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ASSOCIATIONS OF ARMILLARIA ROOT DISEASE IN
JACK PINE WITH *ARCEUTHOBIUM AMERICANUM*

by

Elizabeth G. Hebertson

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Forestry

UTAH STATE UNIVERSITY
Logan, Utah

1995

ABSTRACT

Associations of Armillaria Root Disease in Jack Pine
with *Arceuthobium americanum*

by

Elizabeth G. Hebertson, Master of Science

Utah State University, 1995

Major Professor: Dr. Fred A. Baker
Department: Forest Resources

Relationships between jack pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) and Armillaria root disease (*Armillaria ostoyae* (Romagn.) Herink) were examined to determine how these two disease agents contribute to jack pine (*Pinus banksiana* Lamb.) decline and mortality in the Belair Provincial Forest, Manitoba, Canada. The incidence and extent of Armillaria root disease was strongly related to tree vigor. Dwarf mistletoe infection did not affect either the incidence of *Armillaria* or the mean percentage of root system colonization within vigorous, declining, and dead classes of trees. However, field observations and other analyses indicate that dwarf mistletoe was primarily responsible for jack pine decline and mortality. In dwarf mistletoe mortality centers, *Armillaria* appeared to act opportunistically, extensively colonizing only the stressed trees. Analysis of distributions of percent *Armillaria* colonization revealed that

rapid root system colonization occurred just prior to, or at the time of tree death.

(106 pages)

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Elizabeth G. Hebertson

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INTRODUCTION

Dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) parasitizes jack pine (*Pinus banksinana* Lamb.) throughout the Canadian prairie provinces, and lodgepole pine (*Pinus contorta* var *latifolia* Dougl.) in Alberta (Hiratsuka 1987). Heavy dwarf mistletoe infestation reduces height and diameter growth, decreases seed production, and decreases vigor of host trees (Kuijt 1955; Knutson and Toevs 1972; Hawksworth and Shaw 1984). Branch and stem swellings, knots, and other morphological weakness caused by dwarf mistletoe result in deformity and reduce wood quality (Hawksworth and Johnson 1989). In commercial stands, extensive dwarf mistletoe infestations have resulted in considerable loss of merchantable trees (Hiratsuka 1987). Large witches' brooms and deformities also create difficulties during harvesting operations (Baker et al. 1992). Dead trees in addition to dead brooms and other woody debris pose safety and fire hazards. Deformity and extensive mortality also reduce visual quality in recreational areas (Gilbert and Punter 1984).

A characteristic pattern of tree decline occurs in stands where dwarf mistletoe is the primary agent responsible for mortality. In stands of young, shade-intolerant species, dwarf mistletoe infection centers typically develop around old, mistletoe-infested trees that survived fire, or logging (Baranyay 1970). In lodgepole pine, visible signs of tree decline and mortality become evident in dwarf mistletoe-infested stands within 50 to 100 years (Baranyay and Smith 1972), and jack pine decline and mortality have been observed in severely infested stands approximately 35 years old in Manitoba (Baker pers. comm.). In dwarf mistletoe-infested jack pine stands in Alberta, Muir and Robbins (1973) observed

that mostly dead trees with old mistletoe brooms were found within mortality centers. Heavily broomed living trees often had reduced height growth and dead tops. Mortality caused by this parasite created openings in the forest canopy ranging in size from 50 to 300 feet in diameter (Muir and Robbins 1973). Dwarf mistletoe-infested trees surrounded openings and often had large witches' brooms. Red foliage was characteristic of dead and dying trees (Muir and Robbins 1973). The authors concluded that dwarf mistletoe was the primary agent responsible for death and decline because all mortality centers were infested. Similar observations were made regarding the pattern of tree decline and mortality in dwarf mistletoe-infested jack pine in Manitoba (Fig. 1).

Dwarf mistletoes reportedly occur with insects and other disease agents in some forest pest complexes. Secondary infection by root rotting fungi and insects may contribute to tree death (Muir and Robbins 1973; Hawksworth and Shaw 1984). The weakening effects of dwarf mistletoe may make heavily infested trees less tolerant of insect defoliation and more susceptible to "primary" bark beetle attack including mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) (Parker and Stipe 1974; Johnson et al. 1976; Wagner and Mathiasen 1985). Dwarf mistletoe weakened trees are often attacked by "secondary" bark beetles including *Ips* spp. (Coleoptera: Scolytidae) and wood borers (*Melanophila* spp. (Coleoptera: Buprestidae) hastening their death (Stevens and Hawksworth 1984). Damage resulting from stem infections may provide entry courts for fungal decay pathogens (Hawksworth and Shaw 1984; Filip 1984). Root disease associated with dwarf mistletoe accounted for 11% to 14% of true fir mortality in



FIG. 1. Extensive decline and mortality caused by jack pine dwarf mistletoe in the Belair Provincial Forest, Manitoba, Canada.

northern California forests. Root disease and dwarf mistletoe were also associated in 18% and 28% of the total conifer mortality in the San Bernardino National Forest, and the Laguna Mountain area and Cleveland National Forest, respectively (Byler 1978).

In the Belair Provincial Forest, Manitoba, Canada, *Armillaria* root disease is believed to contribute to jack pine decline and mortality in mature stands heavily infested with *A. americanum* (Baker pers comm.). However, no studies have characterized the relationship between these two disease agents in jack pine. The need for research to examine the role of *Armillaria* in dwarf mistletoe mortality centers became apparent when young red pine (*Pinus resinosa* Ait.) established on former jack pine sites began to experience extensive mortality caused by *Armillaria* root disease.

Because of the severe damage and mortality caused by dwarf mistletoe, past management practices in this forest have dealt primarily with dwarf mistletoe control. After harvesting, heavily infested stands were converted to red pine, a species with high commercial value, and one not susceptible to *A. americanum* (Knowles pers. comm.). However, young red pine in these plantations currently suffer extensive mortality due to *Armillaria* root disease (Moody and Cerezke 1986). Located near the northwestern limit of red pine, young trees in these plantations may experience stress, making them susceptible to *Armillaria* (Hood et al. 1991).

A second explanation of the extensive *Armillaria*-induced mortality in red pine plantations was proposed by Baker (pers. comm.). He suggested that by reducing host vigor, dwarf mistletoe predisposes heavily infected jack pine to *Armillaria*. *Armillaria*

colonizes declining and dead mistletoe-infected trees in jack pine stands, increasing the amount of inoculum. After harvesting, stumps, roots, and debris become food bases, providing *Armillaria* with the energy to infect juvenile red pine. Klein-Gebbinck et al. (1991), Whitney (1988), and Stanosz and Patton (1987) have all described the importance of these inoculum sources in the spread of *Armillaria* root disease to juvenile trees in young stands.

My research examined *Armillaria* root disease associated with jack pine decline in dwarf mistletoe mortality centers located in the Belair Provincial Forest. Jack pine experiencing stress induced by dwarf mistletoe exhibit visible symptoms of decline including open upper crowns, short yellow-green needles, top dieback, and reduced height and diameter growth (Hawksworth and Johnson 1989). These symptoms can serve as a means to assess host vigor primarily influenced by dwarf mistletoe. Hawksworth (1958) showed a relationship between tree vigor and dwarf mistletoe in Rocky Mountain lodgepole pine using four vigor classes based on crown condition described by Taylor (1939). The percentage of board-foot volume in vigorous trees decreased from 20% to 0% as dwarf mistletoe infection increased. Trees with symptoms of poor vigor comprised 66% of the board-foot volume of heavily infected lodgepole stands (Hawksworth 1958).

Basal area increment (BAI) can also serve as an index of a tree's past relative growth and vigor, and is an important characteristic for describing stand and site quality (Daniel et al. 1979). Daniel and others (1979) define BAI as a measure of the capacity of trees or stands to produce xylem elements. Genetics, biotic, physical, and chemical factors of the

environment all influence BAI (Daniel et al. 1979). Jack pine with visible symptoms of decline and reduced BAI resulting from dwarf mistletoe infestation should have greater incidence of *Armillaria* and more extensive root system colonization than vigorous trees.

The first objective of this study was to determine how the incidence and percentage of *Armillaria* colonization was associated with tree vigor as influenced by the incidence of dwarf mistletoe. The second objective was to determine how the incidence and percentage of *Armillaria* colonization was associated with tree vigor as influenced by the extent of dwarf mistletoe infestation. Tree vigor was assessed by visual criteria, including crown shape, extent of brooming, foliage color, terminal leader growth, and BAI.

Understanding associations between dwarf mistletoe and *Armillaria* root disease has important implications for the control and management of these two disease agents. Information about these associations could lead to the development of systems to identify stands at high risk. Harvesting operations, site preparation, and silvicultural treatments could be used to reduce potential problems with *Armillaria* in future plantations.

A REVIEW OF JACK PINE, DWARF MISTLETOE,
AND ARMILLARIA ROOT DISEASE

Understanding relationships between dwarf mistletoe and Armillaria root disease requires a basic knowledge of the biology and ecology of each organism, and how parasitism by each organism affects host vigor. The following discussion reviews the ecology of jack pine, and biological and ecological characteristics of dwarf mistletoe and Armillaria root disease that may influence potential interactions between these two disease agents and their host. These characteristics include disease cycles, spread and intensification, host effects, and associations with other damaging agents in forest pest complexes.

Jack pine

Jack pine forests extend from the Northwest Territories, Canada, through the Canadian prairie provinces, southward into Minnesota, Michigan, and Wisconsin, and eastward to northern New England (Harlow et al. 1979) (Fig. 2). Throughout most of its range, jack pine is an important timber species (French 1967). Jack pine can grow on sandy sites where it is a valuable physiographic climax species (Smith 1962). Its best development, however, occurs north and west of Lake Superior (Harlow et al. 1979).

Having evolved in fire-prone ecosystems, jack pine possess several reproductive characteristics that enable them to successfully populate open sites following fire (Rowe



FIG. 2. General distribution of jack pine (*Pinus banksiana* Lamb.) in North America (adapted from Harlow et al. 1979).

and Scotter 1973; Critchfield 1985). Trees produce seed in cones that exhibit varying degrees of serotiny (Harlow et al. 1979). The cones of some trees remain closed when mature and open with heat, especially that produced by fire (Harlow et al. 1979). Seeds retained in closed cones also allow jack pine to regenerate during any part of the growing season following fire (Critchfield 1985). Other jack pine produce cones that open upon maturity (Harlow et al. 1979). A single jack pine can produce thousands of viable seeds that disseminate well and germinate quickly (Critchfield 1985). Being a very shade-intolerant species (Daniel et al. 1979), jack pine seedlings respond favorably to full-sun exposure, have good growth and survival rates, and are frost hardy (Rowe and Scotter 1973).

Jack pine succession in North American boreal forests begins with large-scale, high-intensity fires that recur during prolonged periods of drought (Heinselman 1973). These intense fires inhibit the growth of grasses, forbs, and shrubs, and consume duff layers, exposing bare mineral soil that provides the best medium for seed germination and seedling survival (Pyne 1984; Critchfield 1985). Following germination, a naturally regenerated jack pine stand may have thousands of seedlings per acre (Smith 1962). The young trees grow rapidly, and as the stand ages, vigorously growing trees outcompete less vigorous trees for light, water, and nutrients (Smith 1962). Natural thinning occurs quickly as stressed trees become overtopped, pass into suppression, and die (Smith 1962).

Fuels begin to accumulate in the stand with increasing numbers of dead trees and

woody debris (Critchfield 1985). Diseases and insect damage hasten mortality. Root rotting and trunk decay fungi make trees susceptible to wind throw and wind breakage, factors that further contribute to fuel loads (Heinselman 1973). In dwarf mistletoe-infested stands, dead trees, branches, twigs, and needles add to ground fuels, and foliage close to the ground and witches' brooms provide ladder fuels capable of carrying fire into tree crowns (Gill and Hawksworth 1964). Understory species such as spruce (*Picea spp.*) and fir (*Abies spp.*) have very flammable foliage that also acts as ladder fuel (Heinselman 1973). Shrubs, herbaceous plants, mosses, and lichens, in addition to litter, duff, and humus, provide other potential sources of fuel (Heinselman 1973).

With suitable weather conditions and an ignition source, stands eventually burn (Heinselman 1973). As with other boreal forest types, vegetation, stand age, successional stage, and fuel factors interacting with climate and site characteristics determine the pattern and intensity of burns in jack pine stands (Heinselman 1973). Significant fires reduce fuels and create openings that allow jack pine succession to begin again (Heinselman 1973).

In the absence of fire, succession in jack pine-dominated communities progresses to fir-spruce-birch in well drained sites, or black spruce-moss types in bogs. However, scattered jack pine can persist in the overstory of spruce-fir forests for over 200 years (Heinselman 1973). On average, jack pine forests have a natural fire return interval of about 100 years, and succession to other species is rare (Heinselman 1973).

The fire ecology of jack pine results in stands of pure composition and even-aged

structure, making them susceptible to disease and insect attack (Daniel et al. 1979).

Dwarf mistletoe, jack pine budworm, and *Armillaria* root disease cause serious losses of jack pine throughout the prairie provinces of Canada (Hiratsuka 1987). Dwarf mistletoes have a particularly unique ecological relationship with jack pine and fire. Dowding (1929) suggested that wildfire was the major factor that influenced the distribution of dwarf mistletoes on jack pine in the sandhill areas of central Alberta.

Fires tend to favor the establishment of early successional, mistletoe-susceptible species (Gill and Hawksworth 1964). In these stands, high intensity fires can eradicate, or impede dwarf mistletoe spread and intensification by simultaneously killing both the host tree and parasitic plant (Zimmerman and Laven 1984). With patchy or infrequent fires, dwarf mistletoe infected trees survive the fire, and dwarf mistletoe can spread rapidly from infected residual trees to regeneration of the same species (Gill and Hawksworth 1964). With increasing infestation, witches' brooms, tree decline and mortality results in a build-up of fuels that predisposes stands to subsequent fires (Brown 1975).

Dwarf mistletoe

Dwarf mistletoes parasitize forest trees in all six genera of the Pinaceae in North America. In both the United States and Canada, dwarf mistletoes are the single most damaging disease agent for many commercially important species, causing unacceptable losses of timber products (Baranyay 1970; Hawksworth and Shaw 1984; Wicker 1984; Moody and Amirault 1992). In the Northern Rockies, heavily infested lodgepole pine stands have reduced rates of height and diameter growth and increased rates of mortality,

and produce less volume than comparable mistletoe-free stands (Hawksworth and Johnson 1989). Baranyay (1970) estimated approximately 9.6 million cu ft were lost annually in lodgepole pine and jack pine stands in Alberta. Significant losses occur in true firs (*Abies spp.*), western larch (*Larix occidentalis* Nutt.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and western hemlocks (*Tsuga spp.*) in the Pacific Northwest (Knutson and Tinnin 1980), and in ponderosa pine and Douglas-fir in the Southwest (Hawksworth and Shaw 1984; Mathiasen et al. 1990).

Dwarf mistletoe is the most damaging agent of jack pine in the Canadian prairie provinces (Hiratsuka 1987). *Arceuthobium americanum* is the primary dwarf mistletoe species that parasitizes jack pine. Figure 3 shows the general distribution of *A. americanum* in North America. Eastern dwarf mistletoe (*A. pusillum* Peck) can also infect jack pine when they grow near infested black spruce (*Picea mariana* (Mill) B.S.P.) in southeastern Manitoba (Laut 1967); however, few aerial shoots are produced and brooms remain small (Knowles pers. comm).

Dwarf mistletoes are small, leafless, chlorophyllous angiosperms belonging to the genus *Arceuthobium* (Wicker and Hawksworth 1988). Dwarf mistletoes have fruits that explosively discharge seeds (Kuijt 1955). On average, seeds are dispersed 15 feet from the parent plant (Hawksworth and Hinds 1965). A mucilaginous substance called viscin covers the seeds, enabling them to stick to objects in their path (Kuijt 1955). The dwarf mistletoe disease cycle begins when seeds adhere to needles of host trees. When moistened by rain, the viscin rehydrates, allowing the seed to slide down the needle to the twig

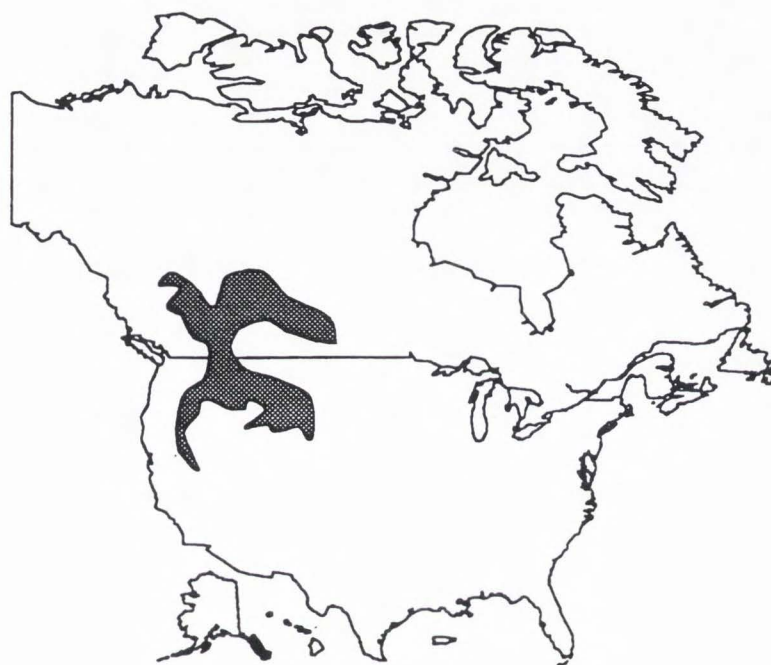


FIG. 3. General distribution of *Arceuthobium americanum* in North America (adapted from Hawksworth and Johnson 1989).

(Hawksworth and Hinds 1965). The germinating seed produces a radicle that elongates and grows along the surface of the branch until it reaches a bud or leaf base (Kuijt 1955). At the infection site, the radicle flattens and produces a primary haustorium that penetrates the bark primarily by mechanical force, although enzymes may be secreted to soften cell walls (Kuijt 1955). From the primary haustorium, haustorial strands extend longitudinally and circumferentially through the host cortex and outer phloem. Radial strands called "sinkers" extend from the haustorial strands into the host vasculature (Alosi and Calvin 1984). The longitudinal strands and radial sinkers comprise the endophytic system of the dwarf mistletoe plant. Because sinkers are closely associated with host xylem, they are believed to absorb nutrients, and facilitate nutrient transport out of the host vasculature (Alosi and Calvin 1984). Pathways for water and nutrients are formed by the apoplastic continuity of xylem contacts and cellulose wall free space (Alosi and Calvin 1984).

The diversion of water, minerals, and photosynthates affects host trees by reducing height and diameter growth rates, increasing mortality, decreasing seed production, and reducing wood quality (Knutson and Toevs 1972; Hawksworth and Shaw 1984). Starch concentrations in needles of both systemically and locally infected lodgepole pine branches are greater than in uninfected branches (Broshot and Tinnin 1986). Wanner and Tinnin (1986) determined that rates of dark respiration are greater in uninfected twigs of lodgepole pine than in infected twigs. The rates of dark respiration for aerial shoots of dwarf mistletoe are greater than in host twigs. Wanner and Tinnin (1986) also found a shift in mass allocation from stem to branch wood in heavily infested trees, which

contributes to reduced timber volume.

Dwarf mistletoe spread

Dwarf mistletoe spreads more rapidly from infested overstory trees to regeneration, than within even-aged stands (Hawksworth 1958). In lodgepole pine approximately 10 to 25 years old, 89% of dwarf mistletoe-infested trees were within 30 feet of infested stands (Gill and Hawksworth 1964). In this same study, dwarf mistletoe-infested trees were found up to 60 feet from infested residual trees or stands. Dwarf mistletoe can also spread more rapidly in open stands than in dense stands. In dense, even-aged lodgepole pine stands, Hawksworth (1958) found that lateral spread of dwarf mistletoe occurred at a rate of 1.2 feet per year. In more open lodgepole stands, with fewer obstructions, the rate of dwarf mistletoe spread increased to 1.7 feet per year (Hawksworth 1958). Similar rates of spread were observed for *A. americanum* in jack pine (Muir and Robbins 1973).

Dwarf mistletoe seeds observed on bird feathers, and on the fur of small mammals suggest that these animals may contribute to long distance spread of the parasite (Nicholls et al. 1984). The occurrence of occasional dwarf mistletoe infection centers in otherwise healthy stands supports these observations (Gill and Hawksworth 1964).

Dwarf mistletoe infection centers typically develop in young stands around old, infested trees that survived fire or logging (Baranyay and Smith 1972). Dwarf mistletoe seeds have greater chances of striking regeneration of larger height and diameter, and consequently a larger percentage of these trees become infested with dwarf mistletoe (Knutson and Tinnin 1980). Initially, infested stands show few signs of dwarf mistletoe

effects (Gill and Hawksworth 1964). In lodgepole pine, broomed trees, trees with spike tops, and mortality become evident in dwarf mistletoe infection centers within 50 to 100 years (Gill and Hawksworth 1964; Baranyay and Smith 1972). Extensive mortality caused by this parasite in heavily infested stands may create openings in the forest canopy. In dwarf mistletoe-infested jack pine in Alberta, these openings ranged in size from 50 to 300 feet in diameter (Muir and Robbins 1973). In stands older than 100 years, heavily broomed, dying, and dead trees are found within mortality centers (Gill and Hawksworth 1964; Baranyay and Smith 1972). In forests experiencing heavy infestations, several large infection centers may merge (Gill and Hawksworth 1964). The intensity of dwarf mistletoe decreases progressively further from infection center boundary (Gill and Hawksworth 1964; Muir and Robbins 1973).

Dwarf mistletoes associated with other damaging agents

Potential association between dwarf mistletoe, insects, and disease agents remains in question (Stevens and Hawksworth 1984). Associated with insects and fungal pathogens, dwarf mistletoes may reduce the longevity of infected trees. In Arizona, ponderosa pine mortality resulting from pandora moth (*Coloradia pandora pandora* Blake (Lepidoptera: Saturniidae)) defoliation was greater in trees heavily infested with dwarf mistletoe than in uninfected trees (Wagner and Mathiasen 1985). The authors speculated that trees weakened by dwarf mistletoe were less tolerant of defoliation than uninfested trees. Defoliation by western spruce budworm (*Choristoneura occidentalis* Freeman

(Lepidoptera: Tortricidae)) did not cause additional growth reduction in Douglas-fir for any dwarf mistletoe severity class (Filip and Parks 1987).

Dwarf mistletoe-weakened trees are often attacked by "secondary" beetles including *Ips* spp. and *Melanophila* spp., hastening their death (Muir and Robbins 1973, Stevens and Hawksworth 1984). The role of primary bark beetles remains uncertain. Stress induced by dwarf mistletoe may predispose trees to aggressive bark beetle attack.

Mountain pine beetles (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)) were more attracted to dwarf mistletoe-infested trees in parts of the Colorado Front Range than uninfested trees (Johnson et al. 1976). In an Idaho study, mountain pine beetle killed a significantly larger proportion of lodgepole pine weakened by dwarf mistletoe than mistletoe-free trees (Parker and Stipe 1974).

Most studies, however, indicate that the thin phloem of dwarf mistletoe-infected trees makes them less attractive to "primary" bark beetles for brood production. Hawksworth and others (1983) did not find significant relationships between dwarf mistletoe infection and phloem thickness of lodgepole pine. Consequently, these trees were not considered suitable for mountain pine beetle brood production. Densities of mountain pine beetle attack and brood production were not significantly different between dwarf mistletoe-infected and -uninfected ponderosa pine (MacCambridge 1980). Per unit area of bark, the total egg gallery length was greater in uninfested trees. McGregor (1978) found less mortality from mountain pine beetle in stands heavily infested with dwarf mistletoe. He attributed the difference to thinner phloem of mistletoe infected trees. The average

phloem thickness of dwarf mistletoe-infected lodgepole pine was 0.12 inches for infected trees, compared to 0.17 inches for uninfected trees, making attack by mountain pine beetle less likely (Roe and Amman 1970).

Cytospora canker (*Cytospora abietis* Sacc.) established in older dwarf mistletoe infections contributed to the mortality of grand fir (*Abies grandis* (Dougl.) Lindl.) branches, especially in stressed trees. Branch mortality in combination with fir engraver attacks and root diseases eventually killed trees (Filip 1984). In four California national forests, root pathogens in combination with dwarf mistletoes accounted for 11 to 28% of total conifer mortality (Byler 1978). Damage resulting from stem infections may also provide entry courts for decay fungi (Hawksworth and Shaw 1984).

Armillaria root disease

Armillaria root disease also contributes to significant jack pine mortality in the Canadian prairie provinces (Mallett 1990). Three species of *Armillaria* have been identified in Manitoba; *Armillaria ostoyae* (Romagn.) Henrink (= *Armillariella obscura* (Pers. ex Secr.), *Armillaria sinapina* Berube and Dessureault, and *Armillaria calvescens* Berube and Dessureault (Mallett 1990). *Armillaria ostoyae* appears to be pathogenic on all hosts and is the species most frequently isolated from dead and declining conifers (Mallett 1990). In young lodgepole, jack, and red pine stands, *A. ostoyae* is particularly prevalent. Little is known about the role and damaging effects of *Armillaria* in older trees (Mallett 1990). With age, trees appear increasingly tolerant of the disease. *Armillaria*-caused mortality is less frequent in older trees and has been associated with tree stress

(Hiratsuka 1987). *Armillaria sinapina* and *A. calvescens* both infrequently infect conifer species; however, the pathogenicity of these two species has not been determined (Mallett 1990).

Armillaria pathogenicity

The occurrence of *Armillaria* root disease has been reported throughout coniferous and deciduous forests worldwide (Wargo and Shaw 1985; Williams et al. 1986). Contradiction surrounded the role of *Armillaria* root disease in North America until morphologic and mating studies lead to the recognition of several different taxonomic and biological species (Watling et al. 1991). Basidiome morphology and mating studies have shown that the genus *Armillaria* contains approximately 40 species (Watling et al. 1991) with nine biological species of *Armillaria* currently recognized in North America (Anderson 1986; Mallett 1990). These species and genotypes of *Armillaria* vary in their pathogenicity (Rishbeth 1982). "Pathogenicity" means the quality or characteristic of being able to cause disease as applied to a genus or species (British Federation of Plant Pathologists 1973, in Gregory et al. 1991). *Armillaria spp.* range in behavior from a nonpathogenic saprophyte to a necrotrophic plant pathogen (Rishbeth 1982; McDonald et al. 1987b, Kile et al. 1991).

As with all diseases, interactions among the environment, the pathogen, and host influence the expression of *Armillaria* pathogenicity (Gregory et al. 1991). Following pathogenicity tests with four English *Armillaria* species, Rishbeth (1985) concluded that "some degree of specificity is shown by *Armillaria* species with respect to the type of

standing tree attacked and its physiological condition." He found that in the absence of any weakening or predisposing factors, *A. mellea* (Vahl: Fr.) could kill a number of broadleaved trees, including birch (*Betula spp.*) and ash (*Fraxinus spp.*). *Armillaria mellea* could also penetrate intact bark and invade tissues with some residual resistance. *Armillaria bulbosa* (Barla) Kile and Watling was a primary colonizer of weakened broadleaved trees. With its ability to induce less exudate production, *A. ostoyae* killed all pines (*Pinus spp.*) in this same study. *Armillaria mellea* and *A. bulbosa* mainly colonized weakened pines (Rishbeth 1985). In other studies, *A. mellea* infected and killed larger percentages of inoculated lodgepole pine seedlings than either *A. sinapina* Berube and Dessureault or *A. ostoyae* (Mallett and Hiratsuka 1988). In contrast, *A. ostoyae* was more pathogenic on lodgepole pine and killed a greater percentage of seedlings than other *Armillaria* species (Mugala et al. 1989). White spruce (*Picea glauca* (Moench) Voss) seedlings were more frequently infected and more likely to die than lodgepole pine seedlings after being inoculated with both *A. ostoyae* and *A. sinapina* (Mugala et al. 1989).

Through enzymatic activity, *Armillaria* penetrates bark tissues and invades host tissues more rapidly than periderm can develop (Rykowski 1975). In experiments designed to study the structural responses to wounding and *A. ostoyae* infection in Scots pine seedlings, *Armillaria* infection delayed the formation of necrophylatic periderm, and reduced the number of cells involved in host tissue structural responses (Wahlstrom and Johansson 1992). In oaks (*Quercus spp.*), phenolic oxidases were greater and oxidized

phenol less in both discolored and *Armillaria*-colonized bark tissue than healthy bark (Wargo 1984).

A number of host factors influence *Armillaria* infection. To inhibit rhizomorph penetration, vigorous trees form layers of secondary cork beneath the point of infection (Morrison et al. 1991). The suberization of cells within newly formed secondary periderm of broadleaved trees has also been shown to inhibit rhizomorph penetration (Rishbeth 1985). Wounded Scots pine (*Pinus sylvestris* L.) seedlings inoculated with *Armillaria ostoyae* produced more lignified cell layers than wounded uninoculated seedlings (Wahlstrom and Johansson 1992).

Exudate production, including resin, gum, and kino in many hosts, restricts mycelial growth (Morrison et al. 1991). Phenolics and other chemical barriers provide the most resistance to penetration and infection by *Armillaria* (Garraway et al. 1991). When root tissue produced lower concentrations of phenolic compounds and other chemical constituents combined with higher sugar production, trees were more susceptible to *Armillaria* (Entry et al. 1991; Entry et al. 1992a). With age, trees appear to increase in both their ability to produce defense compounds and form tissues that provide physical barriers to *Armillaria* colonization (Morrison et al. 1991).

Soil factors, including pH, soil type, and temperature, affect inoculum survival, rhizomorph production, frequency of infection, and tree death. Thus, environment may restrict the distribution of *Armillaria* species. Habitat types characterized by temperature extremes and dry conditions were outside of the ecological range of *Armillaria* species

native to the Northern Rocky Mountains (McDonald et al. 1987a). Dry seasonal conditions may have affected the growth of *A. mellea* rhizomorphs in Britain (Morrison 1976). The dry weight of rhizomorphs produced by *Armillaria* species was greatest in soils with temperatures at 20 C, and lowest in soils with temperatures below 10 C and above 26 C (Rishbeth 1978). Several studies have shown that high pH may either inhibit or enhance the growth of the fungus in soil. *Armillaria mellea* infected a significantly larger proportion of coniferous and broadleaved tree species grown in acid sand soils than in other soil types (Redfern 1978). The incidence of infection in this same study was lowest in alkaline clay. In a different study, total fungal weight and hyphal extension of *Armillaria* in culture increased significantly in soils with a higher pH (Entry and Cromack 1986). *Armillaria ostoyae* was more common in acidic soils than alkaline soils in England (Rishbeth 1982). After inoculating two-year-old lodgepole pine grown in four different soil types with *A. ostoyae*, Blenis and Mugala (1989) showed that sandy loam was more favorable for *Armillaria* growth than either a loam or clay loam soil. The authors speculated that differences may have been due to different levels of water and oxygen, or perhaps the presence of inhibitory substance(s) or organism(s). Common soil bacteria isolated from root free soil, including *Pseudomonas spp.* and *Bacillus spp.*, inhibited *Armillaria* mycelial growth and rhizomorph production in culture (Dumas 1992).

Redfern (1978) demonstrated that trees subjected to conditions of low light intensity such as suppression, shading, or shortened day length were more susceptible to *Armillaria*. In inoculation studies conducted by Davidson and Rishbeth (1988), crown

suppression weakened English oaks and Scots pine, increasing their susceptibility to *Armillaria*. All suppressed trees were colonized by *A. mellea*, *A. ostoyae*, or *A. gallica*. Subdominant oaks and pines were only colonized by *A. mellea* and *A. ostoyae*, respectively.

McDonald et al. (1987b) found that human activity such as road building or previous cutting also increased pathogenicity of *Armillaria* in study sites. Harvesting, site preparation, and planting activities can cut rhizomorphs, stimulate new growth, and increase the amount of potential inoculum for infecting tree regeneration (Redfern 1973).

Disease development and spread

Morrison (1981) discussed *Armillaria* infection and subsequent disease development. In general, *Armillaria* spreads from diseased trees to uninfected trees along root contacts, or by rhizomorphs that grow through the soil. At contact points, mycelia grow from diseased roots to healthy roots. Mycelial fans develop in the outer bark and penetrate to the cambial zone where continued fungal growth occurs. Rhizomorphs penetrate root bark by mechanical and enzymatic means. Eventually, hyphae reach the cambial zone, branching in all directions, and mycelial fans develop within the cambial zone (Morrison et al. 1991).

Several factors may contribute to tree death. Extensive physical disruption of the host's vascular system eventually girdles the infected root. Continued tissue death occurs as the fungus spreads to the root collar and other roots (Morrison et al. 1991). In saplings and pole-sized trees, attacks high on the tap root or root collar hasten host mortality

(Shaw 1980). Host tissues may also die when exposed to metabolic toxins produced by *Armillaria* (Wargo 1984).

Damage caused by Armillaria root disease

Trees infected by *Armillaria* experience reduced height and diameter growth, decayed wood, and mortality (Morrison et al. 1991). *Armillaria* root disease resulted in significant volume loss in infected Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in southeastern British Columbia (Bloomberg and Morrison 1989) and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in Washington (Shaw et al. 1976). Young lodgepole pine, jack pine, red pine (*Pinus resinosa* Ait.), and white spruce suffer extensive mortality due to *Armillaria* root disease in plantations throughout the Canadian prairie provinces (Hiratsuka 1987; Moody and Amirault 1992). *Armillaria mellea* was associated with the decline and death of red spruce (*Picea rubens* Sarg. [*Picea rubra* (Du Roi) Link.]) in mixed hardwood, transitional, and montane boreal forests of New England (Carey et al. 1984). Damage can also leave stands poorly stocked and underproductive, and increase a tree's susceptibility to windthrow (Shaw et al. 1976; Mallett 1992).

Armillaria root disease associated with other damaging agents

Accelerated forest decline and mortality may result from the combined effects of *Armillaria* associated with insect pests and other decay fungi. Root diseases may predispose trees to attack by bark beetles (Coleoptera: Scolytidae) (Cobb 1989). Chemical compounds produced by host trees in response to *Armillaria* infection may

affect the selection and invasion of these trees by beetles (Madziara-Borusiewicz and Strzelecka 1977). *Armillaria mellea sensu lato* was found infecting the root systems of lodgepole pine and ponderosa pine infested with endemic populations of mountain pine beetle in Utah and the northern Black Hills of South Dakota, respectively (Lessard et al. 1985; Tkacz and Schmitz 1986). Kulhavy and others (1984) concluded that resistance of western white pine (*Pinus monticola* Dougl. ex D. Don) to bark beetles decreases through the combined effects of *Armillaria* root disease, white pine blister rust (*Cronartium ribicola* J. C. Fisch), and senescence. The incidence of sugar maple borers (*Glycobius speciosus* Say (Coleoptera: Cerambycidae)) was significantly higher in declining maples infected with *Armillaria calvescens* Berube and Dessureault than in healthy trees (Bauce and Allen 1992).

Defoliation consistently has been associated with *Armillaria* root disease in both deciduous and coniferous trees. *Armillaria ostoyae* penetrated more cell layers in Scots pine seedlings when stressed by defoliation (Wahlstrom and Johansson 1992). In the Northeastern United States, gypsy moth (*Lymantria dispar* L. (Lepidoptera: Lymantriidae)) defoliation has been associated with *Armillaria* since the early 1900's (Wargo and Harrington 1991). Rhizomorph density increased in mixed oak stands after repeated defoliation by the gypsy moth (Twery et al. 1990). Dead and top-killed jack pine defoliated by jack pine budworm (*Choristoneura pinus* Freeman (Lepidoptera: Tortricidae)) had more root system colonization by *Armillaria ostoyae* than fully foliated trees in Saskatchewan (Mallett and Volney 1990). *Armillaria* root disease was associated

with the two-lined chestnut borer (*Agilus bilineatus* Weber (Coleoptera: Buprestidae)) in oaks experiencing stress by defoliation and drought stress (Wargo 1977). Other foliar pathogens, including powdery mildews, blister rusts, and needle blight, enhance *Armillaria* attack (Wargo and Harrington 1991).

Armillaria occurs with other root pathogens, forming root disease complexes commonly encountered in Northwest forests. *Armillaria mellea* was associated with *Phellinus weirii* (Murr.) Gilb., *Heterobasidion annosum* (Fr.) Bref., and *Ceratocystis wagneri* in causing extensive mortality in the Deschutes National Forest, Oregon (Filip and Goheen 1982). Associations among root pathogens may exist by chance, as a result of successional relationships, or from synergistic interactions between fungi (Hansen and Goheen 1989).

METHODS

Site description

Jack pine stands selected for this study were located within the Belair Provincial Forest approximately 100 km northeast of Winnipeg, Manitoba. Formed from the meltwater of retreating continental glaciers, ancient Lake Agassiz once covered this region. As a consequence, the present topography is usually gently sloping, or in the form of narrow, elongated, gently sloping beach ridges (Smith and Ehrlich 1967). Average temperatures range from -18 C in January to 21 C in July, with approximately 457 mm of precipitation annually (Weir 1983).

The soils of study sites include the Sandilands and the Woodridge series. The Sandilands series are Minimal Podzol soils developed on siliceous sandy outwash deposits. The Woodridge series are Orthic Grey Wooded soils developed on sand and gravel beach and outwash deposits, which may be underlain by gravelly deposits 0.76 m below the surface. Both soils are rapidly to well drained, with rapid internal drainage and negligible to moderate surface runoff. The Sandilands soils have very weakly developed horizons distinguished by faint changes in color and reaction. They have a thin discontinuous organic layer, a thin, light brownish grey A horizon, and an indefinite B_{fg} horizon that grades gradually into very pale brown fine sand. The Woodridge soils are characterized by a thin, organic surface layer, a deep, leached, light grayish brown A horizon, and a brown, textural B horizon. The B horizon occurs in the sandy surface mantle and in the underlying stratified gravel and coarse sand (Smith and Ehrlich 1967).

Jack pine was the dominant cover type of the two stands selected as study sites, which comprised 71-100% of the stand. These were mature stands, approximately 50-70 years old, with a crown closure of at least 71%. Understory species used as indicator plants included bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), creeping savin (*Juniperous horizontalis* Moench.), reindeer moss (*Cladonia* spp.), and mountain [slender] rice (*Oryzopsis* spp.).

Establishing transects

Preliminary ground surveys were done to locate dwarf mistletoe mortality centers within jack pine stands. Selected mortality centers were similar with respect to other environmental and physical factors. Dwarf mistletoe infestations were sometimes extensive, making it difficult to discern individual mortality center boundaries and to find trees uninfected by dwarf mistletoe. Consequently, only eight dwarf mistletoe mortality centers with discernible boundaries were selected.

Of the eight potential dwarf mistletoe mortality centers, three were randomly selected for sampling purposes. The three mortality centers ranged from 18 m to 27 m in diameter. A transect was established through the middle of each mortality center on a random compass bearing. To insure that enough uninfected trees would be included in the sample, the transect extended through 20 m of uninfected forest at one end, across the mortality center, and through 20 m of uninfected forest at the other end (Appendix A).

Tree categorization

Crown position, using Kraft's tree classification (Daniel et al. 1979), and a dwarf mistletoe rating (DMR) (Hawksworth 1977) were determined for all trees within 5 m of the transect line. The trees were then categorized into one of six dwarf mistletoe-vigor classes. These classes include: (1) vigorous trees with no mistletoe; (2) vigorous trees with mistletoe; (3) declining trees with no mistletoe; (4) declining trees with mistletoe; (5) recently dead trees with no mistletoe; (6) recently dead trees with mistletoe. The following visual criteria, similar to those described by Taylor (1939, in Hawksworth and Johnson 1989), were used to characterize host vigor as influenced dwarf mistletoe.

Vigorous trees: Trees with a dense, pointed crown and full foliage with good color. Terminal leader growth was among the highest in the stand.

Declining trees: Trees with a sparse, rounded crown and bunchy foliage with poor color. Terminal leader growth was less than one half that of vigorous trees.

Recently dead trees: Trees with a full complement of brown or reddish needles.

Five trees in each tree vigor category were randomly selected as sample trees.

Dominant and codominant trees were primarily selected as sample trees. Dominant trees are defined as those with crowns that rise above the general canopy, and are exposed to full sunlight above and laterally. Codominant trees comprise the main part of the canopy with dominants but are not as tall. They receive overhead light but do not receive as much light laterally (Daniel et al. 1979). However, declining and recently dead dominant and codominant trees were scarce within mortality centers. To sample enough trees from

these vigor categories, intermediate trees were included. The height and diameter at breast height (DBH, 1.4 m above ground) were recorded for each sample tree. Increment cores were taken 0.3 m above the ground. Diagnostic crown symptoms and other types of damage for sample trees were also noted.

Examination of root systems for Armillaria

To determine the incidence and extent of *Armillaria* colonization, the root system and root collar of sample trees were examined. Using pulaskis, vegetation around the sample tree was removed. The root collar and lower bole of each sample tree were debarked and the cambial zone examined for signs and symptoms of *Armillaria*. If more than 75 % of the root collar was infected, primary lateral roots were considered completely infected. Otherwise, primary lateral roots greater than two centimeters in diameter were excavated from the root collar to a distance of 1 m. Once a root was exposed, it was cut at the root collar and at 1 m. Beginning at the proximal end of the cut root, 25-cm sections were examined for signs and symptoms of *Armillaria* root disease, including mycelial fans, rhizomorphs, and lesions. Other symptoms such as resinosis, atypical staining, and decay were also recorded. After each symptomatic root segment was cut and labelled, it was placed in a plastic bag and stored in a cooler. Root samples collected in the field were retained for culturing.

Confirming the presence of Armillaria in sample roots

To confirm *Armillaria* root disease, cultures were made from wood or subcortical

mycelium aseptically removed from lesions, or from stained and decayed wood. Host tissues were initially cultured on Russell's basidiomycete medium (Russell 1956), Kuhlman's medium (1966), and Hutchinson's benomyl medium (Hutchinson unpubl: 2 mg /1 chlortetracycline HCL (Sigma), or 2 mg /1 penicillin G., 30 mg /1 streptomycin sulfate (Sigma), 4 mg /1 Benomyl (Benlate, 50% wettable powder (DuPont) to final concentration of 2 ppm). Samples of root tissue with *Armillaria* mycelial fans were also cultured on these three media to aid in the identification of *Armillaria* in culture and to determine if these selective media would inhibit rhizomorph production. Rhizomorph production provides an easy, macroscopic means for identifying *Armillaria* in culture (Morrison et al. 1991).

To isolate *Armillaria* from sample roots, wood chips were taken from sample roots and *Armillaria*-infected roots and placed onto four plates of each medium. Two plates of each medium were incubated at 20 C and two at 25 C for approximately three weeks, or until cultures produced rhizomorphs. After this time, cultures were examined macroscopically. *Armillaria* was identified by the presence of rhizomorphs and pseudosclerotial plates, and typical crustose appearance. Once it was determined that *Armillaria* cultures could be identified on all three media, only Russell's basidiomycete medium was used for subsequent isolations.

Pure cultures of *Armillaria* were obtained by extracting hyphal tips from the edge of cultures and transferring them onto 2% malt extract agar. These plates were incubated at 20 C. Pure cultures of *Armillaria* were then transferred into vials. Ten cultures were

selected at random and sent to Ken Mallett of the Canadian Forest Service, Northern Forestry Centre, in Edmonton, Alberta, Canada for species determination. *Armillaria* cultures were identified as *A. ostoyae* by vegetative compatibility tests with diploid North American Biological Species (NABS) testers (Mallett et al. 1989).

To calculate the proportion of the root system infected, the number of infected root segments was divided by the total number of root segments for that tree. If *Armillaria* was present on the root collar, the proportion of the circumference infected by the disease was determined. These percentages were calculated only from those roots with visible signs of *Armillaria*, or those where *Armillaria* isolates were obtained by culturing.

Determining basal area increment

Both five- and ten-year BAI were determined from increment cores collected from each sample tree. Cores were mounted and sanded using fine-grained sand paper. The prepared cores were then placed on a sliding bannister stage, and the ten most recent rings were measured using a dissecting scope, and a tree-ring incremental measuring system (TRIMSTM Madera Software, Tucson, AZ) with a Model 4 Digital Display unit (Fred C. Henson Co., Mission Viejo, CA). For calculating BAI, the widths for either the five or ten most recent rings were summed. This value was doubled, then subtracted from the tree's DBH to obtain an estimate of the tree's DBH five or ten years prior to the current year. The basal area of the tree five and ten years ago was calculated by multiplying the estimated DBH by the constant 0.000078545. Subtracting the five- or ten-year basal area from the current basal area gave the basal area increment for the last five or ten years.

Significant growth loss experienced by individual trees may go undetected by examining only differences in mean basal area increment of jack pine in dwarf mistletoe vigor classes. Some trees in each vigor class may have grown exceptionally well or poorly relative to other trees in the same vigor class. Therefore, the difference in the percentage of growth increment during the past five and ten years was determined for each tree. This value was calculated by first subtracting the five-year BAI from the ten-year BAI to determine the amount of increment from six to ten years. Then the six- to ten-year BAI was subtracted from the five-year BAI to determine the difference in increment between these two periods. This value was then divided by the six- to ten-year increment to determine the percent difference in growth increment between these two periods.

Data analysis

A number of relationships between jack pine vigor, dwarf mistletoe, and *Armillaria* root disease were examined using chi-square analysis of row by column proportions (Moore and McCabe 1989), and other nonparametric procedures including an odds ratio (θ) and Goodman and Kruskal's gamma measure of concordance (γ) (Agresti 1990).

A 95% confidence interval was used to determine the significance of values obtained for θ . If the value of 1 was contained within the confidence interval, the value of θ was not considered significant, and indicated no association between the variables tested.

Gamma was also used to test the strength of association between two variables. Values of gamma approaching 1, or $-1 \pm$ the asymptotic standard error, indicated a strong association between variables tested.

Small sample size, however, limited the power of chi-square analysis for detecting significant results. Because standard chi-square analysis does not accurately estimate P -values when some expected cell frequencies are small (Cochran 1954), an interactive program called CHITEST (Romesburg and Marshall 1985) was used to give a better estimate of the P -value. Romesburg and Marshall (1985) provide a complete explanation of the CHITEST program. In summary, to run CHITEST, cell frequencies from the observed table were entered into the program. CHITEST used a Monte Carlo method to generate a large number of tables having the same number of rows and columns and total frequency (N) as the observed table. For each table within this specified sample space, CHITEST calculated the expected cell frequencies. The N counts were allocated within each table in proportion to the expected cell frequencies. Because each table is randomly drawn from the defined sample space, the marginal distributions generally do not equal those of the observed table. CHITEST computes a chi-square value for each table, computes the mean chi-square value of all tables, and estimates the P -value. This P -value is the proportion of all tables generated having chi-square values greater than, or equal to the observed table. A large P -value indicates that a small proportion of tables deviates from the null hypothesis as much, or more than the observed table. The chi-square value and P -value obtained from the observed table are accurate. A small P -value indicates that a large proportion of tables deviates from the null hypothesis as much, or more, than the observed table, and that the chi-square value and P -value obtained from the observed table are inaccurate.

Variables used in regression analysis and ANOVA, including the number of root segments, basal area, five- and ten-year BAI, percent difference in BAI, and percentage of *Armillaria* colonization were tested for normality and equality of variance. All variables with the exception of percent *Armillaria* colonization and BAI were normally distributed. An arcsin transformation was used to normalize percent *Armillaria* colonization data for analysis, and BAI data were normalized by using a \log_{10} transformation.

Associations between jack pine vigor and the incidence and extent of Armillaria root disease

Contingency table analyses, including chi-square analysis and gamma, were used to examine relationships between jack pine vigor and the incidence of *Armillaria* colonization. Vigorous, declining, and recently dead jack pine were categorized according to the presence, or absence of *Armillaria*. Obtaining a significant chi-square value would indicate that the proportions of *Armillaria*-infected jack pine within each dwarf mistletoe vigor class were not equal, and that a relationship existed between these two variables. A significant value of gamma would indicate that jack pine with low vigor tended to have greater incidence of *Armillaria* colonization.

Chi-square analysis and gamma were also used to measure the strength of association between jack pine vigor and the extent of *Armillaria* colonization. For these analyses, four levels of *Armillaria* colonization were compared within each jack pine vigor class. These levels were uninfected (0% colonization), low (1-20% colonization), moderate (21-60% colonization), and high (> 60% colonization), and were representative of the

distribution of percentages of *Armillaria* colonization obtained from sample trees. If less vigorous trees were more susceptible to aggressive *Armillaria* colonization, then a larger proportion of declining and dead trees was expected to have high percentages of root system colonization. Again, gamma would indicate that low vigor is associated with extensive *Armillaria* colonization.

Because reduced growth is indicative of stress induced by dwarf mistletoe, or other agents of decline, trees with low BAI were expected to have more root system colonization by *Armillaria*. Relationships between the extent of *Armillaria* colonization and five- and ten-year BAI were determined by simple regression analysis (Moore and McCabe 1989). Values of r^2 obtained from this analysis were used to determine how much variability in percent *Armillaria* colonization could be explained by its relationship with BAI. A strong negative relationship between BAI and percent *Armillaria* colonization would suggest that slowly growing trees were more extensively colonized by *Armillaria*.

Percent difference in BAI was used as another means to assess tree vigor. A tree with a positive percentage grew more during the most recent five years than during the previous five-year period, suggesting good vigor. A negative percentage of growth increment was assumed to indicate reduced tree vigor. Chi-square analysis was used to examine associations between positive and negative percentages of growth increment, and the incidence of *Armillaria*. *Armillaria* was expected to have colonized a larger proportion of jack pine with negative percentages of growth increment than trees with

positive percentages of growth increment.

Effects of dwarf mistletoe on the incidence of Armillaria and the extent of Armillaria colonization

Nonparametric procedures and two-way analysis of variance were used to determine the effect of dwarf mistletoe infestation on both the incidence of *Armillaria* and the extent of root system colonization. Odds ratios (θ) were computed from 2 x 2 contingency tables of the incidence of both disease agents for vigorous and declining trees. A value for θ could not be calculated for dead jack pine because all trees were colonized by *Armillaria*. High values of θ would indicate that jack pine had greater odds of being infected by both dwarf mistletoe and *Armillaria*, than of being infected by either disease agent alone.

Two-way analysis of variance was used to determine if the incidence of dwarf mistletoe significantly affected the mean percentage of *Armillaria* colonization within each jack pine vigor class. If the percentage of *Armillaria* colonization increased significantly with dwarf mistletoe infestation, then dwarf mistletoe-infested jack pine within each vigor class would have greater mean percentage of *Armillaria* colonization than uninfected trees. Only vigorous and declining trees were included in the analysis of differences in mean percentage of *Armillaria* colonization because all dead trees were completely colonized by *Armillaria*. Contrasts between means were examined by using Tukey's multiple range test (Moore and McCabe 1989).

The amount of dwarf mistletoe infesting individual jack pine was variable. Trees

experiencing stress induced by heavy dwarf mistletoe infestation were expected to have greater incidence of *Armillaria*. Chi-square and gamma values were computed from a contingency table with uninfected (DMR = 0), low (DMR = 1, 2), moderate (DMR = 3, 4), and high (DMR = 5, 6) levels of dwarf mistletoe infestation by the presence or absence of *Armillaria*. The same analyses were used to examine associations between the extent of dwarf mistletoe infestation and the percentage of root system colonization by *Armillaria*. If heavy dwarf mistletoe infestation caused significant decline, jack pines with high DMR's were expected to have higher percentages of root system colonization by *Armillaria* than uninfested, or lightly infested trees.

Associations between dwarf mistletoe infestation and jack pine vigor

Contingency table analysis was used to examine the effect of dwarf mistletoe infestation on jack pine vigor. A chi-square value and gamma were obtained from a 2 x 3 table with presence or absence of dwarf mistletoe by jack pine vigor class. A large chi-square value would indicate that the proportion of jack pine infested with dwarf mistletoe in each vigor class was not equal, suggesting a relationship between these two variables. A significant value of gamma would indicate that jack pine with low vigor tended to be infested with dwarf mistletoe.

To determine how the extent of dwarf mistletoe infestation affected jack pine vigor, the same analyses were conducted using the four levels of dwarf mistletoe infestation described above. A one-way ANOVA was also used to determine if the mean DMR for

trees in each vigor class differed significantly. If heavy dwarf mistletoe infestation was associated with decline, declining and dead trees would have higher mean DMR's than vigorous trees. Because of the small sample size, however, the power of this test for detecting significant differences was low.

Analyses of the number of roots by jack pine vigor, dwarf mistletoe, and Armillaria root disease

Preliminary examination of data collected for each jack pine indicated that vigorous trees had more roots within the 1 m area surrounding the bole than either declining, or dead trees. Analyses were done to explore relationships between the number of roots, jack pine vigor, dwarf mistletoe, and Armillaria root disease. Two-way analysis of variance was employed to determine if the mean number of jack pine roots differed significantly between trees in each vigor class, and to determine if either Armillaria root disease or dwarf mistletoe significantly affected the means in each vigor class. Contrasts between means were examined using Tukey's multiple range test. Strengths of relationships between the number of roots and BAI were determined by simple regression analysis.

RESULTS

A total of 252 jack pine was surveyed within three dwarf mistletoe mortality centers. Table 1 gives the percentage of vigorous, declining, and recently dead jack pines in dominant/codominant and intermediate crown classes. Thirty-eight percent of vigorous trees were infected with dwarf mistletoe. The percentages of declining and recent dead trees infected with dwarf mistletoe were 49% and 60%, respectively (Table 1). The root systems of 46 dominant and codominant trees, and 12 intermediate trees were excavated and examined for signs and symptoms of *Armillaria* root disease. Lateral roots with *Armillaria* often had resinous, soil-encrusted lesions, and colonized portions of live roots distal to these lesions. Rhizomorphs were sometimes found embedded within the resin-soil matrix. Typical advanced decay and mycelial fans were present.

Approximately 45% of sampled jack pine were infected with *Armillaria* root disease, and on those trees, the proportion of root system colonized ranged from 2.1-100%. *Armillaria* had completely colonized the root systems of all eight dead trees, and one declining tree (Fig. 4). These trees had mycelial fans present on both the taproot and root collar. Both *Armillaria* root disease and dwarf mistletoe were present on 28% of the jack pines sampled. Of dwarf mistletoe-infected jack pine, 49% had *Armillaria*.

Associations between jack pine vigor and the incidence and extent of Armillaria root disease

Both the incidence of *Armillaria* root disease (Table 2) and the extent of root system

colonization by *Armillaria* (Table 3) were strongly associated with jack pine vigor assessed by visual criteria. CHITEST analysis of the incidence of *Armillaria* and extent of root system colonization by tree vigor gave small probabilities of obtaining a chi-square value larger than the observed table. The observed chi-square values (18.67, and 51.76) were not consistent with the null hypothesis of homogeneity of row by column proportions. As vigor decreased, a greater proportion of trees and roots was infected by *Armillaria*. Other nonparametric analysis (gamma) showed that the incidence of *Armillaria* and extent of root system colonization tended to increase as vigor decreased, supporting the results given by CHITEST analysis.

TABLE 1. Number of vigorous, declining, and recent dead dominant, codominant, and intermediate jack pine surveyed along transects of three selected dwarf mistletoe (DM) mortality centers

Vigor class	Percentage of trees in each crown class ^a		Total	Percentage of trees infected with DM
	D / C	I		
Vigorous	87%	49%	196	75 (38%)
Declining	11%	41%	46	22 (49%)
Recent Dead	2%	10%	10	6 (60%)
Total	191	61	252	103 (41%)
Percentage of trees infected with DM	82 (43%)	21 (34%)		

^aD, dominant trees; C, codominant trees; I, intermediate trees.

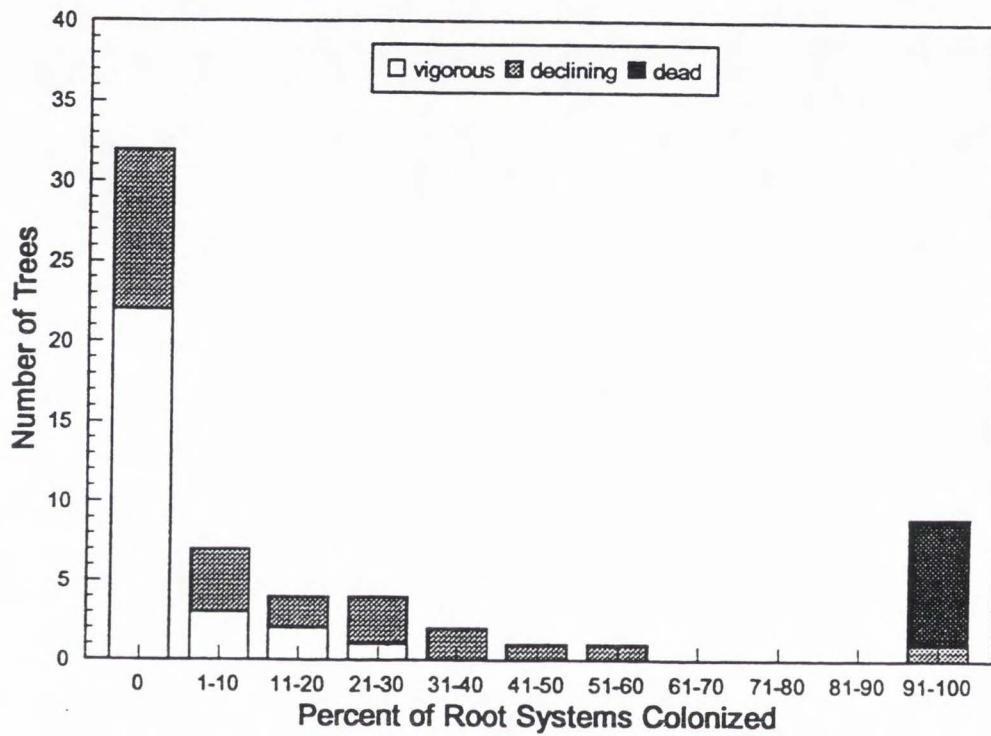


FIG. 4. Colonization of jack pine root systems by *Armillaria*. Mycelial fans were also present at the root collar of all jack pine with 91-100 % root system colonization.

TABLE 2. Association between the incidence of *Armillaria* root disease and jack pine vigor^a

<i>Armillaria</i> infection	Number of trees in each vigor class			Total
	Vigorous	Declining	Dead	
+	5.0 (12.1)	13.0 (10.3)	8.0 (3.6)	26
-	22.0 (14.9)	10.0 (12.7)	0.0 (4.4)	32
Total	27	23	8	58

NOTE: Expected cell frequencies given in parentheses.

^aChi-square value of the observed table, 18.7 ($P = 0.000$); CHITEST mean chi-square value, 2.04 ($P \geq$ observed table, 0.000), $n = 10,000$; $\gamma = -0.831 \pm 0.184$.

TABLE 3. Association between the extent of *Armillaria* colonization and jack pine vigor^a

Extent of colonization	Number of trees in each vigor class			Total
	Vigorous	Declining	Dead	
Uninfected	22 (15.2)	10 (12.4)	0 (4.5)	32
Low (0 < 20%)	4 (4.3)	5 (3.5)	0 (1.3)	9
Med (21% < 60%)	1 (2.8)	5 (2.3)	0 (0.8)	6
High (61% < 100%)	0 (4.7)	2 (3.9)	8 (1.4)	10
Total	27	22	8	57

NOTE: Expected cell frequencies in parentheses. Fifty-seven trees were used in this analysis.

^aChi-square value of the observed table, 51.76 ($P = 0.000$); CHITEST mean chi-square value, 6.07 ($P \geq$ observed table, 0.000), $n = 10,000$; $\gamma = 0.848 \pm 0.156$.

The effect of dwarf mistletoe on the incidence of Armillaria and the extent of Armillaria colonization

Given the present understanding of both dwarf mistletoe and *Armillaria* biology, ecology, and host effects, relationships between these two disease agents in the Belair Provincial Forest seemed likely. However, associations were not apparent in the field during data collection. Examination of transect maps suggested a random distribution of *Armillaria* (Appendix A). For example, some jack pine with extensive brooms, sparse foliage, and stunted growth had root systems with no signs of *Armillaria* or other decay fungi. Other trees, with little or no dwarf mistletoe, had visual symptoms of decline, and at least 25% root system colonization by *Armillaria*.

Contingency table analysis provides no evidence of a relationship between the incidence of dwarf mistletoe and the incidence of *Armillaria* (Table 4). The same tests conducted to examine the strength of association between the incidence of dwarf mistletoe and *Armillaria* within vigorous and declining classes of trees yielded similar results (Tables 5 and 6, respectively). All eight dead trees were colonized by *Armillaria*; consequently, no chi-square statistic, odds ratio, or gamma was computed for this vigor class.

Although no associations were detected between the incidence of both disease agents, dwarf mistletoe-infested trees were expected to have more *Armillaria* colonization than uninfested trees. Figure 5 shows the mean percentage of *Armillaria* colonization on roots of dwarf mistletoe-infested trees and -uninfested trees by vigor class.

TABLE 4. Association between the incidence of *Armillaria* root disease and dwarf mistletoe infection for all jack pine sampled*

Incidence of <i>Armillaria</i>	Incidence of dwarf mistletoe		Total
	+	-	
+	16 (14.8)	10 (11.2)	26
-	17 (18.2)	15 (13.8)	32
Total	33	25	58

NOTE: Expected cell frequencies in parentheses.

*Chi-square value of the observed table, 0.414 ($P = 0.520$); CHITEST mean chi-square value, 3.0 ($P \geq$ observed table, 0.94), $n = 10,000$; $\gamma = 0.171 \pm 0.522$; $\theta = 1.412$, 95% confidence bounds (0.493, 4.042).

Two-way ANOVA indicated that the mean percentage of *Armillaria* colonization was significantly greater in declining jack pine than vigorous jack pine (Table 7). The incidence of dwarf mistletoe had no significant effect on percent *Armillaria* colonization within each vigor class, and there was no significant interaction.

Gamma indicated that increasing levels of DMR were weakly associated with increased incidence of *Armillaria*. However, the chi-square value of the observed table and P -value given by CHITEST was consistent with the null hypothesis of homogeneity of row by column proportions (Table 8).

Associations between jack pine vigor as measured by BAI and both disease agents

Basal area increment varied significantly with tree vigor (Table 9). Vigorous trees had greater mean five- and ten-year BAI than either declining or dead trees. No significant

TABLE 5. Association between the incidence of *Armillaria* and dwarf mistletoe in vigorous jack pine sampled^a

Incidence of <i>Armillaria</i>	Incidence of dwarf mistletoe		Total
	+	-	
+	3	2	5
-	12	10	22
Total	15	12	27

^a $\gamma = 0.111 \pm 0.996$; $\theta = 1.25$, 95% confidence bounds (0.173, 9.019).

TABLE 6. Association between the incidence of *Armillaria* and dwarf mistletoe in declining jack pine sampled^a

Incidence of <i>Armillaria</i>	Incidence of dwarf mistletoe		Total
	+	-	
+	8	5	13
-	5	5	10
Total	13	10	23

^a $\gamma = 0.231 \pm 0.806$; $\theta = 1.60$, 95% confidence bounds (0.302, 8.490).

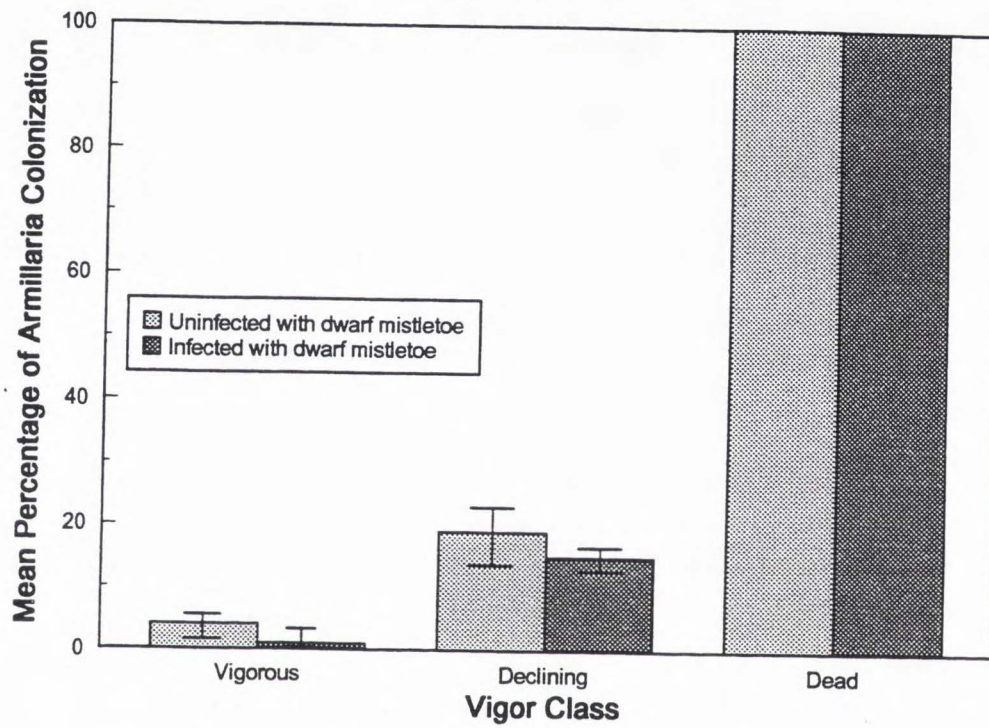


FIG. 5. Mean percentage of *Armillaria* on jack pine roots by host vigor class.

TABLE 7. Effects of jack pine vigor and dwarf mistletoe infection on the percentage of *Armillaria* colonization^a

Source ^b	df	MS	F	p > F
V	1	0.808	9.34	0.004
I	1	0.011	0.13	0.722
V * I	1	0.001	0.01	0.915
Error	46	0.087		

NOTE: Only vigorous and declining trees were analyzed ($n = 50$). Mean percentage of *Armillaria* colonization for vigorous and declining trees, 2.0% and 17.0%, respectively.

^aPercentage of *Armillaria* colonization was normalized using an arcsin transformation.

^bV, jack pine vigor class; I, the presence or absence of dwarf mistletoe.

TABLE 8. Association between the incidence of *Armillaria* and the extent of dwarf mistletoe^a

Incidence of <i>Armillaria</i>	DMR ^b				Total
	0	1-2	3-4	5-6	
+	10 (11.2)	4 (5.4)	5 (4.5)	7 (4.9)	26
-	15 (13.8)	8 (6.6)	5 (5.5)	4 (6.1)	32
Total	25	12	10	11	58

NOTE: Expected cell frequencies in parentheses.

^aChi-square value of the observed table, 2.56 ($P = 0.465$); CHITEST mean chi-square value, 7.04 ($P \geq$ observed table, 0.932), $n = 10,000$; $\gamma = -0.243 \pm 0.392$.

^bSix-class dwarf mistletoe rating system.

differences in mean five- and ten-year BAI were found between declining and dead trees.

The results of analysis to examine relationships between the percentage of *Armillaria* colonization and BAI were inconclusive. Scatterplots of five- and ten-year BAI and the percentage of *Armillaria* colonization revealed an apparent relationship between these two variables (Figs. 6 and 7, respectively). However, simple regression analysis of percent *Armillaria* colonization and BAI gave r^2 values of 0.07, 0.05 for five- and ten-year BAI, respectively. Other analysis of these data has been considered to examine potential relationships further.

The difference between one- to five- and six- to ten-year BAI percentage calculated for all jack pine sampled was highly variable. Values ranged from 183% more increment growth, to 70% less increment growth during the past five-year period as compared with the previous five-year period. Forty-four percent of vigorous jack pine grew less during the past five-year period, but the average tree had 2% positive mean growth

TABLE 9. Comparisons of mean five- and ten-year basal area increment (BAI 5, and BAI 10, respectively) for vigorous, declining, and recently dead jack pine sampled in the three selected dwarf mistletoe mortality centers^a

Vigor class	<i>n</i>	BAI 5 (m ²)	BAI 10 (m ²)
Vigorous	27	0.0019 (0.0013) <i>a</i>	0.0036 (0.0024) <i>a</i>
Declining	23	0.0007 (0.0005) <i>b</i>	0.0017 (0.0011) <i>b</i>
Dead	8	0.0005 (0.0003) <i>b</i>	0.0014 (0.0009) <i>b</i>
All trees	58	0.00012 (0.0011)	0.0025 (0.0021)

NOTE: Means (with standard deviations given in parentheses) followed by the same letter are not significantly different (Tukey's studentized range test, $P \leq 0.05$).

^aBasal area increment data normalized using a \log_{10} transformation.

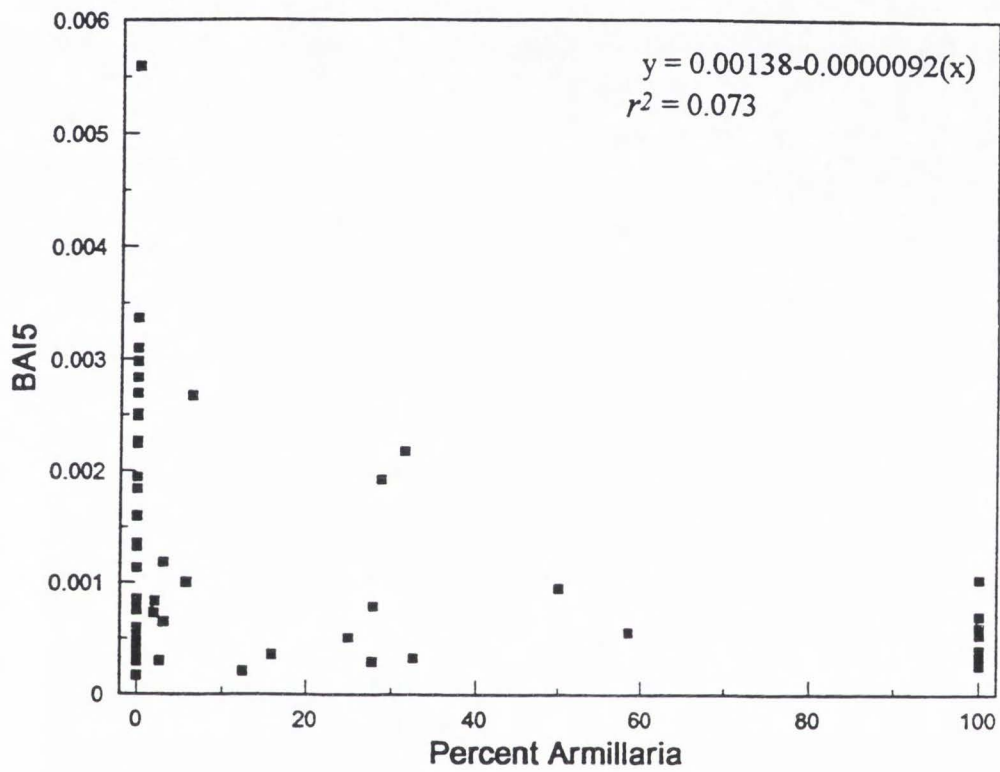


FIG. 6. Five-year BAI in relation to percent *Armillaria* colonization.

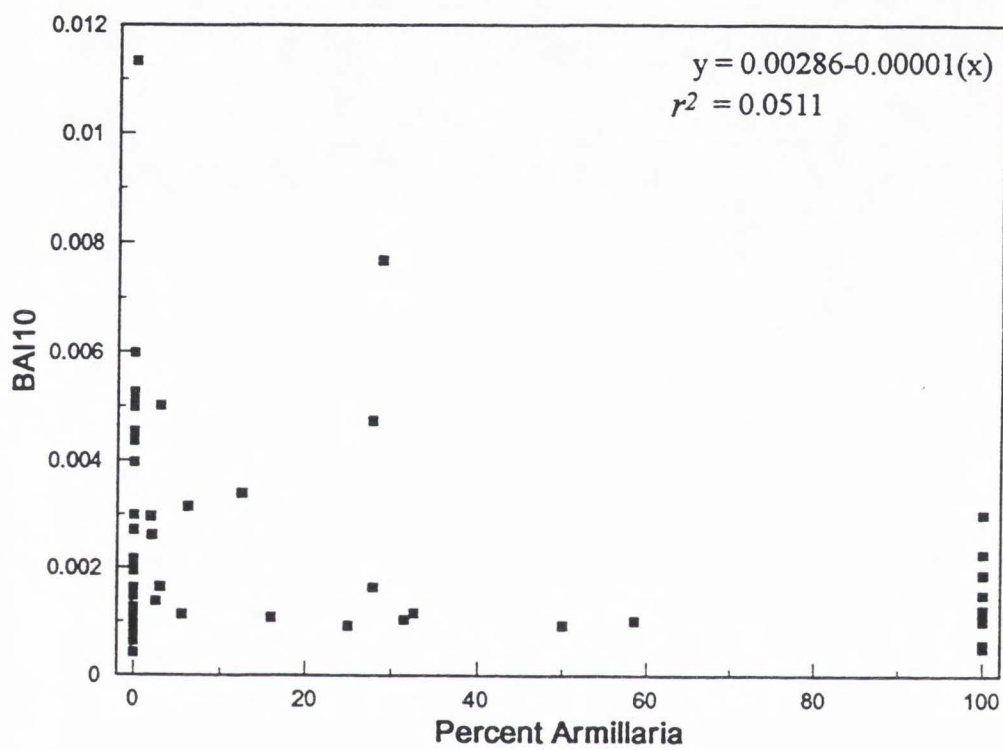


FIG. 7. Ten-year BAI in relation to percent *Armillaria* colonization.

TABLE 10. Association between percentages of growth increment and the incidence of *Armillaria* root disease for all jack pine sampled^a

Growth	Incidence of <i>Armillaria</i>		Totals
	+	-	
+	6 (9.0)	14 (11.0)	20
-	20 (17.0)	18 (21.0)	38
Totals	26	32	58

NOTE: Expected cell frequencies in parentheses.

^aChi-square value, 2.71, df = 1, ($P = 0.10$).

TABLE 11. Association between percentages of growth increment and the incidence of *Armillaria* root disease for dominant and codominant jack pine sampled^a

Growth	Incidence of <i>Armillaria</i>		Totals
	+	-	
+	4 (7.0)	13 (10.0)	17
-	15 (12.0)	14 (17.0)	29
Totals	19	27	46

NOTE: Expected cell frequencies in parentheses.

^aChi-square value, 3.5; df = 1; $P = 0.07$.

increment (sd = 33, Median = 1%). Eighty-four percent of declining and dead jack pine sampled grew less during the past five-year period, with 23% decrease in mean growth increment (sd = 32, Median = 31%).

Chi-square analyses of the association between growth increment and the incidence of *Armillaria* for all jack pine sampled ($P = 0.10$), and for dominant and codominant trees only ($P = 0.07$), suggest that a small proportion of jack pine has both positive growth increment and *Armillaria* (Tables 10 and 11, respectively). Unexpectedly, the numbers of uninfected trees with either positive or negative percent increment growth, and infected trees with negative percent increment growth were approximately equal. These results may suggest that *Armillaria* randomly attacked jack pine in dwarf mistletoe subsequent colonization.

The incidence of dwarf mistletoe also had no effect on the mean five- and ten-year BAI for trees within each vigor category (Tables 12 and 13, respectively). However, one-way analysis of variance to determine mean differences in BAI between uninfected, low, moderate, and high levels of DMR provided evidence that trees with DMR's ≥ 5 had significantly reduced tree growth (Tables 12 and 13, respectively). Small sample size greatly reduced the power of this test for detecting significant results.

Dwarf mistletoe associations with tree vigor

Deleterious effects of dwarf mistletoe infestation on jack pine varied. Contingency table analysis revealed no relationship between the incidence of dwarf mistletoe and tree

TABLE 12. Analysis of the effects of jack pine vigor and the incidence and extent of dwarf mistletoe on mean five-year basal area increment (BAI 5)

	BAI 5 (m ²)				
	Source ^a	df	MS	F	p > F
1. Effects of vigor and the incidence of dwarf mistletoe (+/-) on mean 5 year BAI.					
	V	2	1.088	9.92	0.000
	I	1	0.055	0.50	0.483
	V * I	2	0.040	0.37	0.694
	Error	52	5.701		
2. Effects of vigor and the extent of dwarf mistletoe on mean 5 year BAI (DMR = 0, 1-2, 3-4, 5-6).					
	V	2	0.617	5.62	0.007
	I	3	0.175	1.60	0.203
	V * I	5	0.071	0.65	0.664
	Error	47	5.163		

NOTE: Basal area increment data were normalized by using a log₁₀ transformation.

^aV, jack pine vigor class; I, dwarf mistletoe infection.

TABLE 13. Analysis of the effects of jack pine vigor and the incidence and extent of dwarf mistletoe on mean ten-year basal area increment (BAI 10)

	BAI 10 (m ²)				
	Source ^a	df	MS	F	P > F
1. Effects of vigor and the incidence of dwarf mistletoe (+/-) on mean 10 year BAI.					
	V	2	0.730	8.15	0.001
	I	1	0.129	1.44	0.236
	V * I	2	0.036	0.41	0.669
	Error	52	0.090		
2. Effects of vigor and the extent of dwarf mistletoe on mean 10 year BAI (DMR = 0, 1-2, 3-4, 5-6).					
	V	2	0.384	4.41	0.018
	I	3	0.167	1.92	0.139
	V * I	5	0.089	1.02	0.417

NOTE: Basal area increment data were normalized by using a log₁₀ transformation.

^aV, jack pine vigor class; I, dwarf mistletoe infection.

vigor (Table 14). However, both chi-square and CHITEST analysis suggest that a higher proportion of vigorous trees are associated with low DMR (Table 15). A larger sample might have increased the power of these tests for detecting potential relationships between jack pine vigor and dwarf mistletoe.

*Analysis of the number of roots by
jack pine vigor, dwarf mistletoe,
and Armillaria root disease*

Two-way ANOVA indicated that vigorous trees had significantly more roots than either declining or dead trees (Table 16). The mean number of roots within each vigorclass did not vary significantly between trees infected by either dwarf mistletoe, or *Armillaria* (Table 17). The number of roots was moderately correlated with both five- and ten-year BAI ($r^2 = 0.43$ and $r^2 = 0.45$, respectively). These results suggest that jack pine growth and vigor are related to root system condition.

The lack of association between the number of roots, and dwarf mistletoe and *Armillaria* root disease may have been misleading. Seventy-one percent of the declining and recently dead jack pines sampled had fewer than the average number of roots. Thirty-seven percent of the vigorous jack pine sampled had fewer than the average number of roots for all trees sampled. These vigorous trees had no signs of *Armillaria* root disease in the portion of the root system examined, and little dwarf mistletoe (\bar{x} DMR = 1). Of declining and recently dead trees with more than the average number of roots for all trees sampled, six of nine had more than 28% *Armillaria* colonization, or were heavily infected

TABLE 14. Association between jack pine vigor and dwarf mistletoe infection^a

Dwarf mistletoe	Number of trees in each vigor class			Total
	Vigorous	Declining	Dead	
+	15 (15.4)	13 (13.1)	5 (4.6)	33
-	12 (11.6)	10 (9.9)	3 (3.4)	25
Total	27	23	8	58

NOTE: Expected cell frequencies in parentheses.

^aChi-square value of the observed table, 0.124 ($P = 0.94$); CHITEST mean chi-square value, 2.04 ($P \geq$ observed table, 1.00), $n = 10,000$; $\gamma = -0.064 \pm 0.46$.

TABLE 15. Association of jack pine vigor and the extent of dwarf mistletoe^a

DMR ^b	Number of trees in each vigor class			Total
	Vigorous	Declining	Dead	
0	12 (11.6)	10 (9.9)	3 (3.4)	25
1-2	8 (5.6)	4 (4.8)	0 (1.7)	12
3-4	6 (4.7)	1 (4.0)	3 (1.4)	10
5-6	1 (5.1)	8 (4.4)	2 (1.5)	11
Total	27	23	8	58

NOTE: Expected cell frequencies in parentheses.

^aChi-square value of the observed table, 13.903 ($P = 0.031$); CHITEST mean chi-square value, 6.142, ($P \geq$ observed table, 0.030), $n = 10,000$; $\gamma = 0.227 \pm 0.316$.

^bSix-class dwarf mistletoe rating system.

TABLE 16. Mean comparisons of the number of root segments for vigorous, declining, and dead jack pine sampled in the three selected dwarf mistletoe mortality centers

Vigor class	<i>n</i>	Root segments
Vigorous	27	51 (18.8) <i>a</i>
Declining	23	35 (14.3) <i>b</i>
Dead	8	30 (13.4) <i>b</i>
All trees	58	43 (18.6)

NOTE: Means (with standard deviations in parentheses) followed by the same letter are not significantly different (Tukey's studentized range test, $P \leq 0.05$).

TABLE 17. The mean number of root segments for trees uninfected or infected by dwarf mistletoe and for trees uninfected or infected by *Armillaria*

Mean number of root segments	
<i>Armillaria</i>	
+	40a
-	44a
Dwarf mistletoe	
+	43a
-	42a

NOTE: Means followed by the same letter are not significantly different (Tukey's studentized range test, $P \leq 0.05$).

with dwarf mistletoe (DMR = 5, 6) (Appendix B). These data suggest that vigorous trees with more roots than average remain vigorous until they become weakened by high levels of stress caused by abiotic or biotic factors. Trees with fewer roots than average may be vigorous, but can succumb to the effects of stress more rapidly.

DISCUSSION

Effects of heavy dwarf mistletoe infestation on host vigor have been reported in numerous studies (Hawksworth 1958; Hawksworth and Hinds 1964; Baranyay 1970; Hawksworth and Shaw 1984; Moody and Amirault 1992). Throughout the Belair provincial forest, dwarf mistletoe was believed to weaken infested jack pine, increasing their susceptibility to *Armillaria* root disease. Dwarf mistletoe-infested trees exhibiting poor color, sparse foliage, and reduced growth were expected to have both higher incidence of *Armillaria* attack and greater root system colonization. The incidence of *Armillaria* attack and the percentage of root system colonization were also expected to increase with heavy dwarf mistletoe infestation.

My study shows that jack pine heavily infested with dwarf mistletoe experienced reduced growth and were less vigorous than uninfested or lightly infested trees. As hypothesized, strong associations were found between *Armillaria* root disease and trees with visible symptoms of decline and mortality. Effects of dwarf mistletoe infestation on either the incidence of *Armillaria* or the percentage of root system colonization were not detected. The small sample size limited the power of some statistical tests for detecting significant associations between dwarf mistletoe and *Armillaria*. Methods used to categorize trees, assess the impact of dwarf mistletoe, and determine the extent of *Armillaria* colonization may also explain some of the contradiction in the results. Finally, root system condition and other growth-related factors could have masked the effect of *Armillaria*, dwarf mistletoe, or both disease agents on jack pine vigor and growth. The

potentially confounding effects of each of these factors are discussed below.

Tree categorization

The categorization of trees was based on the assumption that dwarf mistletoe infestation was primarily responsible for visible symptoms of decline. Careful measures were taken to control for other factors having the potential to influence jack pine vigor and subsequently crown condition. The effect of any factor that causes decline and subsequently influences crown condition might have confounded the categorization of jack pine. *Armillaria* root disease itself can produce crown symptoms similar to dwarf mistletoe. As *Armillaria* develops throughout the root systems of infected trees, the foliage gradually becomes chlorotic, stunted, and sparse (Morrison et al. 1991). These symptoms could explain the strong association observed between *Armillaria* root disease and jack pine vigor as assessed by foliage color and density. In studies of growth loss and mortality in Douglas-fir associated with laminated root rot, Bloomberg and Reynolds (1988) noted that categorizing trees using visual symptoms may give unreliable results, especially when attempting to assess the severity of a disease or its effects on host vigor. They found that declining trees actually had greater radial increment than healthy trees on the same plot (Bloomberg and Reynolds 1988).

Assessing the impact of dwarf mistletoe

Several dwarf mistletoe rating systems have been developed that quantify the degree of dwarf mistletoe infestation, and provide an estimate of potential growth loss and

mortality (Hawksworth 1977). Several criteria have been used in these systems to assess the severity of infestations and impact on host trees. To consolidate the various rating systems, and to reduce their subjectivity, Hawksworth (1977) developed the six-class dwarf mistletoe rating system, which has become the most generally applied method for quantifying dwarf mistletoe impacts in the western United States and Canada.

Although the system has been shown to work well for some tree species, including southwestern ponderosa pine (Hawksworth and Johnson 1989) and Rocky Mountain lodgepole pine (Hawksworth 1961), the six-class dwarf mistletoe rating system has two shortcomings. The first is that it does not directly account for the degree of brooming, especially in host/ parasite combinations where the majority of infections develop into systemic brooms (Hawksworth 1977). Consequently, broomed trees are often underrated. Studies have shown that extensive brooming causes significant loss of growth in trees, and decline in vigor. In Newfoundland, Singh and Carew (1989) found that heavily broomed black spruce had significantly reduced diameter growth as compared to non-broomed trees. All dead black spruce with dwarf mistletoe brooms were killed prematurely (Singh and Carew 1989). With ponderosa pines of the same infection class, Hawksworth (1961) found similar results. In another study, pruning large brooms from the lower portions of infected ponderosa pine was shown to improve the vigor of trees and increase their longevity (Lightle and Hawksworth 1973).

Conversely, this rating system tends to overrate trees with numerous light infections, because it only considers the proportion of the crown that is infected, not the type of

infection (Hawksworth 1977). In ponderosa pine and lodgepole pine, heavy infections located in the lower portion of the crown, or light infections distributed throughout the crown, do not always cause a large reduction in growth and an increase in mortality (Parmeter 1978).

For these reasons, in the mortality centers I studied, the six-class dwarf mistletoe rating system might be sensitive to the varied impacts of different types of dwarf mistletoe that infects individual jack pines. This could account for why my observations differed from those of Baranyay and Safranyik (1970). They found that lodgepole pine with individual branch swellings experienced reductions in diameter growth similar to those observed in heavily broomed trees of like dwarf-mistletoe-infection classes, whereas in jack pine, I observed large differences in growth that were a function of the size and number of brooms, of branch swellings, and of the location of infections. On the one hand, the entire crown of severely stunted trees typically consisted of one or two large, dense brooms; on the other hand, some dominant or codominant trees had numerous local infections throughout their crowns. When assigning a dwarf mistletoe rating to each tree, however, I made no attempt to differentiate between types of infection, or to record the exact numbers and locations of infections within tree crowns. I assigned the same DMR to trees with numerous local infections in the crown as I did to trees with one or two dense brooms, even though the effect of the infection on tree growth and vigor was obviously quite different. Therefore, this argues for a decreased likelihood of detecting potential associations between dwarf mistletoe infection and *Armillaria* root disease.

The second shortcoming of the six-class dwarf mistletoe rating system is that in instances where dwarf mistletoe causes rapid decline and mortality, the ratings do not always relate to the severity of the disease. I did not study the spread of *A. americanum* and rates of disease intensification and mortality in jack pine. However, tree damage and extensive mortality appeared to have occurred rapidly in infected stands.

Generally, the DMR of an infected tree increases by one severity class in approximately 15 years (Hawksworth and Johnson 1989). This rate of disease intensification agrees with *A. americanum* infecting lodgepole pine (Hawksworth and Johnson 1989), and *A. cryptopodum* (Engelm.) infecting ponderosa pine (Hawksworth and Geils 1990). These western dwarf mistletoe species, however, appear to kill trees slowly. In lodgepole pine, prior to mortality, the intensification of dwarf mistletoe with time causes detectable loss of growth (Hawksworth 1961). For light to moderately infected (DMR = 2, 3) ponderosa pines, it took dwarf mistletoe approximately 57 years to kill 50% of these trees (Hawksworth and Geils 1990). In comparison, Baker and French found that *A. pusillum* more rapidly kills infected black spruce: Specifically, they found only small differences between the mean diameter growth of dwarf mistletoe-infected black spruce and uninfected trees. This was interpreted to suggest that black spruce dwarf mistletoe killed trees before their diameter growth differed from uninfected trees. Using a disease model based on compound interest, Baker and French (1980) also estimated that in 8.3 years, black spruce dwarf mistletoe kills 50% of the infected trees. After 17 years following infection, nearly 75% tree mortality results. In sum, for black spruce, the rate

of dwarf mistletoe-induced mortality is more rapid than that predicted from DMR, specifically by one DMR severity class.

Arceuthobium americanum also appears to kill jack pine rapidly, particularly when the incidence and intensity of the infestation are severe. Seventy years was the mean age of jack pine sampled in dwarf mistletoe mortality centers. Using DMR to predict the rates of dwarf mistletoe intensification and mortality of jack pine after 70 years, I would expect to observe only those trees initially infected by dwarf mistletoe to have DMRs as high as 5 or 6. I would also expect to observe little tree mortality. However, I observed that in 70 years, dwarf mistletoe had killed sufficient numbers of jack pine to create large, expanding openings within the forest canopy. Surviving trees within these openings mostly had DMRs of 4 to 6. This observation is similar to the level of infestation and the percentage of mortality caused by *A. pusillum* in black spruce in Newfoundland (Singh and Carew 1989). Mean ages of black spruce in these stands ranged from 72 to 76 years. Most infestation levels fell within the range of DMRs of 4 to 5, with mortality averaging 20 to 38%.

Also indicative of the severity of this disease in jack pine is the rapid death of uninfected portions of tree crowns in dwarf mistletoe-infected trees. Some trees with low to moderate DMRs had large, vigorous brooms as indicated by their good foliage color and needle retention. However, uninfected portions of the crowns of these same trees had sparse foliage with poor color. As with other dwarf mistletoe species, this suggests that the diversion of photosynthates, water, and other nutrients to dwarf mistletoe infections

produced severe decline and mortality in uninfected portions of the crowns (Singh and Carew 1989). Because these trees had surviving brooms and large losses in the uninfected crowns, they could have been assigned inflated DMRs. These observations indicate again that the six-class dwarf mistletoe rating system might not be the best method for quantifying the impacts of dwarf mistletoe on infected jack pine.

Determining the extent of Armillaria colonization

Obtaining *Armillaria* isolates from resin-impregnated, or extremely decadent root tissue was difficult. *Armillaria* confirmation was based solely on culture appearance and rhizomorph production. The possibility exists that some *Armillaria* isolates did not produce rhizomorphs in culture or develop characteristics unique to the fungus. Without these characteristics, fungal isolates were not considered to be *Armillaria*. Consequently, the actual percentage of jack pine and jack pine roots infected with *Armillaria* root disease may have been greater in some cases.

Confounding effects of root system condition and other growth-related factors

Extensive functional root systems may help trees tolerate stress-inducing agents (Bloomberg and Reynolds 1985). Dieback in older stands of jack pine attributed to drought and jack pine budworm was more dramatic in trees with less developed lateral and vertical root systems (MacAloney 1944). Following jack pine budworm defoliation, Mallett and Volney (1990) found that dead jack pine or top-killed trees had significantly reduced radial growth. Healthy trees had greater annual volume increment, and larger

root volumes and root weights than trees with dead tops or dead trees. The authors speculated that trees with smaller root volume and root weight did not have adequate food reserves to recover from defoliation easily, leaving them vulnerable to attack by *Armillaria* (Mallett and Volney 1990). Even with 50-60% of their root system infected by decay fungi, balsam fir with extensive root systems were able to maintain growth increment (Whitney and MacDonald 1985).

I found that vigorous jack pine in the three mortality centers sampled had significantly more roots than either declining or dead trees. A large number of roots may have enabled vigorous trees to withstand stress caused by either *Armillaria* or dwarf mistletoe.

In determining tree growth response to infection by laminated root rot, Bloomberg and Reynolds (1985) discussed other sources of variation. Tree size at the time of infection can potentially mask the effects of the disease. Although they may suffer some growth retardation, infected dominant trees can potentially outgrow uninfected trees in lower crown classes. Effects of competition in intermediate and suppressed trees may confound those of root rot. As trees die within mortality centers, the growth of remaining trees may improve due to decreased competition. These types of growth responses have also been observed in laminated root rot-infected Douglas-fir as surrounding trees died (Oren et al. 1985), and in *Armillaria*-infected ponderosa pine after thinning (Filip et al. 1989). Other factors accounting for the high degree of variability in tree growth would include understory vegetation, climate, topography, soils, and genetics (Whitney and MacDonald 1985).

Although associations were not found between *Armillaria* root disease and dwarf mistletoe, the results of this study help explain the ecological roles of *Armillaria* root disease and dwarf mistletoe in this forest. Lack of associations between these two disease agents does not necessarily imply that *Armillaria* has a primary role in causing decline and mortality within these dwarf mistletoe mortality centers. The nature of jack pine decline and mortality observed in the Belair forest, and the observed sequence of *Armillaria* development in the root systems of infected trees, indicated that dwarf mistletoe was the primary agent of decline. Other trends in the data suggest that weakening effects of biotic or abiotic stress-inducing agents, including dwarf mistletoe, allowed for successful *Armillaria* attack and subsequent colonization. *Armillaria* may have contributed to the ultimate death of individual trees.

Patterns of jack pine decline and mortality

Extensive jack pine decline and mortality only occurred in parts of the forest experiencing severe dwarf mistletoe infestations. The apparent pattern of decline and mortality I observed in the Belair was similar to jack pine dwarf mistletoe-related mortality observed in Alberta (Muir and Robbins 1973). Mortality centers were roughly circular openings within the canopy created by fallen dead trees. Living and dead jack pines with extensive brooming occurred in the center of decline and mortality. These trees also often exhibited stunted growth. Extensive brooming was also evident on fallen, older dead trees. In discrete mortality centers, the association between decline and heavy dwarf mistletoe infestations was very apparent. The number of declining and recently killed trees,

and trees heavily infested with dwarf mistletoe decreased progressively outward from the center of mortality (Appendix A).

Also indicative of dwarf mistletoe-induced decline in dwarf mistletoe mortality centers was the presence of secondary organisms in heavily infested trees. Examination of the root collar often revealed secondary beetles and blue stain. Dwarf mistletoe-stressed trees have reportedly been attacked by *Ips* spp. and *Melanophila* spp. (Stevens and Hawksworth 1984). Burnes and others (1985) found that scolytid bark beetles and cerambycid beetles infested jack pine killed by dwarf mistletoe. With scolytid beetle attack, blue stain fungi were also present in these trees (Burnes et al. 1985). Secondary insects and root rotting fungi (species not identified) were believed to hasten mortality of dwarf mistletoe-infested jack pine in Alberta (Muir and Robbins 1973).

Where *Armillaria* acts as a lethal, primary pathogen in forest ecosystems, it causes large expanding mortality centers (Wargo and Shaw 1985). This was not typical of the pattern of tree decline and death in jack pine mortality centers that I studied. Rather, the distribution of *Armillaria*-infected trees was variable with single trees, or small groups of trees scattered throughout the study area (Appendix A). This random pattern of *Armillaria*-related mortality typifies that associated with dieback and decline caused by drought and general tree stress (Kile et al. 1991). Additionally, although all dead trees were colonized by *Armillaria*, extensive colonization was not evident in a number of live dwarf mistletoe-infested trees inhabited by secondary bark beetles and infected with blue stain fungi. These observations support speculations that *Armillaria* acts as an ecosystem

scavenger or secondary pathogen able to successively colonize stressed hosts (McDonald et al. 1987a).

Armillaria development in jack pine root systems

The distribution of percent root system colonization also suggests that *Armillaria* behaves opportunistically in this forest. A histogram of percent *Armillaria* colonization in jack pine roots revealed that 55% of jack pines sampled were uninfected by *Armillaria*. Nineteen percent of the trees sampled had little (1-20%) *Armillaria* colonization, and 13% of sampled jack pine were moderately infected (21-60%). All jack pine in the third group were dead and completely colonized by *Armillaria* (Fig. 4). There is an apparent absence of trees having approximately 61-99% root system colonization. While chance may account for the lack of trees in this part of the distribution, this gap may be evidence of a threshold between decline and tree death. Once such a threshold is exceeded, *Armillaria* rapidly colonizes the entire root system.

Shaw (1980) proposed a sequence of *Armillaria* (*A. mellea*) infection and subsequent disease development for ponderosa pine in south-central Washington. Young trees near edges of root disease mortality centers become infected by rhizomorphs from old-growth stumps colonized by *Armillaria*. Lesions develop at infection sites and girdle the root. The fungus colonizes dead tissue distal to the girdling lesion, with no proximal colonization along roots of living trees. Rhizomorphs from lateral root lesions could initiate lethal tap root and root collar infections in larger, living trees. Attacks high on the taproot and root collar can develop into lethal lesions. Rapid root system and root collar

colonization occurs just prior to, or following tree death. Adverse environmental conditions causing additional stress would hasten tree death (Shaw 1980). Klein-Gebbinck and others (1991) made similar observations of the spread of *A. ostoyae* in young lodgepole pine stands in central Alberta.

In some ways, the observations I made of *Armillaria* colonization on jack pine root systems were similar to Shaw's (1980) proposed sequence of *Armillaria* development. Rhizomorphs were present in the soil and had established epiphytic associations with the lateral roots of living trees. *Armillaria* had initiated infections with successful colonization restricted to distal portions of infected roots. In contrast to Shaw's study, however, I did not observe rhizomorphs penetrating the taproots or root collar of infected trees. Colonization of these portions of root systems was only evident on dead trees and one declining tree, while the taproots and root collars of all other trees were not colonized.

If *Armillaria* behaved as aggressively in jack pine as it does in ponderosa pine, I would have expected fewer uninfected jack pine, and more trees with moderate to high percentages of root system colonization. The distribution of percent *Armillaria* colonization obtained from my data suggests that *Armillaria* infecting live jack pine root systems probably exists at low levels as a weak, secondary pathogen, perthophyte, or saprophyte. Conceivably, rapid root system colonization occurs after trees have been subjected to stress and lose their ability to resist the fungus and death is imminent.

*Stress-inducing agents associated
with Armillaria colonization*

The lack of declining, dominant, and codominant jack pine uninfested with dwarf mistletoe in these mortality centers provided further evidence that *Armillaria* colonized only stressed trees. Initially, only dominant and codominant jack pine were considered for sample trees. However, very few declining dominant and codominant jack pine uninfested with dwarf mistletoe were encountered along transect lines. Due to the scarcity of these trees, intermediate jack pine were included in the sample. Fifty-one percent of the intermediate jack pine surveyed were either declining or dead, and all twelve intermediate trees selected for sampling were either declining or dead. Only one of these trees was heavily infested with dwarf mistletoe, suggesting that light stress due to suppression, or other site-related factors, may have increased these tree's susceptibility to *Armillaria*.

Crown suppression can weaken trees allowing *Armillaria* to colonize root systems (Davidson and Rishbeth 1988). Because suppressed and intermediate trees occupy a subordinate position within the canopy, they receive less light than neighboring dominant and codominant trees (Smith 1962, Daniel et al. 1979). Light stress experienced by these trees results in a reduction of the amount of available energy for defense (Wargo and Harrington 1991). In greenhouse experiments, grand fir (*Abies grandis* Lindl.) and red oak (*Quercus robur* L.) subjected to low light intensities had decreased resistance to *Armillaria* (Redfern 1978). Disease severity increased in conifer seedlings when light and nitrogen were limited as compared to seedlings grown in full light and balanced nitrogen (Entry et al. 1991).

Conversely, 87% of all dominant and codominant jack pine surveyed were vigorous. Of these trees sampled, 85% were uninfected by *Armillaria*. Sixty percent of declining and dead, dominant and codominant jack pines sampled were moderately to heavily infested with dwarf mistletoe, and more than half of these trees were also extensively colonized by *Armillaria*. These findings suggest that dominant or codominant trees are not susceptible to *Armillaria* unless they become stressed by dwarf mistletoe, or other agents.

Relationships between Armillaria root disease and jack pine vigor as assessed by BAI

Regression analysis revealed little correlation between BAI and the percentage of *Armillaria* colonization. However, because the distributions observed in these scatterplots were not linear, regression analysis was not appropriate for determining correlations between these two variables. Scatterplots of five- and ten-year BAI and the percentage of *Armillaria* colonization do suggest a relationship between *Armillaria* and growth loss (Figs. 6 and 7, respectively). The nine jack pines with 100% *Armillaria* colonization had low five- and ten-year BAI. The distributions show that no trees with more than 50% root system colonization had high BAI. To support evidence of the observed relationship between *Armillaria* colonization and BAI, an additional statistical test has been considered. This analysis would involve randomly pairing each BAI value with a percentage of *Armillaria* colonization value producing a new distribution. After numerous runs, the probability of obtaining distributions with high BAI values paired with

high percentages of *Armillaria* colonization values would be calculated. If extensive *Armillaria* colonization was associated with low BAI, the resulting probability would be small ($P < 0.05$). A high probability would suggest that the percentage of *Armillaria* colonization and BAI were associated by chance.

Evidence of an association between extensive *Armillaria* colonization and low BAI does not imply that *Armillaria* was primarily responsible for poor tree growth. These distributions also show that many uninfected jack pine and trees with low percentages of root system colonization had low BAI. Additionally, eight of the nine jack pine with extensive *Armillaria* colonization and low BAI were either intermediate trees, or were heavily infested with dwarf mistletoe (Appendix B). Growth loss caused by crown suppression, dwarf mistletoe, or other stress-inducing agents may explain the low BAI observed in trees.

Other analysis and observations also provide evidence to suggest that *Armillaria* did not contribute to significant growth loss. The percent difference in BAI analysis showed that only 24% of jack pine with an increasing growth increment were infected by *Armillaria*. However, for all jack pine with decreasing growth increment, the percentage of trees colonized by *Armillaria* was approximately equal to the percentage of uninfected trees.

Finally, numerous studies show that host trees with a significant number of roots killed by *Armillaria* or other decay fungi experience reduced height growth and diameter increment (Morrison et al. 1991). In northern Ontario, the mean height and radial

increments of balsam fir with ground level decay were significantly less when compared with trees having no ground level decay after three years (Whitney and MacDonald 1985). Laminated root rot decreased the average stem size and periodic annual increment of infected second-growth Douglas-fir in mortality centers on Vancouver Island (Bloomberg and Reynolds 1985). Young radiata pine (*Pinus radiata*) with 50-100% root collar infection by *Armillaria* (*A. limonea*, or *A. novae-zelandiae*) experienced 19-20% less cumulative mean increment than uninfected control trees (Shaw and Toevs 1977). Douglas-fir in southern British Columbia experienced significant reductions in percent stem volume growth attributed to basal resinosis due to increased mycelial colonization of *Armillaria* (Bloomberg and Morrison 1989). *Armillaria*-infected Norway spruce had significantly less diameter growth than healthy trees (Sokolov 1964 in Morrison et al. 1991).

Contrary to the above studies, examination of excavated roots in my study showed that only one declining and all recent dead trees had extensive *Armillaria* colonization. *Armillaria* did not extensively colonize root systems of vigorous jack pine and cause significant root system mortality. The sequence of *Armillaria* development I observed in jack pine root systems indicates that extensive root system colonization and subsequent root mortality occurred at the onset of tree death.

Based on the results of these findings, a probable explanation for the observed relationship between extensive *Armillaria* colonization and low BAI may be that both *Armillaria* root disease and poor growth are indicative of tree decline.

*Implications of both disease agents
in the Belair Forest*

Associations between dwarf mistletoe and tree vigor indicate that dwarf mistletoe has an important role as a stress-inducing agent in these jack pine stands. Although associations of dwarf mistletoe with *Armillaria* root disease were not detected, tree mortality and damage experienced in stands heavily infested with dwarf mistletoe have important implications for the control of *Armillaria* root disease in future stands. Woody substrates provide food bases capable of maintaining *Armillaria* saprophytically in the soil (Redfern and Filip 1991). From sources including dead roots, stumps, slash, and other woody debris, *Armillaria* can spread and infect young trees (Shaw and Calderon 1977; Redfern 1978; Stanosz and Patton 1987). High rates of *Armillaria* infection in Ontario plantations were attributed to the close proximity of infected trees to stumps (Whitney 1988). In young lodgepole pine stands in Alberta, woody debris and stumps from the previous stand were the major inoculum sources (Klein-Gebbinck et al. 1991). Only 22% of the young trees had been infected by *Armillaria* rhizomorphs growing from the roots of previously infected regeneration.

Because all dead jack pine in my study were completely colonized by *Armillaria*, the root systems of dead trees in dwarf mistletoe mortality centers can potentially become a large inoculum source. I also observed other sources of woody debris that were colonized by *Armillaria*. The buildup of *Armillaria* inoculum in dead trees and woody debris may allow the fungus to spread to root systems of vigorous trees within surrounding mortality

centers. With high inoculum potential, young trees, or dwarf mistletoe-stressed trees appear extremely susceptible to the disease (Hood et al. 1991). The increased probability of *Armillaria* infecting a larger proportion of roots may supercede requirements for stress for successful attack and colonization. In this manner, *Armillaria* root disease may contribute to the expansion of mortality centers.

The buildup of *Armillaria* within dwarf mistletoe mortality centers, in addition to to the buildup of *Armillaria* in stumps created after harvesting jack pine may also explain the prevalence of *Armillaria* in Belair red pine plantations established on these former jack pine sites. The effects of site-related stress experienced by planted red pine and the prevalence of *Armillaria* may increase the susceptibility of young red pine to the disease resulting in the high mortality observed.

Supposing that this is the case, several management options could minimize losses due to *Armillaria* root disease in these plantations. First, following harvest stands, heavily infested with dwarf mistletoe should not be converted to red pine. In Belair plantations, volunteer jack pine regeneration has demonstrated greater vigor and resistance to *Armillaria* root disease than red pine. In *Armillaria* infection centers, red pine are killed by the fungus, whereas jack pine typically have uninfected root systems. Hall and others (1971) found that natural fir regeneration had more well-developed root systems than planted seedlings. Well-developed root systems may give young trees competitive advantages on the site, and the ability to withstand adverse environmental conditions and recover from the effects of stress (Hood et al. 1991). Selecting species more suited to

these sites would minimize volume loss that results from poorly stocked stands due to *Armillaria*-caused mortality.

Secondly, utilize management strategies that maintain forest health. In jack pine stands, dwarf mistletoe control may significantly improve tree vigor, thus reducing mortality and resulting in less *Armillaria* inoculum. Wicker and Hawksworth (1988) described a number of strategies and tactics useful for dwarf mistletoe control that will minimize losses. In stands where jack pine occurs with a mixture of other tree species, selection cutting favors retention of the species mixture over a pure jack stand, and reduces dwarf mistletoe spread. If the management objective is to regenerate jack pine, then the preferred strategy is to remove all overstory trees from the cutting unit, and leave a 70-foot buffer strip between residual stands and regenerated stands. If taking this amount of forested land out of production is not economically feasible, edge infections of the residual stand may be removed. If infested overstory trees are retained for seed trees, they should be cut within the first five years of seedling establishment to prevent spread to young trees. In residential, or recreational areas, where tree removal may not be an option, pruning dwarf mistletoe-infested branches may delay dwarf mistletoe spread. In addition to reducing dwarf mistletoe damage within the stand, the costs associated with these control strategies are considerably less than the costs of stump removal and other inoculum control strategies during site preparation.

Finally, if red pine is the preferred species for planting, reducing inoculum sources in sites prone to *Armillaria* root disease by removing stumps and roots during site

preparation has been shown to provide benefits exceeding the costs (Shaw and Calderon 1977). Delaying planting to allow sources of inoculum to decay may also reduce the amount of *Armillaria* available to infect young trees.

SUMMARY

This study did not find evidence of associations between jack pine dwarf mistletoe and *Armillaria* root disease in the Belair Provincial Forest. Trends in the data, however, indicate that dwarf mistletoe was primarily responsible for jack pine decline and mortality. Extensive decline and mortality were only observed in dwarf mistletoe-infested areas of the forest. The pattern of tree death in mortality centers and the subsequent colonization of dwarf mistletoe infested trees by *Armillaria* was indicative of dwarf mistletoe-induced stress. Severely stunted jack pine often had crowns comprised of large brooms. Analysis of basal area increment data also provided evidence that heavy dwarf mistletoe infestation reduced jack pine growth.

Although two-way analysis of variance and nonparametric procedures showed strong associations between *Armillaria* colonization and jack pine vigor, extensive colonization appears to be related to tree stress. Only dominant and codominant jack pine heavily infested with dwarf mistletoe were extensively colonized by *Armillaria*. Crown suppression caused by light stress or other site-related factors may have predisposed intermediate trees to *Armillaria*.

Patterns of decline and mortality, and the random distribution of *Armillaria*-infected trees in jack pine mortality centers suggest that *Armillaria* acts as an ecosystem scavenger able to successfully colonize stressed trees. Associations between growth increment percentage and the incidence of *Armillaria* support this observation. Only a small proportion of vigorously growing trees was infected by *Armillaria*. *Armillaria* did not

appear to contribute to reduced BAI. Only 24% of jack pine with increasing growth increment were infected with *Armillaria*. For jack pine with decreasing growth increment, the percentage of *Armillaria*-infected trees was approximately equal to the percentage of uninfected trees. Vigorously growing trees are more likely to resist random *Armillaria* attacks, while declining trees succumb to attack and subsequent root system colonization.

Finally, root system examination and distributions of percent *Armillaria* colonization suggest that the fungus probably persists in localized areas of jack pine root systems until trees become stressed. As trees approach death, *Armillaria* rapidly colonizes the remaining root system. Most vigorous and declining jack pine had low percentages of root system colonization. The root collars and taproots of vigorous jack pine were not colonized. Only the root systems of dead jack pine were extensively colonized with mycelial fans present at the root collar and on taproots. Colonization of these portions of the root system was also concurrent with infestation by secondary bark beetles and blue stain fungi, which is again indicative of the secondary nature of *Armillaria* in these mortality centers.

As a secondary disease agent, the potential contribution of *Armillaria* in increasing rates of decline and mortality within heavily infected jack pine stands should remain a concern. The extensive colonization observed in dead trees, stumps, and woody debris has important management implications regarding future losses to the disease in Belair forest plantations. Consideration of these factors could affect decisions regarding the location of future plantations, harvesting operations, and site preparation. Most

importantly, young jack pine grows best on these sites and demonstrates greater resistance to *Armillaria* than red pine. Measures to control dwarf mistletoe are easier and less expensive than stump removal, and will allow optimal jack pine growth on these sites.

This study also demonstrates the limitations of the six-class dwarf mistletoe rating system to accurately assess the effect of dwarf mistletoe on individual trees, particularly in host/parasite combinations where brooming is extensive and mortality great. Further research is needed to investigate how large brooms and other types of dwarf mistletoe infection divert photosynthates, water, and nutrients from host tissues; how dwarf mistletoe stresses host trees measured in terms of productivity, from individual needles of infested branches, to overall productivity of the entire tree; how dwarf mistletoe affects the formation of phenolic compounds and other defense chemicals in roots; how dwarf mistletoe infections influence the number of roots, root system volume, and root system weight; and, how dwarf mistletoe affects the growth and development of the root systems of seedlings and juvenile trees. Other studies could examine relationships between the location of large brooms in tree crowns and their effect on these same factors. This information could lead to the development of methods and rating systems better able to quantify the true impact of dwarf mistletoe infections on individual trees.

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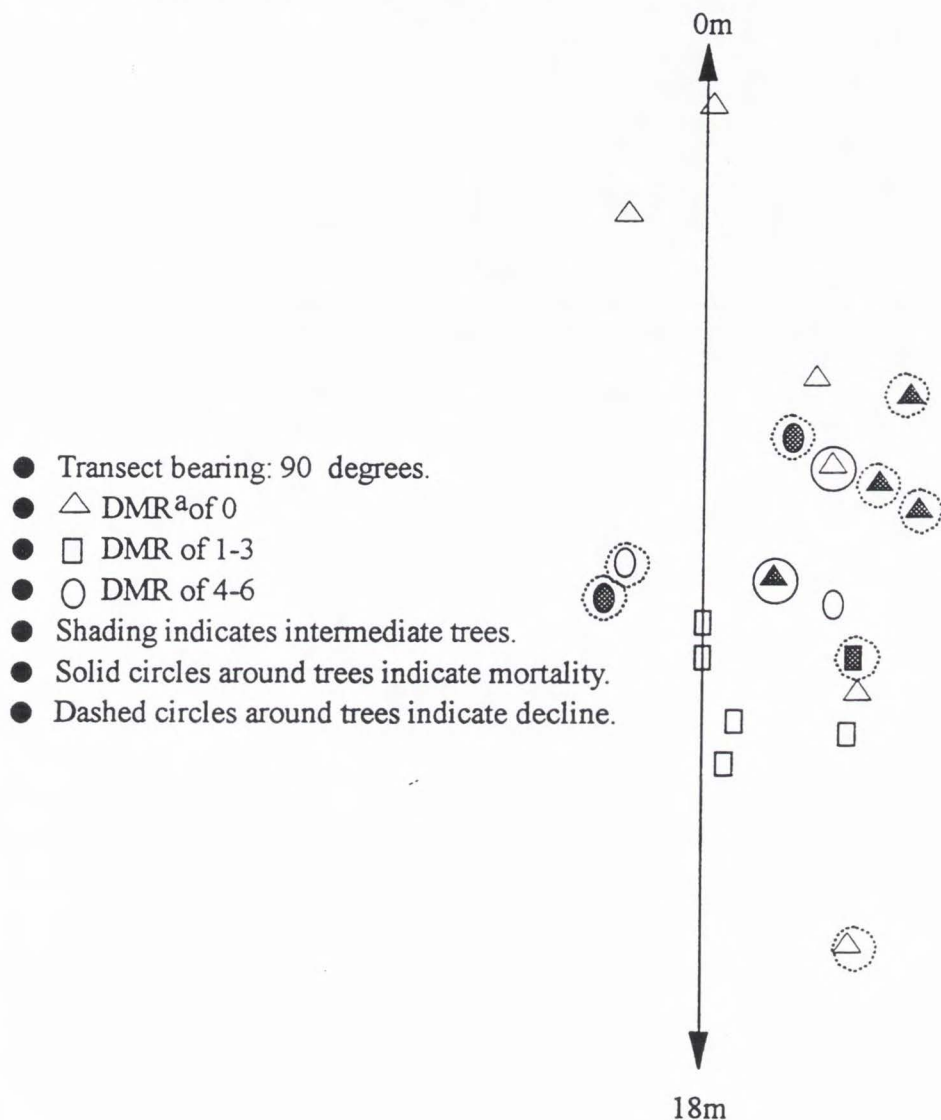
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APPENDICES

Appendix A:
Transect Maps of Dwarf Mistletoe Mortality Centers Sampled

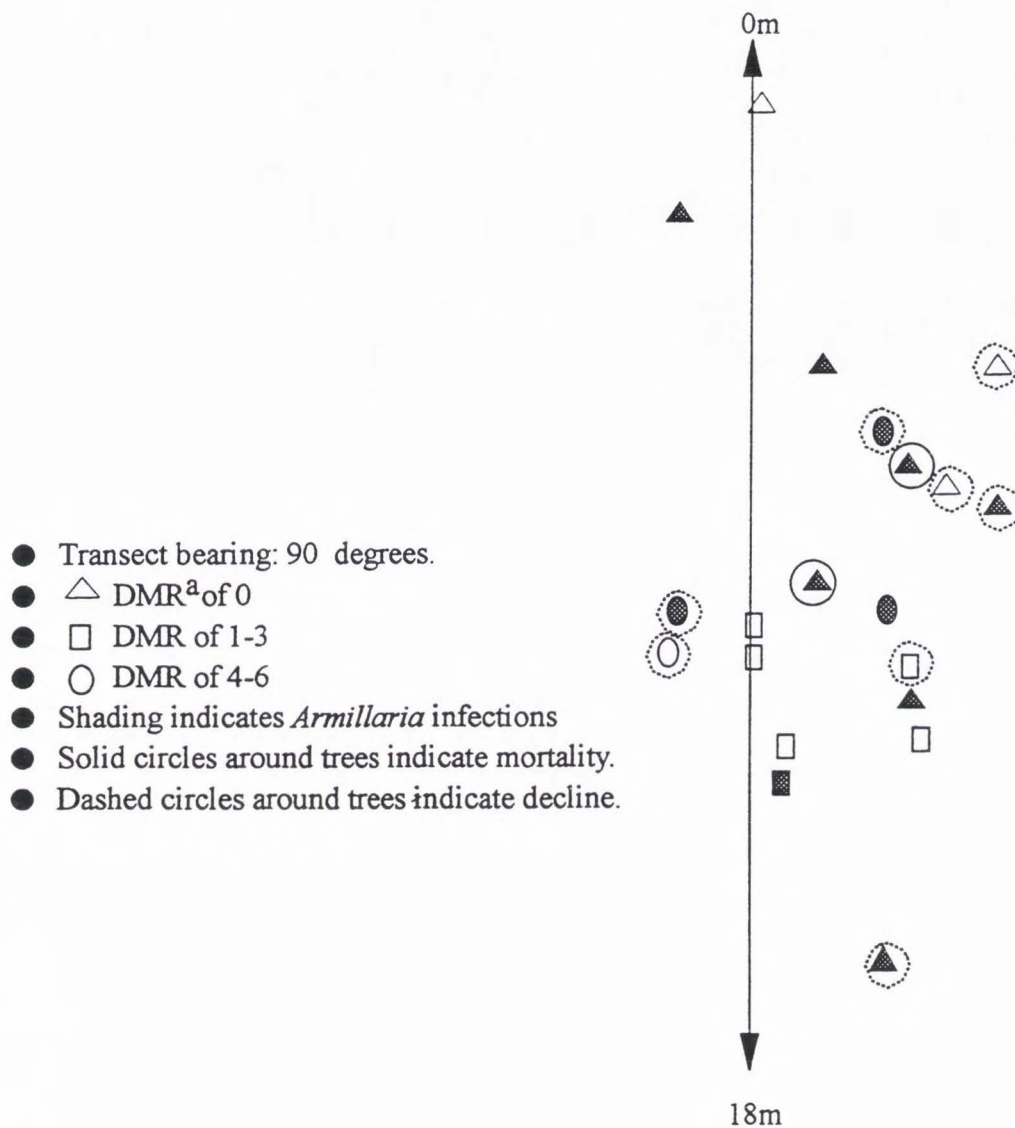
A.1. Distribution of the 20 sampled jack pine in mortality center 1, and their dwarf mistletoe and crown class status.



NOTE: In mortality center 1, only trees sampled for *Armillaria* root disease were mapped. Maps of mortality centers 2 and 3 show the distributions of all jack pine surveyed along transect.

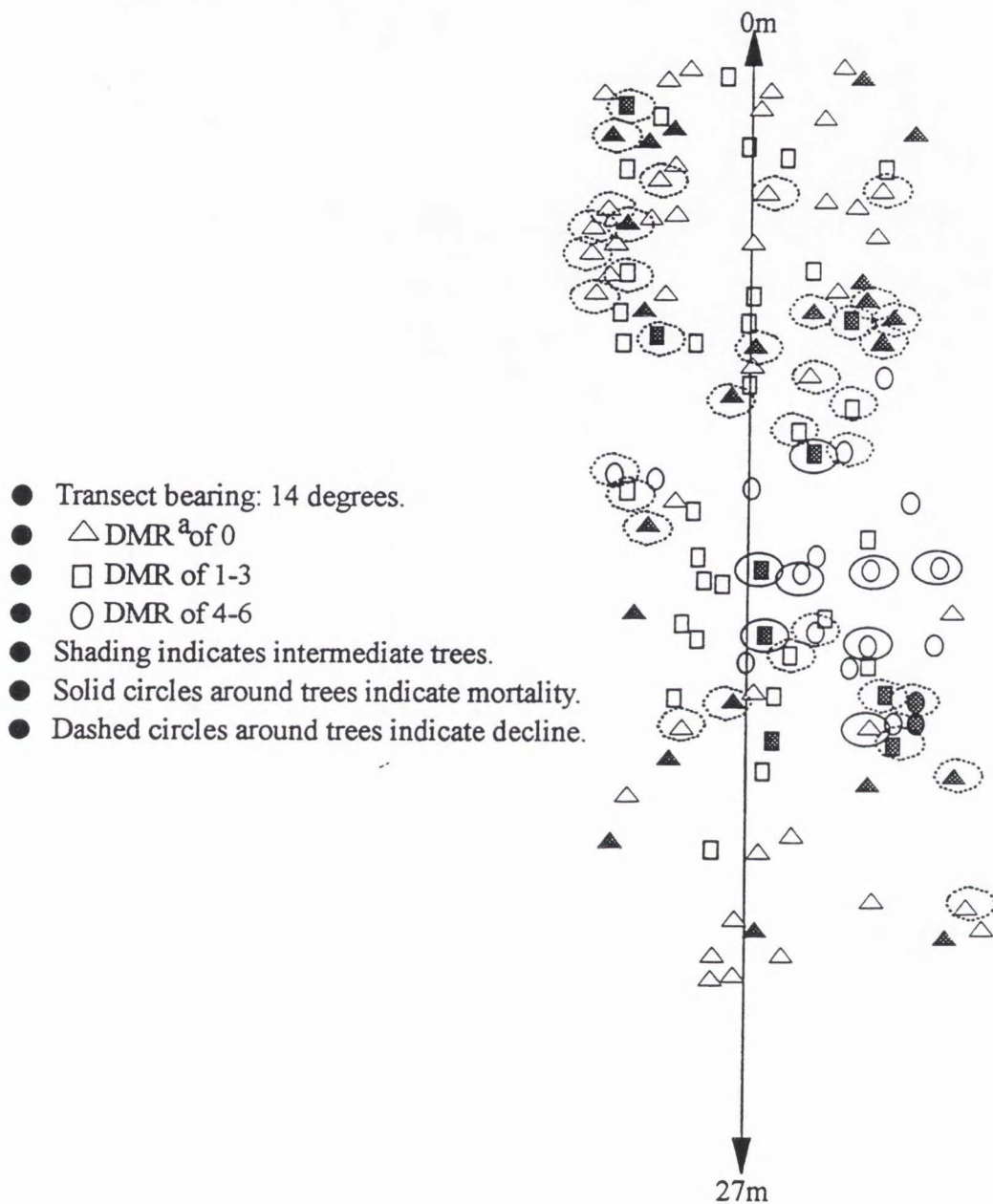
^aDMR; six-class dwarf mistletoe rating system.

A. 2. Distribution of the 20 sampled jack pine in mortality center 1, and their *Armillaria* root disease status.



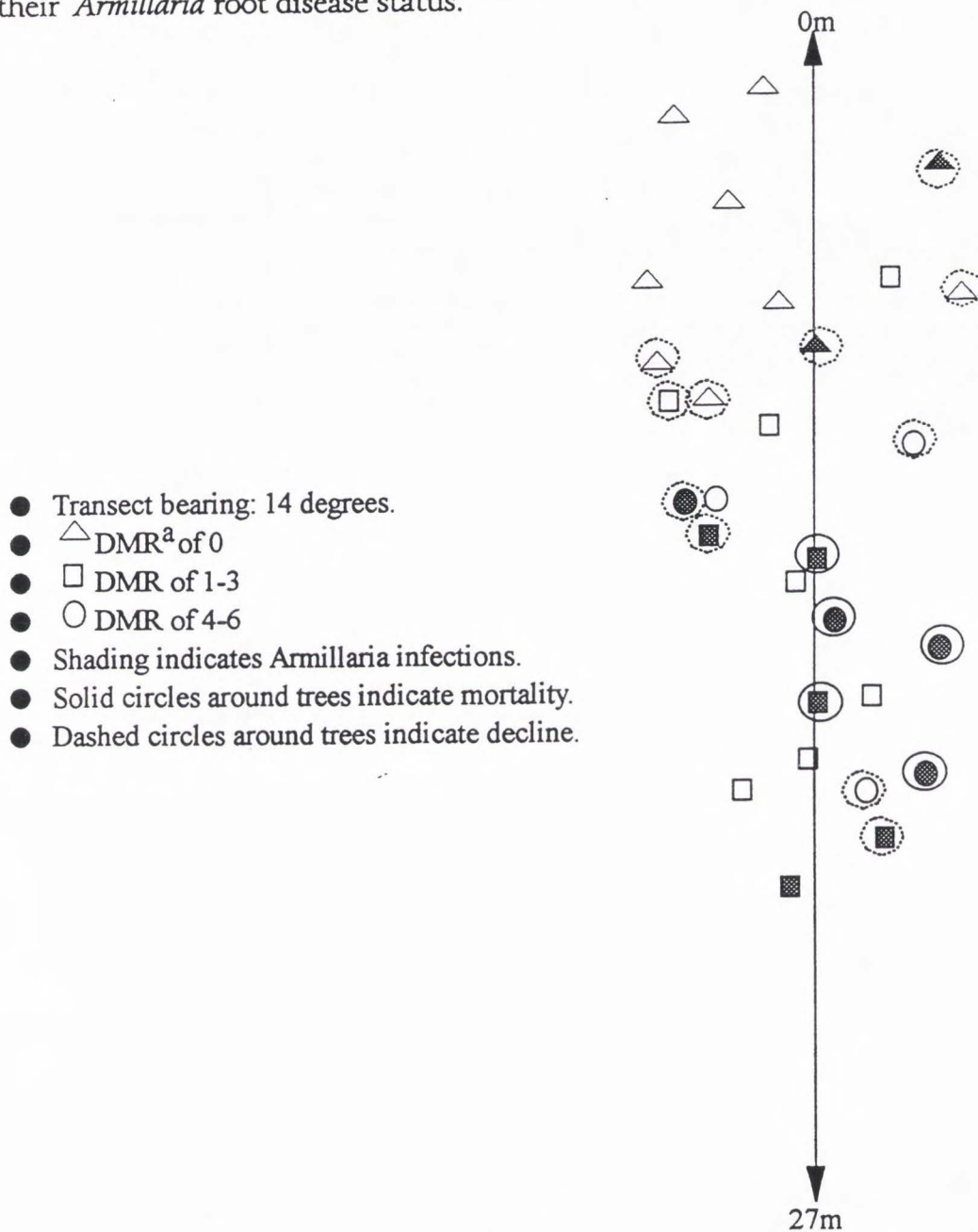
^aDMR; six-class dwarf mistletoe rating system.

A. 3. Distribution of 109 jack pine surveyed in mortality center 2, and their dwarf mistletoe and crown class status.



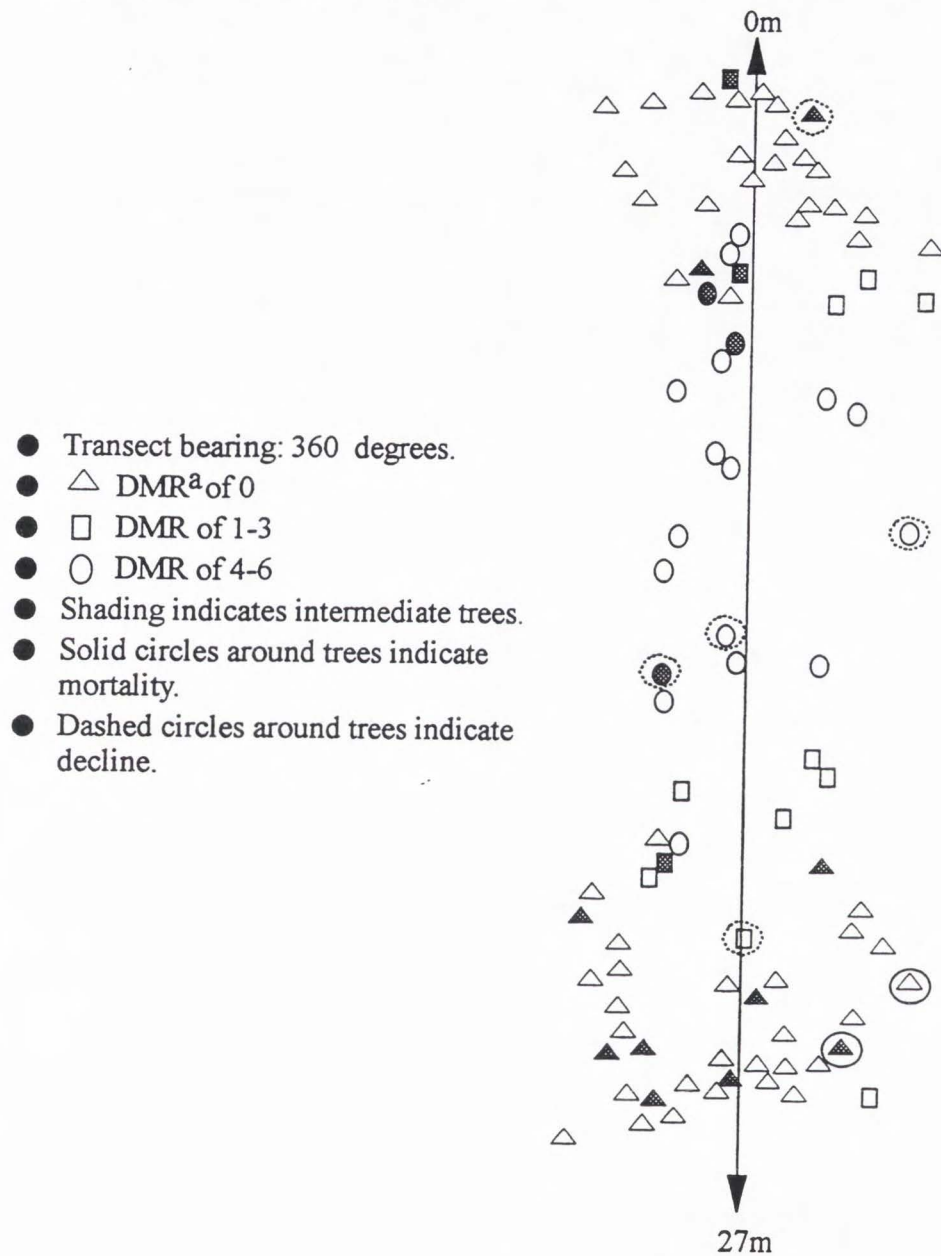
^aDMR; six-class dwarf mistletoe rating system.

A. 4. Distribution of 29 jack pine sampled in mortality center 2, and their *Armillaria* root disease status.



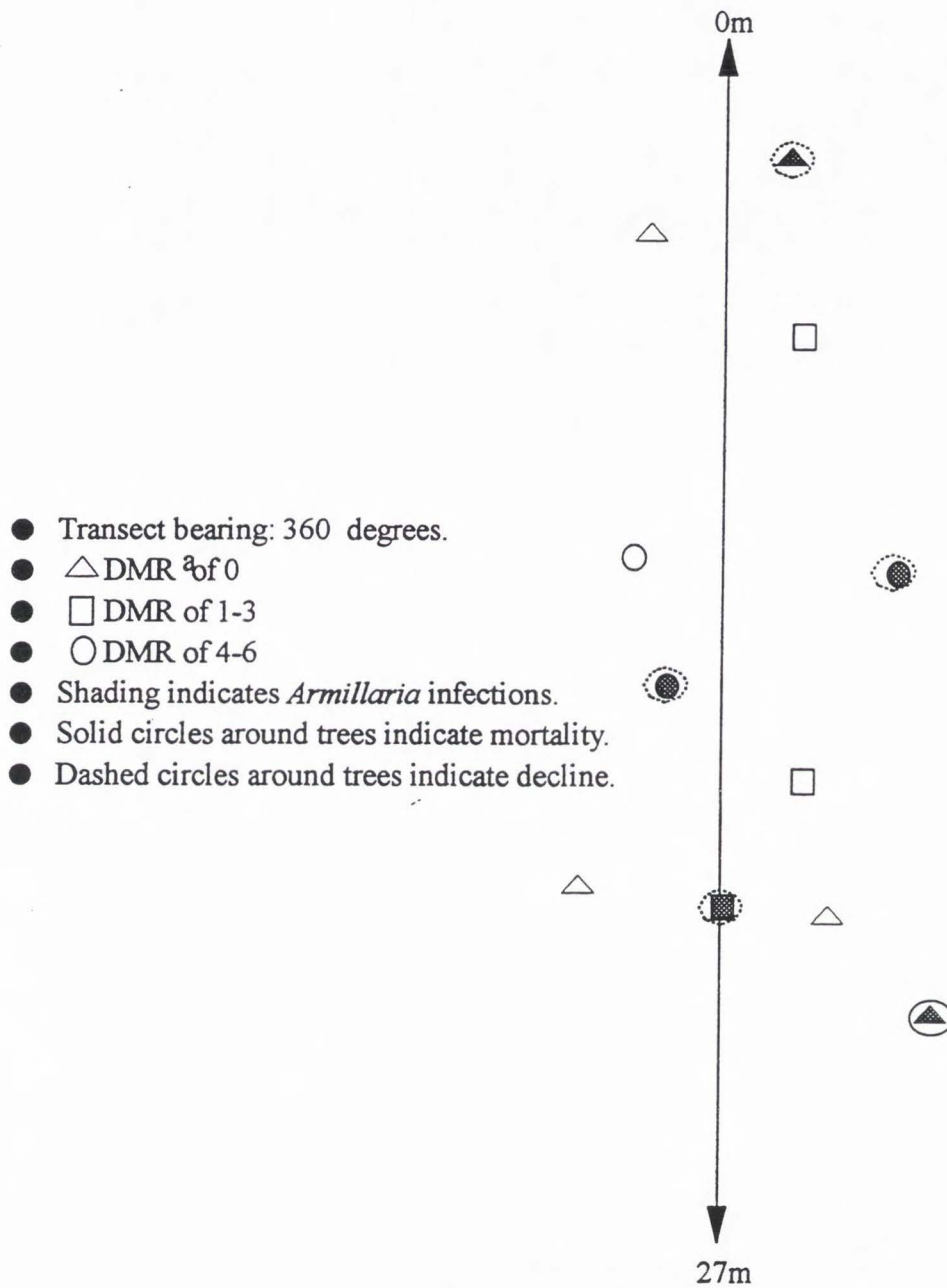
^aDMR; six-class dwarf mistletoe rating system.

A. 5. Distribution of 95 jack pine surveyed in mortality center 3, and their dwarf mistletoe and crown class status.



^aDMR; six-class dwarf mistletoe rating system.

A.6. Distribution of 11 jack pine sampled in mortality center 3, and their *Armillaria* root disease status.



a DMR; six-class dwarf mistletoe rating system.

Appendix B:
Table of Data Collected for Sampled Jack Pine

Appendix B. Data collected for individual jack pine sampled in the three selected dwarf mistletoe mortality centers^a

ID ^b	VC ^c	CC ^d	dbh (cm)	HT (m)	BA (m ²)	BAI 5 (m ²)	BAI 10 (m ²)	Root Segs	DMR	% Arm
3-93	VU	C	21.0	15.0	0.035	0.0028	0.0052	66	0	0
2-105	VU	C	16.6	15.5	0.023	0.0025	0.0044	78	0	0
1-28	VU	C	19.9	11.3	0.031	0.0016	0.0023	65	0	0
2-104	VU	C	13.0	15.5	0.013	0.0008	0.0015	24	0	0
1-1	VU	C	15.1	13.5	0.018	0.0030	0.005	36	0	0
2-111	VU	C	14.5	15.6	0.017	0.0019	0.0040	45	0	0
3-28	VU	C	14.5	12.5	0.017	0.0008	0.0015	39	0	0
3-62	VU	C	10.8	12.5	0.010	0.0005	0.0012	27	0	0
2-109	VU	C	18.0	17.0	0.025	0.0025	0.0050	63	0	0
2-118	VU	C	11.7	14.0	0.011	0.0002	0.0004	24	0	0
1-12	VU	D	19.9	14.0	0.031	0.0019	0.0034	64	0	12.5
1-27	VU	C	19.5	13.0	0.030	0.0042	0.0077	59	0	28.8
3-16	VI	C	19.9	16.0	0.030	0.0056	0.0113	95	3	0
1-5	VI	D	15.8	11.5	0.020	0.0034	0.0052	36	3	0
2-37	VI	C	10.8	13.8	0.010	0.0002	0.0006	25	1	0

ID ^b	VC ^c	CC ^d	dbh (cm)	HT (m)	BA (m ²)	BAI 5 (m ²)	BAI 10 (m ²)	Root Segs	DMR	% Arm
1-6	VI	D	16.4	13.0	0.021	0.0031	0.0051	64	1	0
3-74	VI	C	14.2	10.0	0.016	0.0006	0.0019	74	4	0
2-95	VI	C	14.9	16.4	0.017	0.0022	0.0045	55	1	0
3-22	VI	C	18.0	10.0	0.025	0.0009	0.0016	57	3	0
2-75	VI	C	12.4	15.5	0.012	0.0008	0.0015	25	3	0
2-89	VI	C	17.5	15.0	0.024	0.0023	0.0044	65	5	0
1-4	VI	C	12.5	11.3	0.012	0.0004	0.0010	40	1	0
2-14	VI	C	16.5	17.8	0.021	0.0027	0.0060	56	1	0
2-81	VI	C	12.8	15.3	0.012	0.0007	0.0015	33	3	0
2-64	VI	C	18.5	16.0	0.030	0.0012	0.0030	50	1	2.0
1-3	VI	D	15.5	12.5	0.018	0.0027	0.0050	65	1	3.1
1-14	VI	C	17.8	12.0	0.025	0.0011	0.0031	63	4	6.4
1-19	DU	I	11.5	8.6	0.010	0.0012	0.0045	44	0	0
2-99	DU	C	12.5	16.0	0.012	0.0003	0.00084	36	0	0
1-22	DU	I	11.8	10.8	0.011	0.0003	0.0008	27	0	0
2-96	DU	C	13.0	16.5	0.013	0.0005	0.0013	44	0	0

ID ^b	VC ^c	CC ^d	dbh (cm)	HT (m)	BA (m ²)	BAI 5 (m ²)	BAI 10 (m ²)	Root Segs	DMR	% Arm
2-19	DU	I	9.5	20.0	0.007	0.0003	0.0009	19	0	0
2-102	DU	C	14.2	15.6	0.016	0.0006	0.0014	38	0	2.6
2-11	DU	C	14.0	15.8	0.015	0.0008	0.0016	64	0	3.1
1-7	DU	C	14.3	11.0	0.016	0.0010	0.0016	43	0	27.9
1-20	DU	I	12.7	10.0	0.013	0.0004	0.0009	16	0	50
3-3	DU	I	11.9	11.8	0.011	0.0006	0.0015	*	0	100
2-98	DI	C	13.0	14.5	0.013	0.0008	0.0021	29	1	0
1-15	DI	I	11.0	8.3	0.010	0.0013	0.0030	24	6	0
1-2	DI	I	12.6	9.5	0.012	0.0004	0.0007	16	2	0
2-31	DI	C	16.5	15	0.021	0.0014	0.0027	63	5	0
2-38	DI	C	11.0	13.3	0.010	0.0008	0.0012	27	6	0
1-16	DI	C	13.5	10.0	0.014	0.0010	0.0026	47	6	2.1
2-88	DI	C	12.7	15.0	0.013	0.0004	0.0011	35	5	5.7
1-17	DI	I	11.0	7.0	0.010	0.0005	0.0011	25	6	16.0
2-86	DI	C	12.9	16.0	0.013	0.0003	0.0009	20	1	25.0
2-48	DI	C	16.0	16.5	0.020	0.0022	0.0047	36	3	27.8

ID ^b	VC ^c	CC ^d	dbh (cm)	HT (m)	BA (m ²)	BAI 5 (m ²)	BAI 10 (m ²)	Root Segs	DMR	% Arm
3-20	DI	C	10.7	8.5	0.009	0.0003	0.0010	19	6	31.6
3-72	DI	C	13.5	8.3	0.014	0.0006	0.0012	52	5	32.7
3-27	DI	C	12.6	11.0	0.012	0.0003	0.0010	47	1	58.5
1-37	MU	I	9.0	7.0	0.006	0.0003	0.0005	34	0	100
1-18	MU	I	9.9	7.0	0.008	0.0004	0.0010	12	0	100
3-33	MU	C	13.2	11.3	0.013	0.0006	0.0012	*	0	100
2-34	MI	C	15.1	14.0	0.018	0.0005	0.0023	48	6	100
2-36	MI	C	15.5	14.0	0.019	0.0006	0.0019	*	4	100
2-80	MI	I	11.0	14.0	0.010	0.0003	0.0006	*	3	100
2-78	MI	I	10.3	12.0	0.008	0.0007	0.0011	24	3	100
2-40	MI	C	14.6	15.0	0.017	0.0010	0.0030	34	6	100

^aID, tree identification number; VC, tree vigor class; CC, crown class; dbh, diameter at breast height; HT, tree height; BA, basal area; BAI 5, five year basal area increment; BAI 10, ten year basal area increment; Root Segs, the number of 25 cm root segments within 1 m of the bole examined; DMR, the six-class dwarf mistletoe rating system; % ARM, the percentage of root segments infected with *Armillaria*.

^bThe first number designates the mortality center, the second, designates the individual tree within the mortality center.

^cV, vigorous; D, declining; M, dead; U, uninfected; I, infected.

^dD, dominant; C, codominant; I, intermediate.