0	66.7	41.5	0.0	0.0	94
% ARMILLARIA	92.9	85.4	70.0	86.4	81.2	86.7	63.4	61.5	25.0	155
% PHELLINUS	0.0	12.2	0.0	34.1	6.2	0.0	17.1	30.8	75.0	38
% ARM & PHEL	0.0	9.8	0.0	22.7	6.2	0.0	4.9	7.7	12.5	19
% of DISTURBED PLOTS with ARM.	90.9	85.0	50.0	100.0	83.3	90.0	70.6	0.0	0.0	81
% of UNDISTURBED PLOTS with ARM.	100.0	85.7	75.0	95.5	75.0	80.0	79.2	84.6	87.5	92

Correlation analysis was used to determine which of the factors examined (*i.e*, disturbance, site index, elevation Phellinus severity) was responsible for the greatest amount of variation in *A. ostoyae* severity (the dependent variable). Prior logging disturbance was the most closely correlated variable out of those analyzed (r = 0.329). The correlation coefficients for the other factors were: site index -0.016, elevation 0.040, and Phellinus severity -0.168. The critical correlation coefficient for n=200, and α=0.05 is $\pm$ 0.138.

Armillaria ostoyae severity vs Disturbance

Armillaria ostoyae severity was significantly higher in plots within both the ICH and the IDF zones when these plots also contained evidence of prior logging activity (Fig. 4). This relationship was significant in both the combined zone analysis and the individual analyses for the ICH and IDF zones (Table 34). The relationship was also significant for both of the zones when two disturbed classes were included with the undisturbed class. As mentioned earlier (page 83) there were two disturbed classes. The difference between the two was based on whether or not the evidence of disturbance was in or out of the plot.

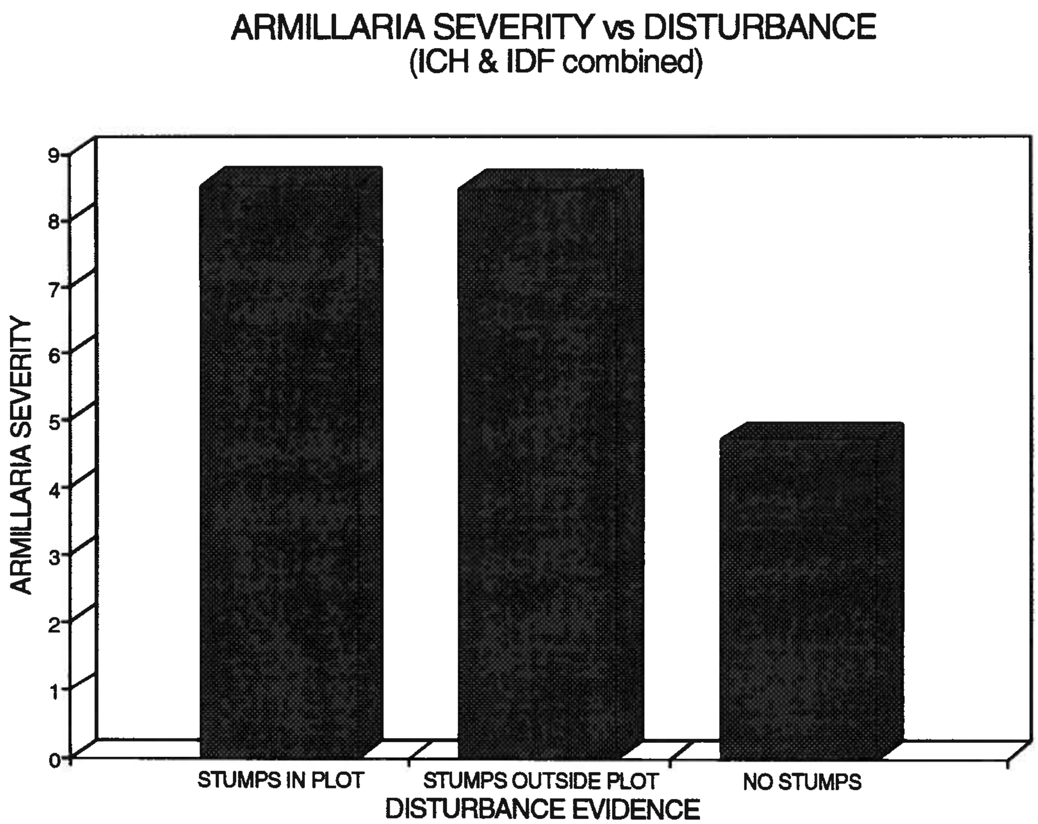

FIGURE 4. ***Armillaria ostoyae*** **severity compared between disturbed and undisturbed plots (ICH and IDF combined)**

TABLE 34. ANOVA results for *Armillaria ostoyae* severity vs disturbance class in the ICH and IDF zones

SOURCE	SUM OF SQUARES	DF	MEAN-SQUARE	F-RATIO	p
BETWEEN GROUPS	723.219	2	361.609	14.544	0.000
WITHIN GROUPS	4947.811	199	24.863		

Prior disturbance did not influence the presence of *A. ostoyae* on a site. Plots that contained evidence of prior disturbance were no more likely to exhibit signs of *A. ostoyae* infection than those plots that were not disturbed. Of the 94 disturbed plots from the entire study area, 81 were also diseased (86.2%). Of the 108 undisturbed plots, 92 were diseased (85.2%).

Armillaria ostoyae Severity vs Elevation

The correlation between *Armillaria ostoyae* severity and plot elevation data was determined to assess whether elevation within the ICH and IDF zones influenced the distribution and impact of the disease (Fig. 5). The plot elevations in the study area ranged from 410m to 1440m. There was no significant relationship between *A. ostoyae* severity in plots and their elevation ($r=0.040$, $n=202$, $p=0.596$).

Elevation did influence the distribution and impact of *P. weirii*. This relationship was significant in both the ICH and the IDF zones. There was significantly more *P. weirii* in the plots at lower elevations than those higher up the slope ($r=-0.197$, $n=202$, $p=0.005$). The possibility that logging disturbance was confounding the results tested above was examined. A one-way ANOVA was used to test whether or not the mean elevation of the undisturbed plots was significantly different from that of the disturbed plots. There was no significant difference between the two. The mean elevation of the disturbed plots was 849.7m while that of the undisturbed plots was 831.7m.

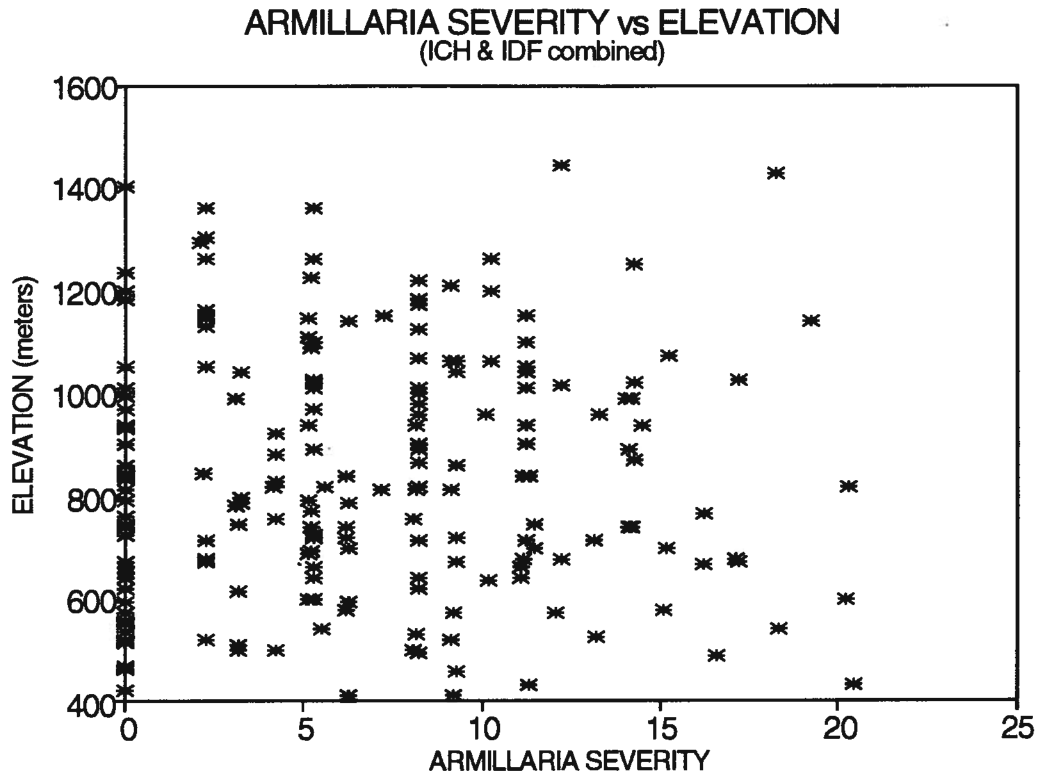

FIGURE 5. The relationship between *Armillaria ostoyae* severity and plot elevation in the ICH and IDF zones

Armillaria ostoyae Severity vs Site Index

There was no significant relationship between *A. ostoyae* severity and site index using the site indices for interior Douglas-fir (r=-0.016, n=202, p=0.824).

Armillaria ostoyae Severity vs Biogeoclimatic Site Unit

There were no significant differences in *A. ostoyae* severity among site units within either of the zones (Fig. 5). A one-way analysis of variance of *A. ostoyae* severity versus site unit within both zones proved to be insignificant (Table 35). The *A. ostoyae* severity was significantly different between the two zones (T-test statistic=-3.150, p=0.002) being significantly higher in the ICH than in the IDF.

TABLE 35. ANOVA results for *Armillaria ostoyae* severity vs biogeoclimatic site unit in the ICH and IDF zones

SOURCE	SUM OF SQUARES	DF	MEAN-SQUARE	F-RATIO	p
ICH zone					
BETWEEN GROUPS	67.601	5	13.520	0.507	0.770
WITHIN GROUPS	3572.271	134	26.659		
IDF zone					
BETWEEN GROUPS	104.722	2	52.361	1.863	0.164
WITHIN GROUPS	1658.389	59	28.108		

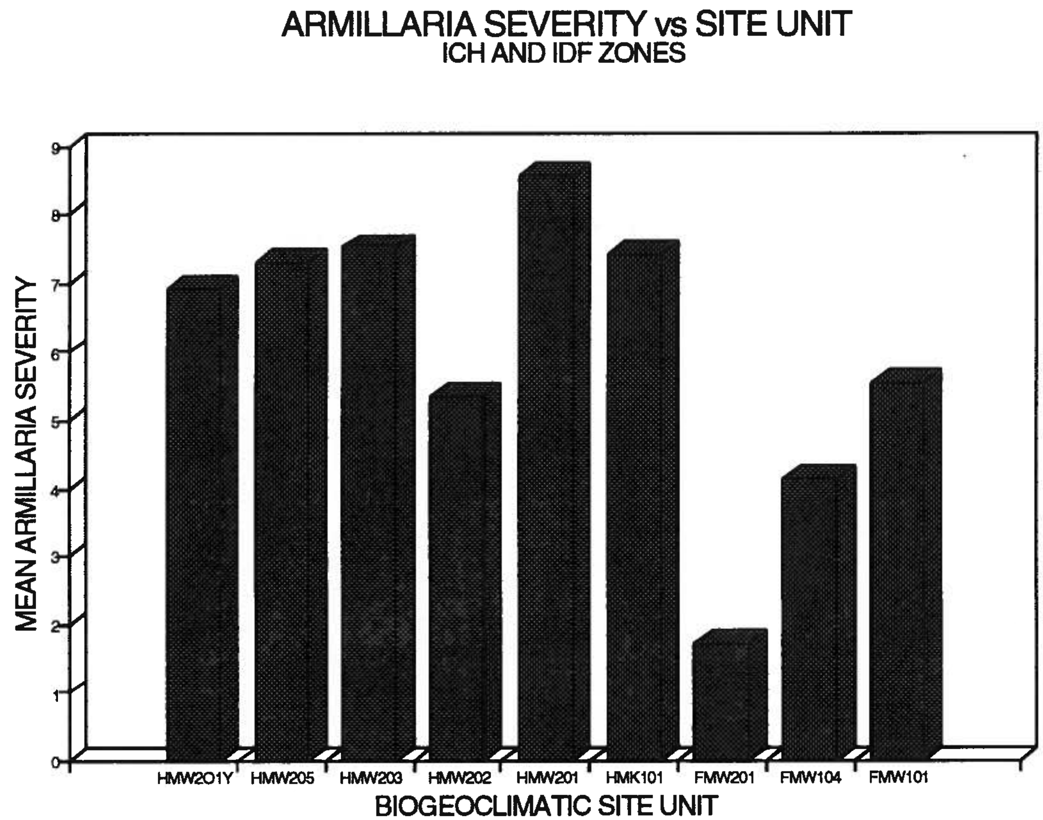

FIGURE 6. The relationship between *Armillaria ostoyae* severity and biogeoclimatic site unit in the ICH and IDF zones

The individual tree results described earlier indicated that only western redcedar had significantly different proportions of trees infected between site units. Thus, it is not surprising that the combined species analysis did not indicate any significant differences in *A. ostoyae* severity among site units.

Armillaria ostoyae Severity vs Timber Volume

There were significant differences in mean conifer volume among the four *A. ostoyae* severity classes (page 88) for the ICH and IDF zones combined (Table 36). Plots with severity class 15 had significantly lower mean conifer volumes than those in the other three classes.

TABLE 36. ANOVA results for *Armillaria ostoyae* severity vs conifer volume in the ICH and IDF zones individually and combined

SOURCE	SUM OF SQUARES	DF	MEAN-SQUARE	F-RATIO	p
ICH and IDF					
BETWEEN GROUPS	431.302	3	143.767	7.378	0.000
WITHIN GROUPS	3858.261	198	19.486		
ICH					
BETWEEN GROUPS	348.290	3	116.097	5.852	0.001
WITHIN GROUPS	2698.169	136	19.839		
IDF					
BETWEEN GROUPS	111.611	3	37.204	2.123	0.107
WITHIN GROUPS	1016.591	58	17.527		

There was significantly less conifer volume in *A. ostoyae* severity class 15 than in any of the other severity classes in the ICH zone (Table 37). There were no significant differences among the *A. ostoyae* severity classes in the IDF zone.

TABLE 37. The relationship between *Armillaria ostoyae* severity and conifer volume with the number of plots in each severity class and the associated mean conifer volume/plot (m^3/ha) for the ICH and IDF zones

	ICH ZONE		IDF ZONE	
Arm. Severity Class	#Plots	Conifer m^3/ha	#Plots	Conifer m^3/ha
0	21	510	26	363
5	53	508	15	459
10	48	437	15	361
15	18	266	6	208
Total Plots	140		62	

The relationship between birch volume and *A. ostoyae* severity was significant for both the IDF zone and the ICH zone (Table 38).

TABLE 38. ANOVA results for *Armillaria ostoyae* severity vs paper birch volume in the ICH and IDF zones

SOURCE	SUM OF SQUARES	DF	MEAN-SQUARE	F-RATIO	p
ICH zone					
BETWEEN GROUPS	7.821	3	2.607	3.122	0.028
WITHIN GROUPS	113.571	136	0.835		
IDF zone					
BETWEEN GROUPS	3.224	3	1.075	3.826	0.014
WITHIN GROUPS	16.294	58	0.281		

Paper birch volume was significantly higher in those plots in *A. ostoyae* severity class 15 in the combined zone analysis. For both of the zones individually the only significant differences in paper birch volume among the four severity classes was between Class 5 and Class 15 (Table 39).

Differences in total volume among the four *A. ostoyae* severity classes were also tested. With both zones combined the ANOVA was significant. There was significantly less total volume in the most severely infected class than in the other three classes. Significant difference in total volume were found in the ICH zone was among severity classes 15, 0 and 5. Severity class 15 had significantly lower volume than class 0 and class 5 but not class 10.

There was no significant difference in total volume among the four severity classes in the IDF zone.

TABLE 39. The relationship between *Armillaria ostoyae* severity and birch volume with the number of plots in each severity class and the associated mean birch volume/plot (m^3/ha) for the ICH and IDF zones

	ICH ZONE		IDF ZONE	
Arm. Severity	#Plots	Birch m^3/ha	#Plots	Birch m^3/ha
0	21	20.0	26	14.5
5	53	21.0	15	4.0
10	48	27.7	15	26.7
15	18	57.2	6	42.7
Total Plots	140		62	

The Relationship between *Armillaria ostoyae* and *Phellinus weirii* in the ICH and IDF Biogeoclimatic zones

The IDF zone had significantly more plots infected with *P. weirii* than the ICH zone. Thus, it appears that this disease possibly prefers drier sites found in the IDF. The relationship between *A. ostoyae* and *P. weirii* is not clear. Results from the first field season indicated that the two diseases are not as compatible on the same site as once believed. The correlation analysis of the two disease severity ratings from the two zones combined was significant ($r=-0.170$, $n=202$ $p=0.016$). Within the ICH zone, the occurrence of the two diseases appeared to be independent of each other. The two diseases did not occur together any more often than would be expected completely randomly. Within the IDF zone, *P. weirii* occurred together with *A. ostoyae* less often than would be expected if they were randomly distributed (Table 40).

TABLE 40. Test of independence between *Armillaria ostoyae* and *Phellinus weirii* in the ICH and IDF zones

ICH ZONE:		ARMILLARIA	NO ARMILLARIA	TOTAL
	PHELLINUS	15 (17.85)	6 (3.15)	21
	NO PHELLINUS	104 (101.15)	15 (17.85)	119
	TOTAL	119	21	140

Chi-square=3.569, Critical Chi-square=3.841

IDF ZONE:		ARMILLARIA	NO ARMILLARIA	TOTAL
	PHELLINUS	4 (9.9)	13 (7.1)	17
	NO PHELLINUS	32 (26.1)	13 (18.9)	45
	TOTAL	36	26	62

Chi-square=11.59, Critical Chi-square=3.841
(expected values are bracketed)

These relationships could not be tested using the data collected on Larch Hills. Out of the 32 plots examined, *P. weirii* occurred in 12 and *A. ostoyae* occurred in all but two of the plots. All of the plots that contained evidence of *P. weirii* also contained evidence of *A. ostoyae*. Since nearly 100% of the plots were infected with *A. ostoyae* it was not possible to test for independence between the two diseases.

3.4 Discussion

3.4.1 The Ranking of Conifer Species Based on Incidence of *Armillaria ostoyae* Infections in the ICH and IDF Zones

Morrison's (1981) ranking of tree species susceptibility was based on trees that were known to have been infected. A susceptible species was one that once infected was soon killed. Resistant species were rarely killed when infected. Western larch has been considered one of the most resistant conifer species within the southern interior of B.C.(Morrison 1981). Hagle and Goheen (1988) also considered western larch to be one of the most *A. ostoyae* resistant species based on their observations in mature stands in the Intermountain Northwest area of the United States. The question of western larch being more resistant than other conifer species was reviewed in this research. The methods used in this study differed considerably from those of Morrison (1981). In this study, the species were ranked based only on the presence of above ground symptoms of *A. ostoyae*. It was not known whether or not a symptomless tree had been infected by the disease. Work by Morrison in the ICH suggests that the proportion of conifer trees infected in this zone ranges from 60-100%, based on below ground evidence (pers. com.). Thus, the probability that the symptomless trees were not challenged by *A. ostoyae* is low. Despite differences in methods, the ranking of certain conifer species as more "susceptible" than others in this study differed considerably from those found by Morrison (1981) listed on page 9. The proportions of trees infected for three species were compared to a Douglas-fir standard measure of disease incidence (Table 30). The proportion infected for Douglas-fir, western redcedar, western larch and lodgepole pine varied between the ICH and IDF zones on both the Hunter's Range and Larch Hills sites. The proportion infected for the three species varied significantly from the Douglas-fir standard. This variation among the four sites made it impossible to state definitively which species was proportionately more frequently infected. Whether a species was more "susceptible" than another appeared to depend more on site than on species characteristics.

The K-values (Table 30) represented a quantitative ranking of disease incidence. Since the proportion infected for each species varied significantly from the standard, the confidence level in the K-values is low. Despite this, the K-values still indicated differences in *A. ostoyae* infection incidence among the four major species. Douglas-fir had the lowest relative rate of infection of the four species. Lodgepole pine and western redcedar had considerably higher rates of infection. Western larch was also more heavily infected than Douglas-fir though not to the same degree as lodgepole pine and western redcedar.

The fact that the relative proportions of trees infected, for most conifer species, varied from site to site was made clear by examining the two zones within each study area individually. Within the ICH zone on Hunter's Range the proportion of western larch infected with *A. ostoyae* was significantly less than that of any of the other conifer species (Table 26). However, the proportion of western larch infected was significantly greater than the proportion of Douglas-fir infected in the IDF zone in that study area. The results from the Larch Hills indicated that the proportion of western larch infected with *A. ostoyae* was not significantly less than that of any of the conifer species in both the IDF and ICH zones. The proportion of Douglas-fir and lodgepole pine infected in the Larch Hills was considerably less than that found in Hunter's Range, while the opposite was found for western larch.

The species ranking based on incidence of *A. ostoyae* infection in the Larch Hills (Table 27) differed from that determined in the Hunter's Range data (Table 26). The reasons for this could lie in the difference in species composition between the two sites. There were significantly more western larch trees on the Larch Hills site and significantly fewer western redcedar. It is possible that the reason the proportion of larch trees infected was significantly greater than that found on Hunter's Range was due to the higher stocking of that species on Larch Hills. When a species is relatively abundant on a site, it is perhaps easier for disease to spread within that species than to spread between individuals of differing species. Trees of the same species would have the same root form and would tend to graft roots between individuals. Trees of different species that were adjacent to each other, would be less likely to have roots in contact due to differences in root system form. The proportion of total stocking consisting of Douglas-fir did not differ significantly between the two sites, nor did the proportion of that species infected. The same was true for lodgepole pine. However, for western larch, the proportion of total stocking on the Larch Hills site was significantly greater than that on Hunter's Range and the proportion of trees infected was also significantly greater.

More work is required to determine definitively whether or not western larch is indeed more resistant than Douglas-fir and other conifer species. More work is required in general regarding the ranking of species susceptibility to *A. ostoyae* in the southern interior of British Columbia. The Larch Hills would appear to provide an excellent study area to test for the relative differences in species susceptibility to *A. ostoyae*. Hadfield (1984) stated that it is dangerous to make generalizations about the susceptibility of tree species to Armillaria root rot. It is quite apparent from the results of this research that his statement was quite sound.

3.4.2 The Influence of Prior Disturbance on the Expression of *Armillaria ostoyae* in the ICH and IDF zones

Past logging disturbance was closely associated with high *A. ostoyae* severity in plots in both the ICH and the IDF zones. The correlation between prior disturbance and *A. ostoyae* severity had the highest r-value of any of relationships for any of the site factors examined in this study. Differentiating between the evidence of disturbance inside the plot and that outside did not significantly affect the strength of the relationship (Fig. 4). Both measures of disturbance had very similar effects on the severity of *A. ostoyae* within the plots. There were significantly higher *A. ostoyae* severity ratings on those plots that exhibited evidence of past logging disturbance than those that were not disturbed.

The past logging disturbances did not affect the area of forest land infected with *A. ostoyae*. There was a roughly equal proportion of plots infected in those areas that had no evidence of disturbance as those that did. Of the plots that were disturbed, 86.3% were also diseased, while 85.3% of the undisturbed plots were diseased. However, the *A. ostoyae* severity rating of the disturbed plots did differ significantly from that for the undisturbed plots. Thus, the proportion of trees infected in the disturbed areas was significantly higher than the proportion of trees infected in the undisturbed areas. These results agree with those of Shaw *et al.* (1976) in their study of *A. mellea* in south central Washington. They found that the area of *A. mellea* infection following cutting remained essentially constant, but the volume losses more than doubled. The effects of cutting history on the incidence of root disease that Byler *et al.*(1987) observed in the Crow Creek compartment, Lolo National Forest, Montana differed from those found in Hunter's Range. They found that cutting history increased both the severity of infections and the incidence of root disease. Ten percent of the stands in their study had some evidence of past disturbance. In those stands, the proportion of plots with root disease damage was roughly double that of plots that had no evidence of past cutting. These differences aside, there is certainly evidence to suggest that partial cutting in mature stands increases the probability of losses to *A. ostoyae*.

3.4.3 The Influence of Elevation on Root Disease Expression

The influence of elevation on root disease activity has been examined in several studies in the Intermountain Northwest region of the United States. Hobbs and Partridge (1979) examined the incidence of root rots along an elevation gradient in mixed conifer stands in northern Idaho. They reported that *A. mellea* was not affected by elevation, describing its occurrence as ubiquitous. They found that *P. weirii* was affected to some degree by elevation and that this root disease was generally found below 1500m elevation in that region. The Hunter's Range results agree with those found by Hobbs and Partridge (1979). There was no significant relationship between the elevation of a plot and the incidence or severity of *A. ostoyae* infection. *Phellinus weirii* incidence was dependent on elevation. There was significantly more *P. weirii* infections at lower elevations. Williams and Marsden (1982) found that the probability of root disease center occurrence was inversely related to elevation. Their study did not differentiate between *A. ostoyae* and *P. weirii*; thus, their conclusions were not necessarily contrary to those found in this study.

3.4.4 The Relationship between *Armillaria ostoyae* Distribution and the Biogeoclimatic Site Classification in the Southern Interior of B.C.

Several studies in the Intermountain Northwest region of the United States have related both incidence and severity of root disease to the habitat classification system used in that area (Byler *et al.* 1987, Hagle 1985, McDonald *et al.* 1987). None of the literature regarding *A. ostoyae* in the southern interior of B.C. has connected the incidence and severity of the disease with the BEC system at any finer detail than the zonal level. This research was designed to describe differences in the role of *A. ostoyae* within two of the zones on a more detailed scale.

The results of this study indicated there were no significant differences in the incidence and severity of *A. ostoyae* among site units in either zone. The only individual tree species in which the site unit appeared to influence the proportion of trees infected was western redcedar.

The proportions of Douglas-fir, lodgepole pine, western larch and western hemlock that were infected did not differ significantly among site units.

The lack of significant differences in *A. ostoyae* incidence among site units was probably due, in part, to the manner in which the site units were identified at each plot. The difference between some of the site units was sometimes decided by the presence or absence of a single plant species. However, the differences between the driest and wettest site units within a zone would have been obvious.

The proportion of western redcedar trees that were infected was significantly less in the more moist site units than in the drier ones within the ICH. There was, however, a significantly greater proportion of western redcedar infected in the ICH than in the drier IDF zone. Thus, greater moisture did not appear to reduce the probability of western redcedar becoming infected on the larger zonal scale. This apparent discrepancy could be explained on the basis of differing levels of inoculum between the two zones. The ICH zone simply had more *A. ostoyae* inoculum than the IDF zone; thus, any trees within the ICH were at a greater risk of becoming infected. If both zones had the same levels of inoculum, then perhaps western redcedar would have had a lower proportion of trees infected in the ICH than in the IDF zone.

There were significant differences in the incidence and severity of *A. ostoyae* between the two zones based on the Hunter's Range data. The ICH zone had a significantly greater proportion of diseased plots than the IDF zone. These results agree with those of Byler *et al.*(1987) and Hagle (1985) who both found that the more productive habitat types suffered the most severe damage. These results are in contrast to those found by McDonald *et al.*(1987) who stated that the most productive sites in National Forests of the inland western United States showed low incidence of *A. ostoyae*. McDonald *et al.*(1987) stated that the incidence of the disease showed a strong tendency to decrease as stand productivity increased. It is apparent that the latter argument is not the case in the southern interior of B.C. The ICH zone is after all the most productive zone in the interior of B.C. (Meidinger and Pojar 1991).

3.4.5 The Relationship Between *Armillaria ostoyae* Severity and Stand Productivity in Terms of Timber Volume

There has been very little research done on the impacts of *A. ostoyae* on forest productivity in terms of timber volume in the southern interior of B.C.. The ICH zone is the second most productive forest zone in Canada, yet it quite possibly has the highest incidence of *A. ostoyae* of any forest zone in the country. This study indicates that *A. ostoyae* is wide spread in some areas of the zone. It is clear that *A. ostoyae* cannot be killing all trees or the ICH would not be nearly as productive as it is. The results of this study indicate that there was a significant relationship between *A. ostoyae* severity class and conifer volume in the ICH zone and the ICH and IDF zones combined. There was no significant relationship between conifer volume and *A. ostoyae* severity class in the IDF zone. However, the most severely infected plots in the IDF had considerably less conifer volume than the less infected plots (208 m^3/ha vs 459 m^3/ha, Table 37).

Whether these relationships between *A. ostoyae* severity class and conifer volume were significant or not depended in part on how the severity classes were defined. The methods used in this study combined plot severity ratings into four classes (page 88). Combining the plot severity ratings into a greater number of smaller classes could yield different results. The same could be said for fewer large classes. Regardless of how the severity classes are defined, it is apparent that the most severely infected stands in both zones have considerably less conifer volume than less severely infected stands. It is also clear that *A. ostoyae* can be quite prevalent in a stand without having a significant negative impact on conifer volume (Table 37). In the ICH zone conifer volumes did not drop significantly until *A. ostoyae* severity class 15. Thus in this zone, perhaps as many as 40% of the stems could have shown signs of infection with as many as 30% having Class 3 infections, before volumes decreased.

There was also a significant relationship between paper birch volume and *A. ostoyae* severity class in the ICH and IDF zones combined. Plots with a severity rating greater than 14.0 had significantly greater birch volumes than those plots with lower *A. ostoyae* severity ratings (Table 39). The fact that there was a significant relationship was in part an artifact of the methods used to determine the *A. ostoyae* severity rating. The rating was based on the proportion of conifer trees infected out of the total number of conifers. In those plots with a small conifer component and a large birch component a single infected conifer translated into a high proportion of conifers infected. Thus, such areas with high *A. ostoyae* severity ratings would quite likely have a large birch component. This is probably not far from the truth in the majority of the stands in the ICH. Often those areas most heavily infected with *A. ostoyae* are converted from conifer to deciduous forest types. If the severity ratings were based on the proportion of trees infected out of the total trees including birch, the ratings would underestimate the effects of *A. ostoyae* in these stands. The severity rating used in this study incorporates the effects of severe *A. ostoyae* infestations on species composition.

3.4.6 The Relationship Between *Phellinus weirii* and *Armillaria ostoyae*

The results regarding the relationship between *A. ostoyae* and *P. weirii* in this research reflect the differences in opinion among the various workers who have examined this subject. The results from the original study on Hunter's Range are reported in Table 40. They indicate that the occurrence of the two diseases was independent of each other in the ICH zone, and was significantly negatively related in the IDF zone. This is contrary to the results of Filip and Goheen (1982) who found that the two diseases were often found in association with each other. The ICH results, in part, support the claim of Hansen and Goheen (1989) who attribute the association between the two diseases to chance and to primary-secondary relationships. Primary-secondary relationships refer to situations where a host is infected by a pathogen, such as *P. weirii*, but not killed. The vigor of the infected host is reduced making it more vulnerable to *A. ostoyae*. Such relationships would result in more frequent association between the two diseases than random. Attributing the relationship between the two disease to chance is probably most appropriate for the ICH. The negative relationship between *A. ostoyae* and *P. weirii* in the IDF zone requires more study.

In the Larch Hills *P. weirii* was only found in association with *A. ostoyae*. None of the *P. weirii* infected plots contained evidence of only that disease. All *P. weirii* plots also contained evidence of *A. ostoyae* infections. This result is hardly surprising since 30 out of 32 plots exhibited evidence of *A. ostoyae* infections.

3.4.7 The Value of Surveying for *Armillaria ostoyae* in Mature Stands in the ICH and IDF zones

The follow-up study concerning root disease survey methods revealed that an average of 16.1% of the infections in that study would not have been identified with the methods used in the Hunter's Range study the previous year. These results have important implications for forest managers who are required by regulations in this province, to carry out root disease surveys in areas believed to be infected. Clearly, the amount of root disease detected in a stand has a great deal to do with the methods used to survey that stand. The effort required to find the additional 16.1% of *A. ostoyae* infections was considerable. In order to find all of these infections the bark had to be removed from the lateral root up to a distance of 30cm from the root collar. Had the roots been excavated even further, the amount of infection in these stands would no doubt have been higher. The question then becomes: " What is the appropriate degree of accuracy required in a root disease survey?". From the forest manager's viewpoint, does it matter if a root disease survey has missed 16% of the actual number of infections in a stand?

It is quite clear that *A. ostoyae* is present in the majority of sites within the transition between the ICH and IDF biogeoclimatic zones. Thus, it appears the value of surveying for the presence of *A. ostoyae* in this area is minimal. The results from the plantation study in Chapter 2 indicated that the relationship between *A. ostoyae* infections in stumps and plantation mortality was poor. Thus, the results from a root disease survey would not significantly improve any predictions of future plantation health. These two arguments combined seriously question the value of *A. ostoyae* surveys in the ICH and ICH/IDF transition portions of the southern interior of B.C.

CHAPTER 4 CONCLUSIONS

Several important conclusions may be made based on the results of this research. A word of caution should be included with these conclusions as they are based on a small number of study areas. With regards to the behavior of *A. ostoyae* in plantations, six clear conclusions may be made. First, the negative impacts of brushing in plantations within the ICH are quite obvious. *Armillaria ostoyae* is present in the majority of sites within the Interior Cedar Hemlock zone. The results from the two 1969 plantations examined in Chapter 2 illustrate very clearly the impact of brushing stands in this zone. The losses to *A. ostoyae* in the unbrushed plantation were significantly less than those suffered in the brushed plantation.

Second, the proximity of infected stumps to trees in 25-year-old plantations does not significantly increase the probability of those trees becoming infected. The proximity of infected stumps to trees in 10-year-old plantations does influence the probability of those trees becoming infected. This conclusion is drawn from the comparison of the two different plot sizes used in the study of *A. ostoyae* in plantations. Using a smaller plot size did not improve the relationship between the infected stumps and infected trees in the older plantation. The opposite was found in the younger plantation. This has very important implications for free growing surveys and the current policy of the Ministry of Forests in B.C.. This policy states that any tree within three meters of a stump infected with *A. ostoyae* cannot be considered free growing. The results of this research indicate that the distance that a tree is from an infected stump is not strongly related to the probability of that tree becoming infected. Trees in the 25-year-old plantation had survived 25 years in close association with infected stumps.

Third, the question of ranking species susceptibility to *A. ostoyae* requires more study in both young and mature stands. Whether or not western larch is significantly more resistant to *A. ostoyae* infection than the other conifer species is not certain. The relationship between *Phellinus pini* and western larch survival in mature (120-year-old) stands also deserves more research. *Phellinus pini* had a significant impact on western larch survival in the mature stand surveyed on Larch Hills. Before western larch is prescribed on a large scale as the species of choice in areas infected with *A. ostoyae* in the ICH, the relationship between this tree species and both *A. ostoyae* and *P. pini* in mature stands should be studied further.

Fourth, the use of lodgepole pine in plantation management in the ICH zone should be reviewed. The results from the mature stands indicated that lodgepole pine suffered one of the highest rates of mortality due to *A. ostoyae* of any of the conifer species. Douglas-fir was significantly more tolerant to this pathogen than lodgepole pine in the mature stands.

Fifth, the fact that a mature stand may be quite heavily infected with *A. ostoyae* does not necessarily mean that a future plantation, following harvest on that area will not be productive. The results from the unbrushed 1969 plantation show that the overall stocking level in the 25 year old plantation was the highest of the four plantations although the prior stand was heavily infected with *A. ostoyae*. Although a fairly large proportion of the stocking was made up of ingress there was still over 400 stems/ha of the original planted stock. As mentioned above, any additional entries into that plantation for brushing or spacing would place the health of the young stand at a much greater risk. It should be kept in mind that if the intended stand composition is largely based on a single species, it will not be realized. The presence of *A. ostoyae* on a site ensures species diversity.

The sixth conclusion based on the plantation study is concerned with the use of root disease surveys for predicting future losses in plantations. The number of infected stumps was the stump measure most highly correlated with losses in plantations. The size of the infected stumps as measured by stump basal area was not as highly correlated. Neither of these stump measures were very strongly correlated. It may be concluded from these results that intensive surveying for root disease in mature stands prior to harvest may not be useful. The estimates of future losses in the plantations would simply not be very accurate. Furthermore, the accuracy of estimates of infection prior to harvest are equally as poor due to the difficulties associated with accurately assessing the amount of infection. In order to accurately estimate the number of infected trees, a considerable amount of effort is required. The costs of obtaining accurate estimates of *A. ostoyae* infection in mature stands are not offset by substantial gains in the accuracy of predictions of future losses in plantations.

There are four major conclusions to be drawn from the study of *A. ostoyae* in mature stands in the ICH and the ICH/IDF transition zones. First, as already mentioned, the ranking of species by the incidence of infection differs considerably from the ranking of species susceptibility that is most prevalent in the literature. The ranking of species based on the incidence of infection depends more on the relative abundance of that species on a site and the site itself than on the species. Additional research is required to determine more definitively the rankings of conifer species suceptibility to *A. ostoyae*.

Second, the use of the BEC system beyond the zonal scale to predict the incidence and severity of *A. ostoyae* in the southern interior is not appropriate. The incidence and severity of the disease within site units in the ICHmw2, and IDFmw1 variants did not differ significantly.

Third, of the site factors recorded for each plot, logging disturbance was most closely associated with high *A. ostoyae* severity. Those plots with evidence of past logging disturbance had significantly higher *A. ostoyae* severity ratings than the undisturbed plots.

Fourth, although most of the plots in the ICH zone contained trees that were infected with *A. ostoyae*, the conifer volume of the majority of these plots was not negatively affected. Only in the most severely infected plots did the volume drop significantly. Few plots were in that category. The fact that only the most severely infected plots had significantly lower conifer volumes in the ICH, helps to explain some apparent contradictions. The ICH is considered one of the most productive ecological zones in Canada, yet *A. ostoyae* is prevalent throughout the zone. However, it is not likely that the volumes currently being harvested off mature stands in the ICH will be realized in the future, under the current forest management strategies. As pointed out in both the plantation and mature stand studies, disturbance whether from brushing or partial cutting significantly increases the severity of *A. ostoyae*. If both of these treatment options continue to be prescribed, particularly brushing, the productivity of the ICH zone will no doubt decline.

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APPENDIX

APPENDIX 1

Appendix 1.1 List of Abbreviations for Tree Species

Abbreviation	Common Name	Scientific Name
At	trembling aspen	*Populus tremuloides* Michx.
Bl	subalpine-fir	*Abies lasiocarpa* (Hook.) Nutt.
Ep	paper birch	*Betula papyrifera* Marsh.
Cw	western redcedar	*Thuja plicata* Donn ex D. Don
Fd	Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
Hw	western hemlock	*Tsuga heterophyla* (Rafn.) Sarg.
Lw	western larch	*Larix occidentalis* Nutt.
Pl	lodgepole pine	*Pinus contorta* Dougl. ex Loud.
Pw	western white pine	*Pinus monticola* Dougl. ex D. Don
Se	Engelmann spruce	*Picea engelmanni* Parry ex Engelm.

Appendix 1.2 Biogeoclimatic Ecological Classification System Abbreviations

Abbreviation	Classification
BEC	Biogeoclimatic Ecological Classification
ICH	Interior Cedar Hemlock zone
IDF	Interior Douglas-fir zone
ESSF	Engelmann Spruce Subalpine fir zone
MS	Montane Spruce zone
SBS	Sub-boreal Spruce zone
IDFmw1	Shuswap moist warm Interior Douglas-fir variant
IDFmw2	Thompson moist warm Interior Douglas-fir variant
ICHmw2	Shuswap moist warm Interior Cedar Hemlock variant
ICHmk1	Kootenay moist cool Interior Cedar Hemlock variant

Appendix 1.3 List of Acronyms Used for Data Analyses

Abbreviation	Definition
DRC	diameter at root collar
ARMSEVB	proportion of stumps infected prior to harvest
ARMSEVA	proportion of stumps infected both before and after harvest
STMPBEFR	number of stumps infected before harvest
STMPAFTR	total number of stumps infected
BABEFOR	total basal area in m2/ha of stumps pre-harvest
BAAFTER	total basal area in m2/ha of stumps infected
CONSTEMS	number of healthy conifer regeneration/ha
PROINFCT	proportion of conifer regeneration infected out of total conifer regeneration
TREINFCT	number of conifer stems infected

Infected refers to infections with *Armillaria ostoyae*