Visible versus actual incidence of Armillaria root disease in juvenile coniferous stands in the southern interior of British Columbia

D.J. Morrison, K.W. Pellow, D.J. Norris, and A.F.L. Nemec

Abstract: The relationship between aboveground symptoms and belowground incidence of *Armillaria ostoyae* (Romagn.) Herink on conifers in 13- to 24-year-old stands was investigated at five sites in each of the dry, moist, and wet climatic regions in the Nelson forest region, British Columbia. All trees >1.3 m in height in 0.01-ha circular plots centred on a tree killed fewer than two or more than five years previously or located where there were no symptomatic trees were removed from the soil by an excavator. The location and host response at each *A. ostoyae* lesion on root systems were recorded. Significant differences in belowground incidence were seen among climatic regions and plot types, with distance from the centre of plots, and between planted and naturally regenerated trees. Belowground incidence was related to the percentage of putatively colonized stumps within and adjacent to plots. There were significant differences among climatic regions in the intensity of infection, host reaction to infection, and percentage of diseased trees showing aboveground symptoms. These results have implications for interpreting results of surveys for Armillaria root disease in juvenile stands and for tending of such stands.

Résumé : Cette étude porte sur la relation entre les symptômes présents sur les parties aériennes et l'incidence d'*Armillaria ostoyae* (Romagn.) Herink sur les racines de conifères dans des peuplements âgés de 13 à 24 ans. L'étude a été réalisée dans cinq sites dans chacune des zones climatiques sèche, semi-humide et humide, de la région forestière de Nelson, en Colombie-Britannique. Tous les arbres plus hauts que 1,3 m dans des parcelles circulaires de 0,01 ha ayant comme centre un arbre mort il y a moins de deux ans ou plus de cinq ans, ou se trouvant dans un lieu exempt d'arbres portant des symptômes, ont été extraits du sol avec une excavatrice. La position des lésions dues à l'*A. ostoyae* sur le système racinaire et la réaction de l'hôte ont été notées. L'incidence du champignon sur les racines différait significativement selon la zone climatique, le type de parcelles, la distance à partir du centre de la parcelle et selon que les arbres avaient été plantés ou provenaient de la régénération naturelle. L'incidence du champignon sur les racines était reliée au pourcentage de souches apparemment colonisées à l'intérieur ou à proximité des parcelles. La sévérité de l'infection, la réaction de l'hôte et le pourcentage d'arbres malades montrant des symptômes sur les parties aériennes étaient significativement différents selon la zone climatique. Ces résultats peuvent avoir un impact sur l'interprétation des résultats des relevés du pourridié-agaric dans les jeunes peuplements et sur la façon de traiter de tels peuplements.

Introduction

In many temperate coniferous forests, *Armillaria ostoyae* (Romagn.) Herink causes lethal primary root disease throughout the rotation (Kile et al. 1991). In North America, incidence of mortality in juvenile stands can be as high as 2% per annum (Filip and Goheen1995; Livingston 1990; Morrison and Pellow 1994; Singh and Richardson 1973; Whitney 1988; Wiensczyk et al. 1996) with cumulative mortality reaching 15–20% by age 20 years (Morrison and Pellow 1994; Whitney 1988). Killed and symptomatic infected trees are found in groups of two or three in these young plantations and natural stands, and there may be many disease centres per hectare (Morrison and Pellow 1994; van der Kamp 1995).

In many jurisdictions, juvenile stands are assessed for stocking and health, especially prior to stand-tending operations, recognizing that high levels of disease could jeopardize the owner's investment. Currently, surveys for Armillaria root disease use declining leader length and chlorotic foliage to recognize suspect diseased trees and basal resinosis and subcortical mycelial fans to confirm disease. Results of surveys are presented as proportions of trees killed or symptomatic, percentage of stand area occupied by disease centres, or as number of centres per hectare. A recent survey of research needs (Nevill et al. 1995) identified survey methodology for Armillaria root disease as a high priority.

Armillaria ostoyae is the cause of Armillaria root disease of conifers in western North America (Wargo and Shaw 1985), and isolations from diseased trees indicate that it is the only species causing primary disease on conifers in British Columbia (Morrison et al. 1985; White et al. 1998). In British Columbia, *A. ostoyae* occurs south of about 53°N

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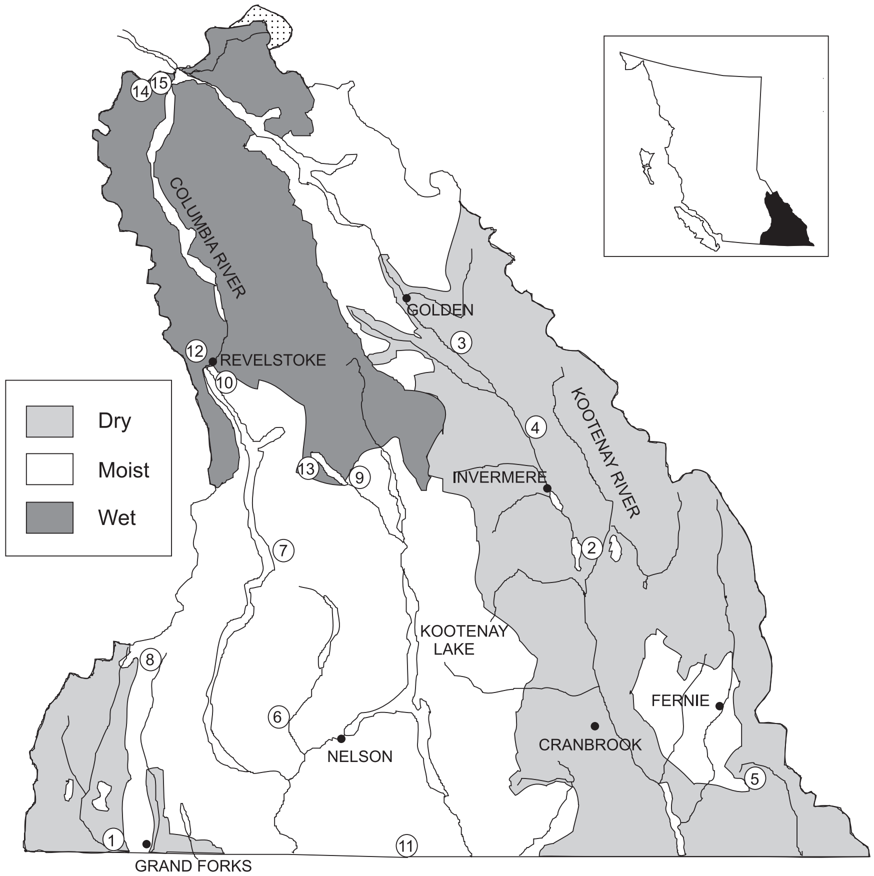
D.J. Morrison[1] and K.W. Pellow. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Road, Victoria, BC V8Z 1M5, Canada.
D.J. Norris. British Columbia Ministry of Forests, Nelson Forest Region, 518 Lake Street, Nelson, BC V1L 4C6, Canada.
A.F.L. Nemec. International Statistics and Research Corp., P.O. Box 496, Brentwood Bay, BC V8M 1R3, Canada.

[1]Corresponding author. e-mail: dmorrison@pfc.forestry.ca

Fig. 1. Distribution of the dry, moist and wet climatic regions and location of the 15 stands in the Nelson forest region (after Braumandl and Curran 1992).



(Morrison et al. 1985) on most species of conifers (Allen et al. 1996). In the southern interior, Armillaria root disease is found in most biogeoclimatic subzones in the dry, moist, and wet climatic regions (Braumandl and Curran 1992; Lloyd et al. 1990). Juvenile stands in these subzones frequently have 1–2% annual mortality, which may cause unstocked openings (Hopkins and Stewart 1992; Morrison and Pellow 1994). Moderate to high incidence of dead and symptomatic trees raises questions for silviculturists about long-term productivity and the wisdom of investing in stand tending.

In five Ontario plantations, Whitney et al. (1989) showed that an average of 58% of coniferous trees without aboveground symptoms were infected by *Armillaria obscura* (Pers.) Herink (= *A. ostoyae*), up to 28% of major roots on these trees were infected, and up to 4.2 times as many infected as dead trees occurred on 0.01-ha plots. These results suggest that current survey methods for Armillaria root disease based only on aboveground symptoms and signs can neither accurately estimate actual disease incidence in a stand nor assess the potential for future mortality of asymptomatic infected trees.

The primary objective of this project was to determine the relationship between incidence of aboveground symptomatic trees and overall incidence of infected trees at sites in the dry, moist, and wet climatic regions of the southern interior of British Columbia. Secondary objectives were to determine belowground incidence of infected trees in the vicinity of trees dead fewer than 2 and more than 5 years, representing active and inactive disease centres and to assess the potential for future mortality by measuring the location of lesions on roots and observing host response at lesions.

Methods

Site selection

Silviculturists in the districts of the British Columbia Ministry of Forests in the Nelson forest region were canvassed for information on biogeoclimatic subzones in which management of juvenile stands is a priority. Lists of candidate sites were compiled from the stand inventory system. Candidate sites were visited and assessed against the following criteria: accessible by road, suitable terrain for an excavator, uniform stocking and species composition on the site, and low to moderate incidence of Armillaria root disease. Sites with a high incidence of centres were avoided, because they would not contain sufficient area to accommodate asymptomatic plots (see below). In subzones of each of the dry, moist, and wet climatic regions (Braumandl and Curran 1992) five sites were selected for study (Fig. 1). Table 1 lists the attributes of the 15 sites and stands.

Plot types

At each site, 3–4 ha were examined for possible plot locations. Plots were of three types: (*i*) centred on a regeneration tree killed five or more years previously (inactive disease centre); (*ii*) centred on a regeneration tree killed two or fewer years previously (active

Table 1. Location and attributes of five juvenile coniferous stands sampled for Armillaria root disease in each of the dry, moist, and wet climate regions of the Nelson forest region.

Climate region[a]	Site No.	Biozone[a]	Location	Stand age	Species composition[bc]		Stems/ha
					Planted	Natural	
Dry	1	IDFdm1	49°09′N, 118°33′W	13		$Pl_{98}Lw_1Fd_tBl_t$	4560
	2	IDFdm2	50°16′N, 115°43′W	19	Pl_{98}	Fd_2Lw_t	1500
	3	Msdk	51°04′N, 116°34′W	17		$Pl_{83}Fd_{14}Se_1Cw_1$ Pw_t Bl_t	3960
	4	Msdk	50°50′N, 116°11′W	18		$Fd_{58}Bl_{26}Pl_{14}Se_2$ Pw_t	3020
	5	ESSFdk	49°17′N, 114°43′W	24		$Bl_{83}Se_{16}Fd_1Pl_t$	2980
Moist	6	ICHdw	49°34′N, 117°44′W	19	Fd_{47}	$Cw_{16}Pw_{16}Pl_{10}Hw_6$ Lw_5Se_t	2180
	7	ICHmw2	50°18′N, 117°39′W	19	Fd_{63}	$Hw_{14}Cw_{14}Pw_8$ Se_t	1750
	8	ICHmw2	49°39′N, 118°20′W	16		$Pl_{88}Pw_7Se_3Bl_2Fd_t$ Lw_tHw_t	4000
	9	ICHmw2	50°32′N, 117°18′W	21	Fd_{73}	$Pw_{10}Cw_9Hw_5$ Se_2 Bl_1	2580
	10	ICHmw3	50°49′N, 118°W	14	Fd_{67}	$Pw_{16}Hw_{12}Cw_4$ Pl_1	1880
Wet	11	ESSFwc1[d]	49°05′N, 116°53′W	19	Se_{80}	$Bl_{14}Pl_6$	2730
	12	ICHwk1	51°02′N, 118°20′W	20	Fd_{54}	$Hw_{20}Cw_{12}Se_{12}$ Pw_1	2000
	13	ICHwk1	50°37′N, 117°31′W	19	Fd_{53}	$Cw_{23}Hw_{11}Bl_9$ Se_2 Pw_1	1980
	14	ICHvk	52°04′N, 118°24′W	19	Se_{64}	$Hw_{29}Cw_5Bl_1$ Pw_1	2570
	15	ICHvk	52°02′N, 118°20′W	17	Fd_{65}	$Hw_{17}Cw_{12}Se_4$ Pw_1Bl_t	1990

[a]See Braumandl and Curran (1992).
[b]Bl, subalpine fir; Cw, western redcedar; Fd, Douglas-fir; Hw, western hemlock; Lw, western larch; Pl, lodgepole pine; Pw, western white pine; Se, Engelmann spruce.
[c]Percentage of species in the stand (*t*, <1%).
[d]Braumandl and Curran (1992) describe the ESSFwc1 as moist-wet.

disease centre); and (*iii*) located where no trees showed aboveground symptoms. Trees killed two or fewer years previously retain at least some needles, all fine twigs, and have intact bark, while those killed more than 5 years ago lack needles and fine twigs, have cracked, sloughing bark and checked wood, and often have sporophores of wood decay fungi on their stems. Potential plot locations were flagged, and five of each plot type with uniform stocking and species composition were selected. Plots centred on a tree dead for more than 5 years did not contain more recently killed or living symptomatic trees. Plots centred on a tree dead two or fewer years often contained older dead or symptomatic trees or both. A plot radius of 5.65 m (0.01 ha) was chosen because in stands with a high incidence of symptomatic trees plots with a larger radius would often overlap adjacent disease centres.

Measuring trees in plots

In plots, all living trees more than 1.3 m in height were tagged. Species, diameter at breast height (DBH), origin (planted or natural), location (azimuth and distance from plot centre), and aboveground symptoms of Armillaria root disease (basal resinosis confirmed by mycelial fans) were recorded for each tree. These data were also recorded for diseased dead trees, but these trees were not tagged. The location, species, and diameter of stumps of the previous stand within plots and for about 2 m beyond the plot boundary were recorded also. Stumps were not examined for signs of colonization by *A. ostoyae* because they were too decomposed by insects and fungi in the dry region; elsewhere, many stumps, although intact, were too large to remove with the excavator, especially in the wet region, or their removal would cause unacceptable soil disturbance. The percentage of stumps putatively colonized by *A. ostoyae* within and adjacent to plots was estimated by viewing plot maps and designating stumps likely to be the inoculum source for adjacent trees with belowground infection.

Removing trees and assessing root systems

All trees in plots were carefully pulled from the soil by an excavator with a grasping attachment (see Morrison and Mallett 1996). The 15 sites were done by four skilled operators, each with a similar size of machine; one operator did two thirds of the sites.

Most roots broke during removal of trees from the soil. Roots several centimeters in diameter that broke at or near the root collar were recovered while those more than 2 m from the root collar and less than 2 cm in diameter were usually lost. Roots girdled and decayed by *A. ostoyae* usually broke distal to the proximal margin of an infection where decay was advanced. We assumed that the length of root recovered was proportional to total root length for all species and diameters. Nothing was observed during assessment of root systems to suggest that this assumption was not valid.

Root systems were examined for infection by *A. ostoyae*. Only mycelial fans in the bark or cambium were accepted as evidence of infection. For each tree, the number of primary roots and the number with *A. ostoyae* lesions were recorded. For each lesion, root order (primary, secondary, or tertiary), root diameter, distance from root collar, lesion length, and host reaction (lesion callused or progressive) were recorded.

Statistical analysis

Data were analyzed using the SAS statistical package (SAS Institute Inc., Cary, N.C.). Arcsine transformation of percentage data did not change *p* values. The relationships between belowground incidence of the root disease and climatic region, distance from the plot centre (within or without 3 m), and tree origin (i.e., natural or planted) were investigated by fitting the following logistic regression model by the method of maximum likelihood estimation:

$$p_{ijkluv}(d) = \frac{1}{1 + \exp(\mu + \alpha_i + \tau_j + \lambda_k + \phi_l + \alpha\phi_{il} + \tau\lambda_{jk} + \tau\phi_{jl} + \beta d + \delta_{ijklu} + \varepsilon_{ijkluv}}$$

where $p_{ijkluv}(d)$ is the probability that a tree with DBH d is infected belowground when the tree is located in climatic region i, is located in plot type j, is in distance class k from the plot centre, has origin l, and is growing under the conditions present in site u and plot v; μ is a measure of the overall level of infection; α_i is the effect of climate; τ_j is the effect of plot type; λ_k is the effect of proximity to the plot centre; ϕ_l is the effect of tree origin; $\alpha\phi_{il}$ is the interaction between climatic region and origin; $\tau\lambda_{jk}$ is the interaction between plot type and distance from the plot centre; $\tau\phi_{jl}$ is the interaction between plot type and origin; βd is the effect of tree diameter; and δ_{ijklu} and ε_{ijkluv} are the site and plot effects, respectively. After adjustment for differences in the diameter distribution of the trees, overall effects of interest were investigated by testing the statistical significance of appropriate contrasts of the parameter estimates. The adequacy of the fitted model was assessed by carrying out a Hosmer–Lemeshow (1989) test and by plotting the associated observed versus fitted frequencies. The test revealed no significant lack of fit of the model (p = 0.2072). Analysis of variance was used to test for differences among climatic regions in the percentage of stumps putatively colonized, among measures of disease intensity and host response, and among climatic regions for detection of diseased trees. When differences were found, means were compared using Student–Newman–Keul's test at α = 0.05. Microsoft® Excel was used to determine the line of best fit for disease incidence in relation to stumps putatively colonized (Fig. 5).

Results

The old-growth stands at the 15 sites that preceded the juvenile stands were primarily of 80- to 100-year-old lodgepole pine (*Pinus contorta* Dougl. ex Loud. var *latifolia* Engelm ex S. Wats.) in the dry region, of ca. 100-year-old mixed conifers in the moist region and of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) up to 300+ years old in the wet region. There were an average of 8.1, 5.6, and 3.0 stumps per plot with a mean diameter of 29, 30, and 46 cm in the dry, moist, and wet climatic regions, respectively.

In addition to *A. ostoyae*, *Heterobasidion annosum* (Fr.:Fr.) Bref., *Cronartium ribicola* J.C. Fisch., and *Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka were observed on trees at several sites. *Heterobasidion annosum* caused butt rot in about 1% of planted Douglas-firs at five sites in the moist and wet climatic regions that had western hemlock in the previous stand. The incidences of *C. ribicola* and *E. harknessii* on western white pine (*Pinus monticola* Dougl. ex D. Don) and lodgepole pine, respectively were less than 10%.

Soil adhered to nearly all root systems after removal. During removal of the soil by hand, fewer *A. ostoyae* rhizomorphs were observed on root surfaces and in the surrounding soil at sites in the dry region than in the moist and wet regions.

In the nine stands in the moist and wet regions with both planted and natural regeneration (Table 1), tree ages varied by only 1 or 2 years, but planted trees were larger, 8.2 versus 4.9 cm DBH, and had a greater rooting radius, 1.21 versus 0.98 m.

During analysis of results, it became evident that the ESSFdk site (Table 1) in the dry climatic region differed markedly from the other four sites in that region with respect to disease parameters such as belowground incidence (see Fig. 5), disease intensity, and host response. Values of parameters for the site were typical of those for sites in the moist and wet climatic regions. The site is located at the foot of a slope, and seepage and summer precipitation apparently maintain moist soil throughout most of the growing season. Data from this site were omitted from analyses of climatic region, stumps putatively colonized, intensity of infection, and detection.

Belowground incidence of diseased trees

Climatic region

There were significant differences (p < 0.0001) in the percentage of trees with belowground infection among climatic regions. The incidence of infected trees at sites in the dry region (8%) was significantly less than in the moist (33%) and wet (26%) regions (p < 0.0001 in both cases).

Plot type

The percentage of trees with belowground infection differed significantly (p < 0.0001) among the three plot types. Incidence in asymptomatic plots was significantly less (p < 0.0001) than in plots centred on a dead tree (Fig. 2). There was no difference in incidence between plot types centred on trees dead fewer than two or more than five years (p = 0.36).

In the 25 asymptomatic plots in each climatic region, nine in the dry, one in the moist and four in the wet did not contain trees with belowground infection. In seven plots centred on a dead tree, six dry and one wet, the centre tree was the only one infected in the plot.

Distance from plot centre

The percentage of trees with belowground infection was calculated for 0–3 m and 3.1–5.65 m from the plot centre for each plot type (Fig. 3). Tests of contrasts (adjusted for diameter effects) indicated that, as expected, there was no difference in incidence of infected trees within and without 3 m from the centre of asymptomatic plots (p = 0.1611). However, there were significant differences in plots centred on a tree dead for fewer than 2 years (p = 0.0004) and more than 5 years (p = 0.0052).

Tree DBH and origin

Tree DBH had a significant effect (p = 0.0001) on the probability of a tree being infected below ground. For planted and naturally regenerated trees within and without 3 m from the plot centre, probability of infection increased by about 0.16 as DBH increased from 5 to 15 cm (Fig. 4). Tree origin, planted or naturally regenerated, had a significant effect on the probability of infection at moist sites, where infection was significantly higher (p < 0.0001) in planted than natural trees.

Tree species

Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and lodgepole pine occurred in all climatic regions, while western hemlock, western redcedar and western white pine were found only in the moist and wet regions, and western larch (*Larix occidentalis* Nutt.) was only in the dry and moist regions. In plots centred on a dead tree, belowground incidence on all species was highest in the moist climatic region and lowest in the dry region. Values for Douglas-fir, subalpine fir, spruce, and hemlock were 45–53% in the moist region, 30–37% in

Fig. 2. Belowground incidence of trees with *Armillaria ostoyae* in 0.01-ha plots centred on a tree killed fewer than two (<2) or more than five (>5) years previously and located where there were no symptomatic trees (asym) in the dry, moist, and wet climatic regions of the Nelson forest region. Columns with different letters are significantly different as determined by the Student–Newman–Keuls test (α = 0.05).

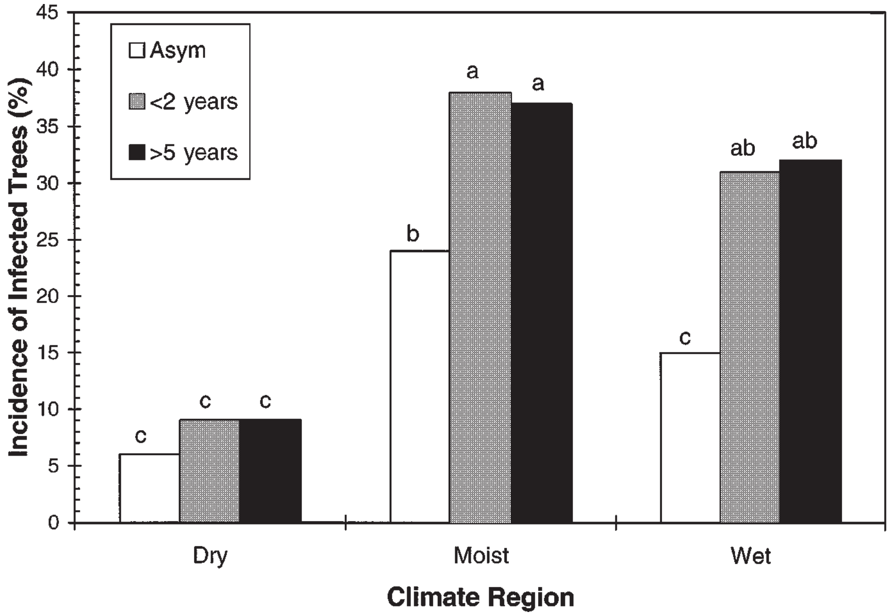
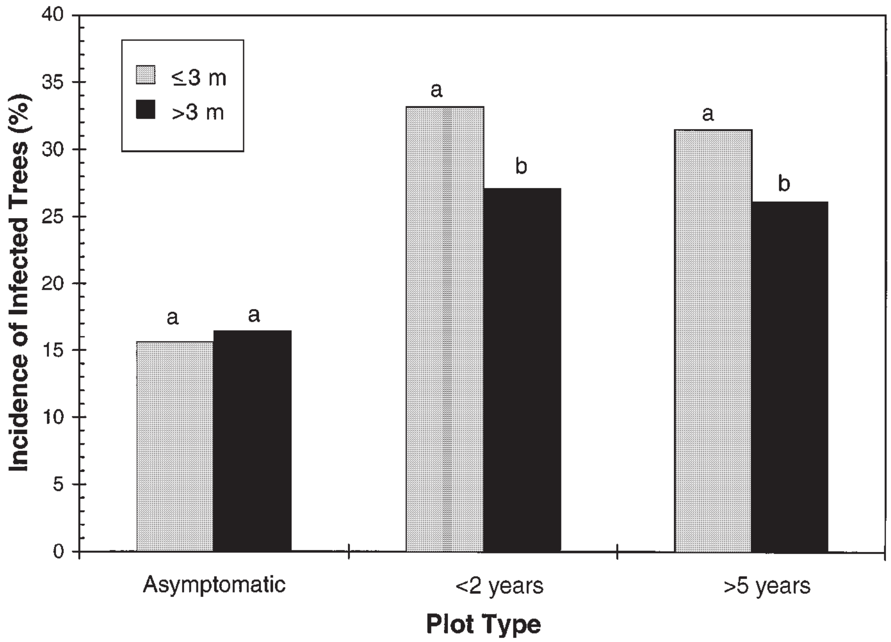


Fig. 3. Belowground incidence of trees with *Armillaria ostoyae* within and without 3 m of 5.65 m radius plots centred on a tree killed fewer than two (<2) or more than five (>5) years previously and located where there were no symptomatic trees (asymptomatic). For each plot type, values in columns with different letters are significantly different as determined by the Student–Newman–Keuls test (α = 0.05).



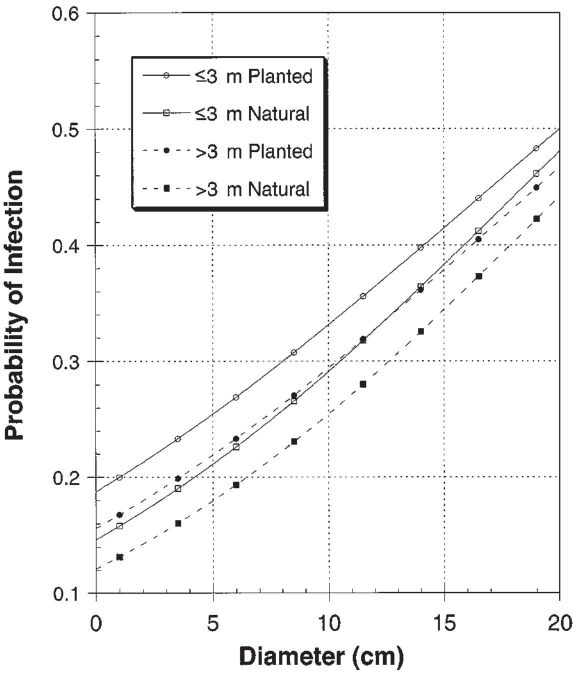
the wet region, and 10–20% in the dry region; those for lodgepole pine, cedar and white pine were lower, 20–27% in the moist, 10–27% in the wet, and 7% in the dry. The value for the small number of larch was 35%.

Percentage of stumps putatively colonized

There were significant differences among climatic regions (p = 0.003) and plot types (p = 0.036) in the percentage of stumps putatively colonized. The value for the dry region (19%) was significantly less than those for the moist (61%) and wet (68%) regions, and it was significantly lower in and around asymptomatic plots (36%) than in those centred on a tree dead more than five (58%) or fewer than two years (60%).

The percentage of trees in plots with belowground infection was related to the percentage of stumps that were putatively

Fig. 4. Estimated probabilities of belowground infection by *Armillaria ostoyae* for planted and naturally regenerated trees up to 20 cm DBH within and without 3 m from the plot centre averaged over all sites and the three plot types. The logistic regression model was used to generate the curves.



colonized in and around plots (Fig. 5); the R^2 value was 0.61.

Intensity of infection

The number of lesions and percentage of primary roots with one or more lesions were used as measures of the intensity of infection on a tree. (In the latter case, a primary root includes its secondary and tertiary branches.) There were significant differences (p = 0.0001) among climatic regions in the number of lesions per infected tree with the value for the dry region (1.8) being significantly lower than those for the moist (2.9) and wet (3.1) regions. There were no significant differences among plot types in the number of lesions per tree. However, there were significant differences (p = 0.0004) among plot types in the percentage of primary roots infected; the value for dead fewer than 2 years (40%) was significantly greater than those for dead more than 5 years (36%) and asymptomatic (33%) plots. There were no differences in the percentage of primary roots with lesions among climatic regions or within and without 3 m from the plot centre.

Host reaction to infection

Resin production at *A. ostoyae* infections was a response common to all coniferous species, although the amount of resin produced varied, being least by western redcedar and greatest by pines. All *A. ostoyae* lesions on roots or the root collar were classified as either callused or progressive; a progressive infection shows no evidence of callus production by the host (see Morrison et al. 1991 for photographs of callused (Fig. 5.4) and progressive (Fig. 5.8) lesions). For trees with more than one progressive infection, the one nearest the root collar classified the tree. The percentage of infected trees with progressive infection differed significantly (p = 0.002) among climatic regions with the dry region (78%) being significantly higher than either the moist (54%) or wet (56%) regions, but it was similar for the two plot types centred on dead trees; in each climatic region, the percentages for asymptomatic plots were 4–7% lower than those for plots centred on a dead tree. On 40–50% of trees with at least one progressive infection, the lesion was at the root collar (Table 2). Another 36–45% of progressive infections were within 50 cm of the root collar. In each climatic region, the percentage of trees with progressive infections was similar within and without 3 m from the plot centre.

Detection of infected trees

For plots centred on dead trees, the number of diseased or dead trees, including the centre tree, showing aboveground root collar symptoms was tallied and the percentage of all diseased trees that was detectable aboveground was calculated and averaged for each site. There were significant differences (p = 0.010) among climatic regions in the percentage of trees with belowground infection that showed aboveground symptoms. In the dry region, the percentage (51%) was significantly higher than in the moist (28%) and wet regions (23%); the percentage was consistently, but not significantly, higher for the dead fewer than 2 years plot type than the more than 5 years type (Fig. 6).

Discussion

These juvenile stands regenerated naturally or were planted or a combination of both following clear-cutting of the previous mature stand. Studies in undisturbed mature stands in the dry and moist climatic regions found that about 10 and 80% of trees, respectively, had localized *A. ostoyae* infections (D.J. Morrison and K.W. Pellow, unpublished data; E. Allen, Canadian Forest Service, Pacific Forestry Centre, personal communication). At dry sites, infected trees occurred singly or in small groups whereas at moist sites only small groups of uninfected trees were found. After logging, the stumps and root systems of infected trees are colonized and become inoculum (Filip 1979; Shaw 1980;Woods 1994). Trees regenerated adjacent to colonized stumps may be infected by rhizomorphs or by transfer of mycelium at root contacts.

The significantly lower belowground incidence of infection by *A. ostoyae* in the dry region compared with the moist and wet regions could be attributed to the following factors: fewer (putatively) colonized stumps and shorter lived inoculum in stumps (Cruickshank et al. 1997); lower frequency of transfer at root contacts (Cruickshank et al. 1997) and fewer rhizomorphs; and lower probability of infection for smaller, naturally regenerated trees. These factors could also account for the larger number of infection-free plots and the smaller number of lesions per infected tree in the dry region. The dry climate apparently affects the ability of trees to resist infection, as evidenced by the significantly higher proportion of progressive infections. As a result, the percentage of trees showing aboveground symptoms in the dry region was twice that of the moist and wet regions. The lower incidence in the wet region than the moist one, although not

Fig. 5. Percentage of trees in juvenile coniferous stands infected by *Armillaria ostoyae* belowground versus the percentage of putatively colonized stumps in three plot types in the dry, moist, and wet climatic regions of the Nelson forest region. The solid squares are the data points for the ESSFdk site.

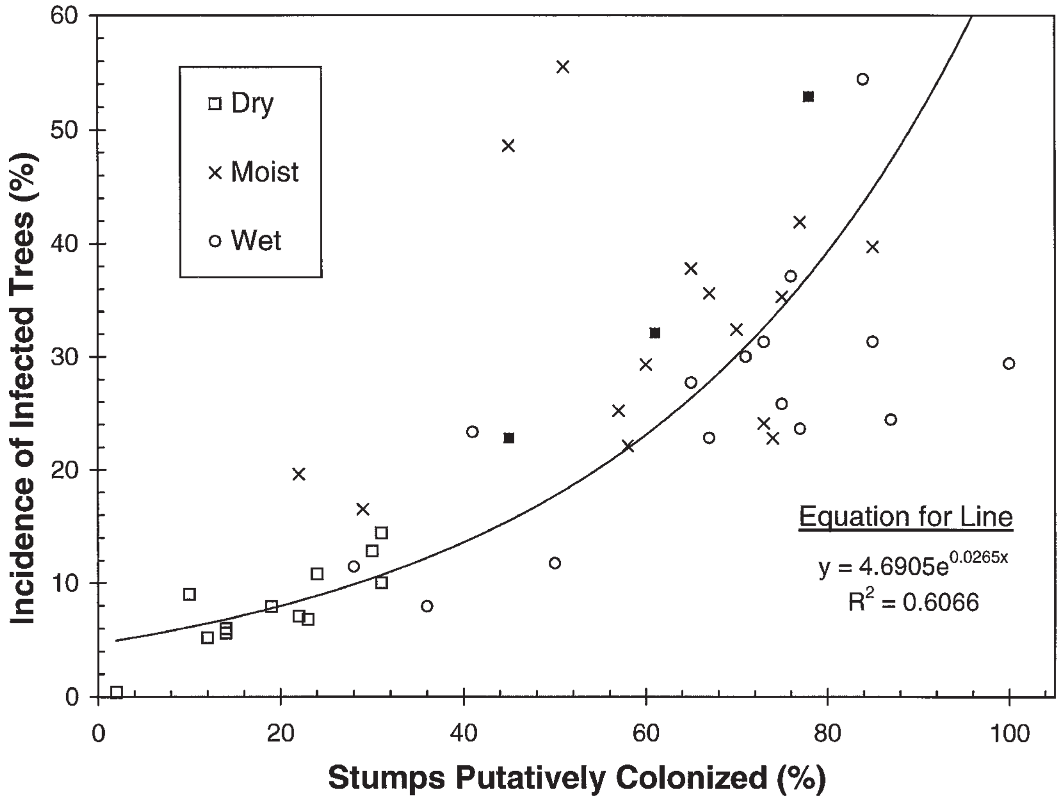


Table 2. Number of trees with belowground infection, the percentage of those trees with progressive infections, and the percentage of trees with progressive infections at the root collar and at 1–50, 51–100, and more than 100 cm from the root collar.

Climate region	No. of infected trees	Trees with progressive infection (%)	Trees with progressive infections at given distances to progressive infection[b] (%)			
			Collar	1–50 cm	51–100 cm	>100 cm
Dry[a]	149	78	38	49	12	1
Moist	574	54	50	36	10	4
Wet	444	56	44	39	14	3

[a]ESSFdk site omitted.
[b]Progressive infection is not callused.

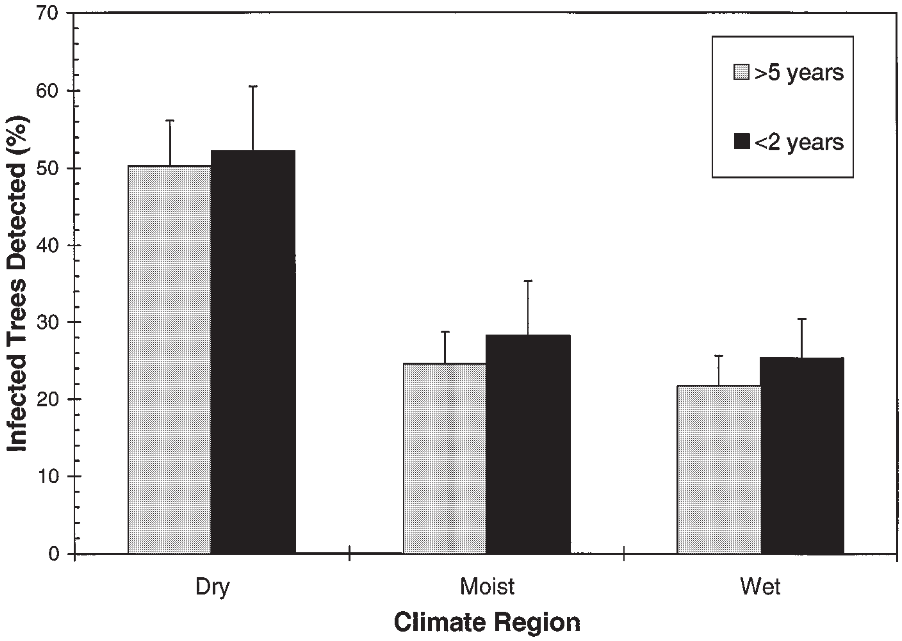
significant, might be due to the smaller number of stumps in the former and the possible negative effects of locally high soil moisture on stump colonization and inoculum longevity (Chang 1996; Cruickshank et al. 1997).

The importance of climatic region to disease epidemiology is clearly shown by the incidence of disease on sites 1 and 8 in the dry and moist regions, respectively, which both regenerated naturally to lodgepole pine following logging of the mature lodgepole pine stands. The numbers of stumps and the age and stocking of regeneration were similar at the sites. Belowground incidence was 7% in symptomatic plots in the dry region and 24% in the moist region. The influence of moisture on disease incidence seen in this study differs from that recorded by Whitney (1984) on black spruce (*Picea mariana* (Mill.) BSP) in Ontario, where incidence of Armillaria root disease decreased with increasing moisture. However, the relative soil moisture scales used in British Columbia and Ontario may not be comparable.

Although the ESSFdk site (Table 1) was located in the dry climatic region, its values for disease parameters such as belowground incidence, intensity of infection, and host response were typical of those for sites in the moist and wet regions, and in retrospect it is a moist site. Hence, in applying these results it is important to recognize that portions of a site may be drier or wetter than the average that classifies the site and that disease epidemiology may vary as a result.

These juvenile stands can be viewed as mosaics of patches containing trees showing aboveground symptoms of Armillaria root disease and patches free from such trees. Thus, the results of this study are applicable to sites showing low to high aboveground incidence of Armillaria root disease because diseased and disease-free strata were sampled.

Fig. 6. Percentage of trees (±SE) with *Armillaria ostoyae* belowground that could be detected from aboveground symptoms on 0.01-ha plots centred on a tree killed fewer than two (<2) or more than five (>5) years ago in the dry, moist, and wet climatic regions of the Nelson forest region.



In the apparently disease-free stratum, at least two thirds of plots contained trees with belowground infection, and in those plots without infected trees either inoculum was not present or the fungus was unable to spread. In addition, fewer colonized stumps and lower inoculum potential, as evidenced by lower disease intensity (i.e., incidence of infection at the root collar, primary roots infected and lesions per diseased tree) on diseased trees could also account for the significantly lower incidence in asymptomatic plots compared with plots centred on a dead tree.

In no climatic region were there significant differences in belowground incidence between plots centred on a recently killed tree and one killed more than 5 years previously. Plots of the former type usually contained old dead trees also. There were no differences in the percentage of infected trees with progressive infections among plot types centred on dead trees for any climatic region. Why has the incidence of mortality declined in plots centred on trees dead for more than 5 years? It may be that inoculum potential is lower in these plots resulting in slower spread of *A. ostoyae* in roots.

In the moist and wet climatic regions, the two planted species, Douglas-fir and spruce, had a significantly higher belowground incidence of infection than the naturally regenerated species. Similar differences in incidence between seeded and planted trees have been observed (Singh and Richardson 1973; Kessler and Moser 1974). However, there is no evidence that juvenile trees of the coniferous species studied herein differ in susceptibility to infection by *A. ostoyae*. The length of roots and hence the area occupied by a root system is greater for dominant than suppressed trees and increases with tree age (McMinn 1963). The probability of a tree becoming infected depends on tree size (Bloomberg and Morrison 1989; Hrib et al. 1983; Rosso and Hansen 1998), number of roots and rooting habit (Reynolds and Bloomberg 1982) as well as on the amount and quality of inoculum around it. Planted and natural trees on each of the nine sites where both occurred were of similar ages; however, planted trees had a larger DBH and had greater average rooting radius resulting in a 45% larger rooting area. These differences could account, in part at least, for the higher incidence among planted trees and for the increasing incidence with increasing DBH.

Surveys for Armillaria root disease in juvenile stands use dead and symptomatic trees to estimate incidence. The results of this study could influence interpretation of survey results and decisions relating to stand tending. Although up to one third of asymptomatic plots did not contain any infected trees, overall in asymptomatic plots, 6, 24 and 15% (Fig. 2) of trees in the dry, moist and wet climatic regions, respectively, had belowground infections. Therefore, in juvenile stands infested with Armillaria root disease, asymptomatic infected trees can be expected to occur in most parts of the stand that appear to be disease free. Mortality among these infected trees should also be expected because one half to three quarters of them have progressive infections. In the vicinity of symptomatic trees, belowground disease incidence increased to 9, 37, and 31% in the three climatic regions; however, in the dry region only about one half of the diseased trees and one quarter in the moist and wet regions showed aboveground symptoms. Consequently, to estimate actual disease incidence, estimates based on aboveground symptoms must be multiplied by a factor appropriate for each climatic region.

Studies by Whitney et al. (1989) and Wallis and Bloomberg (1981) found that aboveground symptoms underestimated incidence of infection belowground by *A. obscura* and *Phellinus weirii* (Murr.) Gilbn., respectively, by about one half. The effect of underestimating the incidence of Armillaria root disease on predictions of yield at rotation age can be seen in the results of runs of the Prognosis model with its root disease extension (Stage et al. 1990), as adapted for the southern interior of British Columbia. The estimated average yield for disease-free sites in the dry climatic region (540 $m^3·ha^{-1}$) was reduced by 10% when visible incidence was used to initialize the model versus 35% when actual incidence was used.

Higher disease incidence within 3 m of the dead tree at the plot centre than without was seen only in plots in the dry and wet climatic regions. This suggests that in these climatic regions symptomatic trees indicate the location of concentrations of inoculum. In contrast, at moist sites incidence was uniform within and without 3 m, indicating uniform distribution of inoculum over large areas. These patterns of incidence in juvenile stands reflect the amount and distribution of potential inoculum in mature stands, as described above.

These juvenile stands are entering a critical period with respect to future development of Armillaria root disease and especially of incidence of mortality. It is unlikely that stumps of the previous stands, colonized by *A. ostoyae* 15–25 years ago, are effective inoculum sources for increasing the incidence of infected trees or intensity of infection on a tree. Excavations have shown that the fungus has exhausted and been replaced in roots less than 5 cm in diameter and in the outer few centimetres of larger roots on 20- to 25-year-old stumps (D.J. Morrison, unpublished results). As juvenile stands age, root systems enlarge, overlap, and develop contacts with those of adjacent trees. The incidence of future mortality in these stands will depend primarily on host resistance, on the incidence of infected trees, on the number and location of progressive infections on them, and on continuous recruitment of these infected trees as new inoculum. Without recruitment of new inoculum, inoculum potential will decline and an equilibrium likely will develop between host and pathogen. A similar scenario was described by Reaves et al. (1993) for a juvenile ponderosa pine (*Pinus ponderosa* Dougl ex Laws.) stand in Washington state.

In the dry region, the high percentage of diseased trees with progressive infections (78%) at or within 50 cm of the root collar (86%) could result in a moderate amount of mortality in the short term. However, the low overall incidence of diseased trees on dry sites (13%) could mean that long term mortality will be low. Although the percentage of trees with progressive infection is lower (55%) in the moist and wet regions, the incidence of diseased trees is two to three times that of the dry region. Hence, the risk of future mortality in the moist and wet regions could also be moderate in the near term. In a 25-year-old, moist region plantation continuing mortality among trees of all diameter classes resulted in development of expanding disease centres and unstocked openings (Morrison and Pellow 1994). It is likely that mortality will continue in such stands as long as there is a supply of suscepts and inoculum with sufficient potential to cause progressive infection on them.

The stocking in all of these juvenile stands (Table 1) is higher than the ca. 1200/ha recommended in Braumandl and Curran (1992). Consequently, some stands could be considered for precommercial thinning, which would reduce stocking to an optimal level and select preferred species as crop trees. On sites infested by Armillaria root disease, precommercial thinning could be counterproductive if it caused an increase in mortality such that stocking fell below prescribed levels. Precommercial thinning in infested juvenile stands increases *A. ostoyae* inoculum when infected trees are cut and the stumps and roots are colonized (Cruickshank et al. 1997) and could upset a developing host–pathogen equilibrium. The risk to crop trees at thinned sites in the dry climatic region could be lower than in the moist and wet regions, because incidence of infected trees is lower, inoculum longevity is less, and tree to tree spread occurs less frequently (Cruickshank et al. 1997). The increase in inoculum can be minimized by not cutting trees in the larger diameter classes, because as van der Kamp (1995) and this study showed, they are more likely to be infected; in addition, they constitute larger more extensive inoculum sources than small diameter trees. The risk to crop trees at many sites in the moist and wet climatic regions may be unacceptably high. However, the higher frequency of callusing at lesions in the moist and wet regions may reduce the risk, especially if the frequency increases with age. The critical factor is inoculum potential and the amount of future mortality could depend on whether precommercial thinning increases inoculum potential to a level that will overcome host resistance.

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