

# Symptom development and mortality rates caused by *Armillaria ostoyae* in juvenile mixed conifer stands in British Columbia's southern interior region

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## ABSTRACT

Plots were established in 20 juvenile mixed conifer stands in the Interior Cedar Hemlock biogeoclimatic zone of British Columbia's southern interior region in western Canada to assess mortality and host response to infection in the form of basal lesions caused by *Armillaria ostoyae*. Western redcedar showed significantly lower mortality and a higher proportion of callused lesions at the root collar than Douglas-fir and western hemlock. Mortality decreased with increasing tree diameter for all species; however, the rate of decrease was markedly greater for western redcedar than Douglas-fir or western hemlock. Results from logistic regression analysis showed that the probability of Douglas-fir being killed is 14.6 times greater than western redcedar in these juvenile stands. Because western redcedar displayed significant resistance to *A. ostoyae* at both the root and stand level, this species represents an excellent choice as a significant stand component with more susceptible conifers. Should susceptible conifers succumb to *Armillaria* root disease, western redcedar will likely fill in the stand.

## 1 | INTRODUCTION

In the southern interior of British Columbia (B.C.), Canada, *Armillaria ostoyae* (Romagn.) Herink (also referred to as *A. solidipes* in North America) poses a serious threat to sustainable forest management because harvesting creates stumps that, unless removed, increase the amount and potential of *Armillaria* inoculum that renders residual or regenerated trees at risk for infection by *Armillaria*. The problem is exacerbated when susceptible hosts, for example Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.), are used for regeneration or replanting in *Armillaria*-infested sites. Cumulative mortality in juvenile stands can be as much as 20% by age 20 years (Morrison & Pellow, 1994; Vyse et al., 2013), and numerous small disease centres may coalesce to form unstocked or understocked openings in the stand.

Few options are available to mitigate potential losses due to *Armillaria* root disease. Mechanical removal of stumps is an effective means to reduce the amount of *Armillaria* inoculum and woody substrates that would otherwise be available to the fungus, which minimizes the extent of *Armillaria*-caused mortality in the regenerating stand (Cleary et al., 2013; Morrison et al., 2014). A less intrusive option is to regenerate tree species that are killed less frequently by *A. ostoyae*. In B.C., no woody hosts have been found that show complete immunity to *A. ostoyae*. Generally, all conifers less than 15-years-old are highly susceptible to *A. ostoyae*-caused mortality, but after this age, some conifers become more tolerant to *A. ostoyae* (Cleary et al., 2008 and references therein). For example, western larch (*Larix occidentalis* Nutt.) shows considerable resistance to the fungus, but only after it reaches about 20–25 years of age (Robinson & Morrison, 2001). However, in young regenerating stands, mortality

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in western larch can be extremely high, exceeding that observed in Douglas-fir (Vyse et al., 2013).

The ability of a host to impede *A. ostoyae* infection and restrict its spread within host tissue by compartmentalization may serve to reduce overall losses to crop tree production. Earlier examinations of western redcedar (*Thuja plicata* Donn ex D. Don) trees naturally infected with *A. ostoyae* (Cleary, unpublished data) and results from field inoculation trials (Cleary et al., 2012), showed that western redcedar contains *A. ostoyae* infections more frequently than Douglas-fir and western hemlock. The question remains whether this observed resistance at the individual root level in western redcedar translates into reduced infection and mortality in mixed species stands. Therefore, the objective of this study was to assess and compare *A. ostoyae* symptom development and mortality in juvenile stands predominated by Douglas-fir with a component of western redcedar.

## 2 | MATERIALS AND METHODS

The study sites were located in the Thompson-Okanagan and Kootenay-Boundary regions in southeastern B.C. in the low- to mid-elevation (400–1500 m) forests of the Interior Cedar Hemlock (ICH) biogeoclimatic zone. In this part of the province, the ICH zone is often referred to as the Interior Wet Belt due to the substantial amount of precipitation and warm moist conditions that prevail. The ICH is the most productive zone in the interior forests and supports the greatest diversity of tree species (up to 15 coniferous and broadleaved species depending on the subzone or variant) than any other ecological zone in B.C. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar are the two most common species that dominate old-growth stands in most ICH subzones. Other common species include Douglas-fir, lodgepole pine (*Pinus contorta* Douglas ex Louden var. *latifolia* Engelm. ex S. Watson), western larch, Engelmann spruce (*Picea engelmanni* Parry ex Engel.), western white pine (*Pinus monticola* Dougl. ex D. Don) and paper birch (*Betula papyrifera* Marsh.), among others. The structure and composition of forests located in the ICH zone have been influenced by a number of disturbances including clearcut harvesting, fire, insect outbreaks and diseases caused by pathogens, such as *A. ostoyae*. The ICH climatic region has a higher incidence of infection by *A. ostoyae* than relatively wet (e.g. Engelmann Spruce–Subalpine Fir) or relatively dry (e.g. Interior Douglas-fir) climatic regions in the southern interior of B.C. (Morrison et al., 2001), and in all but the driest and wettest site series in the ICH, *A. ostoyae* is universally present (Cleary et al., 2008).

For the study, 20 juvenile mixed conifer stands were selected for surveying in the moist-cool (mk) or wet cool (vk) subzones of the ICH zone based on the following criteria: Douglas-fir was a main component of the species mixture (preferably planted) with western redcedar and western hemlock uniformly mixed throughout; moderate to high levels of *Armillaria* root disease present based on symptoms (i.e. foliar chlorosis, thinning crowns, reduced growth of current year's leader and resinosis on conifers) and signs (sub-cortical mycelial

fans at the root collar); and stand age between 15 and 30 years. Stand attributes for all selected sites are shown in Supplementary Table S1.

At each site, transects were established across the stand, starting at least 30 m from the stand edge or landing. At each 50-m stop position, the closest dead coniferous tree killed by *A. ostoyae* greater than 3-cm diameter at breast height (dbh) encountered within a 20-m search radius was considered as a potential plot-centre tree. A 10-m radius plot was centred around the plot-centre tree provided a second set of criteria was met based on visual assessment of the following criteria: at least 10% infection by *A. ostoyae* (lethal and non-lethal) in conifers in the plot, and a minimum number of trees (Douglas-fir and western redcedar) per plot that each comprise >10% of the species composition. Within a plot, the dbh and disease status of each tree (living and dead) greater than 3-cm dbh, regardless of species, was recorded. *Armillaria* infection was confirmed by the presence of sub-cortical mycelial fans or impressions of such fans in resin-soaked or necrotic bark, or both, in all trees suspected of being infected or killed by *A. ostoyae*. The plot-centre tree was not part of the sampling. Soil was removed from the root collar area on all surveyed trees, and the root collar was examined for evidence of old or current basal lesions caused by *A. ostoyae*. Infections at the root collar of living trees were classified as either 'progressive' or 'callused'. Standing dead or downed trees killed by other biotic agents or abiotic factors were also recorded. A minimum distance of 50 m between transect lines avoided any overlap with adjacent plots.

The proportion of trees killed or infected by *A. ostoyae* was determined by species for each plot and site. Frequency data for species mortality were analysed by chi-square tests. To assess the effects of *A. ostoyae* on the probability of host species mortality, the following logistic model was fitted to the data [i.e.  $\log p/(1-p) = a + b(\text{dbh})$ ] where 'p' is the probability of mortality and 'a' and 'b' are regression coefficients with diameter x (mm) for the two species tested (western redcedar and Douglas-fir). The Hosmer–Lemeshow goodness of fit test was used to test whether the model fits the data adequately. All statistical analysis was done using SPSS statistical package (SPSS Inc.).

## 3 | RESULTS AND DISCUSSION

The sample population comprised 51 plots across 20 sites and a total of 7175 trees (Table S1). The number of trees per plot across all sites ranged between 67 and 299 (average 140). Across all sites, the mean proportion for Douglas-fir and western redcedar was similar at 33.0% and 31.3%, respectively. With the exception of western hemlock, Douglas-fir and western redcedar, the number of other host species in these mixed stands was too low to compare incidence. Cumulative mortality caused by *A. ostoyae* ranged between 4.3% and 32.2% with an average of 11.4% (Table S1). Incidence of infection (including live, infected trees) was 1.1- to 3.2-fold higher than mortality; however, the actual (belowground) incidence was almost certainly

TABLE 1 Proportion of trees by disease status category for all tree species tallied in plots.

Disease status	Douglas-fir	Western hemlock	Western redcedar	Willow	Black cotton-wood	Trembling aspen	Red alder	Douglas maple	Paper birch	Grand fir	Western larch	Lodgepole pine	Engelmann spruce	Western white pine	Total
Healthy	0.69	0.78	0.95	0.74	0.99	0.95	1.00	1.00	0.99	1.00	0.72	0.73	0.86	0.64	0.81
Infected by <i>A. ostroyae</i> (PROGRESSIVE) <sup>a</sup>	0.06	0.07	tr <sup>b</sup>	-	-	-	-	-	-	-	0.02	-	0.06	0.02	0.03
Infected by <i>A. ostroyae</i> (CALLOSED) <sup>c</sup>	0.01	0.04	0.03	-	-	-	-	-	-	-	-	-	-	-	0.02
Dead (KILLED by <i>A. ostroyae</i> )	0.25	0.11	0.02	0.02	-	-	-	-	-	-	0.23	0.18	0.08	0.14	0.12
Dead (unknown/other factors)	tr <sup>d</sup>	0.00	tr <sup>d</sup>	0.24	0.01	0.05	-	-	0.01	-	0.02	0.09	-	0.19	0.02
Total	1 (n = 2396)	1 (n = 1220)	1 (n = 2169)	1 (n = 277)	1 (n = 94)	1 (n = 21)	1 (n = 2)	1 (n = 5)	1 (n = 485)	1 (n = 24)	1 (n = 90)	1 (n = 11)	1 (n = 139)	1 (n = 242)	1 (n = 7175)

<sup>a</sup> Progressive lesions are defined as infections at the root collar that lack evidence of necrophylactic periderm formation in the bark or compartmentalization. Lesions appeared as browned tissue in advance of mycelial colonization.

<sup>b</sup> tr = proportion of trees with progressive lesions at the root collar was less than 0.005.

<sup>c</sup> Callused lesions are defined as infections at the root collar that were compartmentalized and spread of the fungus had been stopped.

<sup>d</sup> tr = proportion of trees killed by unknown/other factors was less than 0.005.

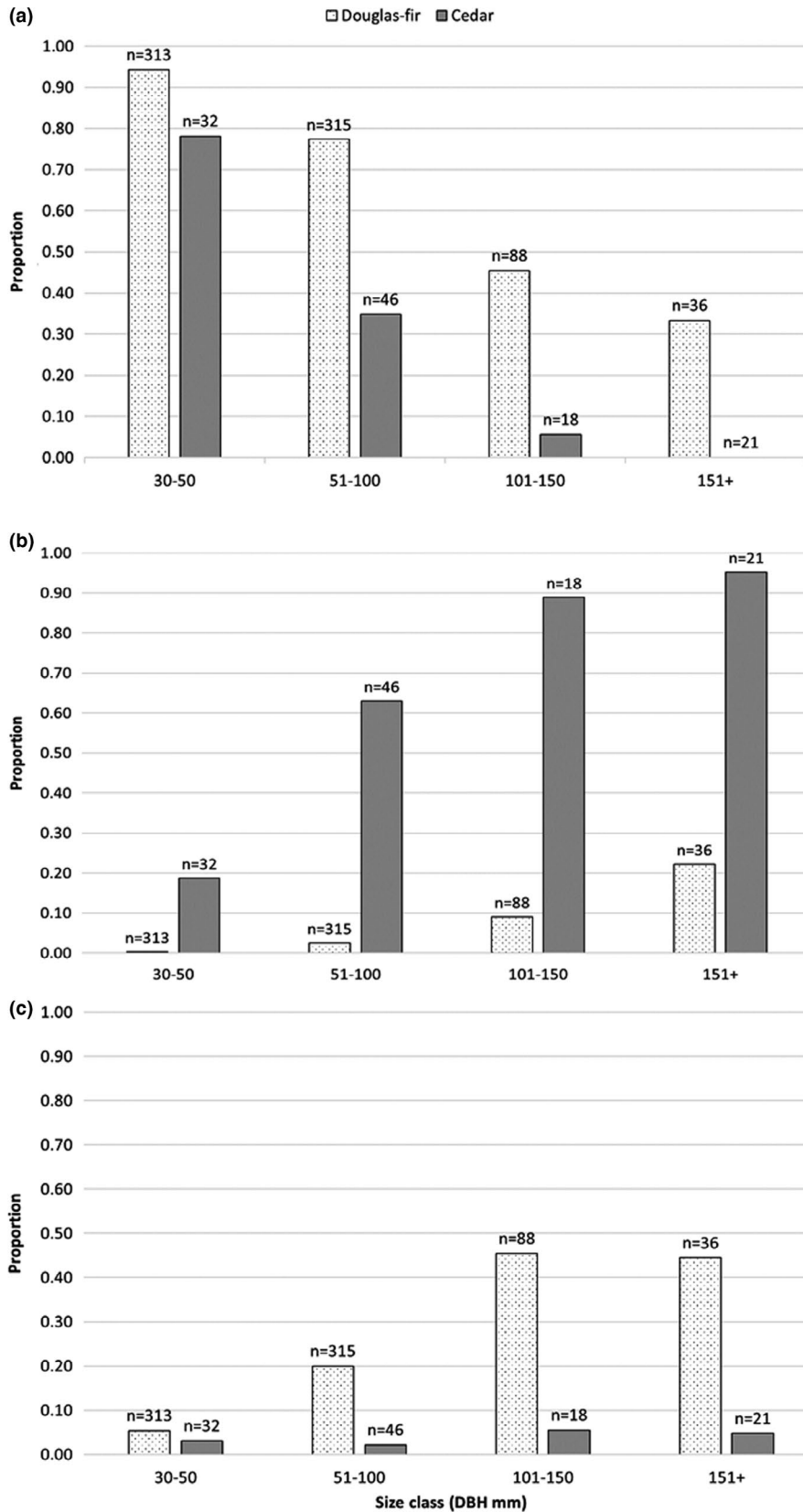


FIGURE 1 (a) Mortality, (b) callused lesions at the root collar, and (c) progressive lesions at the root collar in Douglas-fir and western redcedar as a proportion of the total number of trees with signs or symptoms of *Armillaria ostoyae* by diameter class.

higher than was visually detected because only the root collars, not entire root systems, were examined. The two sites with the highest proportion of Douglas-fir (Mabel Lake\_2 and Trinity Valley) also showed the highest cumulative mortality (mainly of Douglas-fir) and

the smallest margin between mortality and aboveground incidence (which includes also live, infected trees, Table S1). These stands were among the youngest (15- to 16-year-old) and already approximately one-third of the crop trees had been killed by *Armillaria* root disease.

### 3.1 | Comparison of Douglas fir and western redcedar

Significant differences ( $p < 0.0001$ ) were observed in the incidence of mortality between Douglas-fir and western redcedar at all sites. Overall, 25% ( $n = 2396$ ) of the Douglas-fir trees were killed by *A. ostoyae* compared to only 2% ( $n = 2169$ ) of the western redcedar trees (Table 1). The logistic model indicated that probability of mortality among trees infected by *A. ostoyae* depended on both species and dbh ( $\beta = -2.683$ ,  $p < 0.0001$ ). The incidence of mortality was significantly greater in the smaller diameter classes than in the larger ones for both tree species and western redcedar mortality was consistently lower than that of Douglas-fir. Although the incidence of mortality decreased with increasing tree size for both species, the rate of decrease was noticeably greater with western redcedar compared to Douglas-fir (Figure 1a). The Hosmer–Lemeshow test was not significant suggesting that the logistic model adequately fits the data ( $\chi^2 = 3.733$ ,  $p = 0.880$ ). The logistic model calculated the corresponding odds ratio which indicated that in young juvenile stands in the southern interior of B.C., the probability of a Douglas-fir being killed ( $\text{Exp}\beta$ ) is 14.6 times greater (95% C.I. = 10.57, 20.71) than western redcedar.

Among trees with symptoms of *A. ostoyae*, the incidence of compartmentalization and callusing at the root collar was significantly higher in western redcedar (61%,  $n = 117$ ) than in Douglas-fir (3%,  $n = 752$ ). Callused lesions at the root collar on cedar typically appear as a flattened area at the base of the stem and fluting of the trunk as a result of effective barrier zone formation and lateral ingrowth of callus from the edge of the injured cambium. The proportion of infected trees showing compartmentalization and callusing increased with increasing tree size for both western redcedar and Douglas-fir, but the increase was markedly greater for western redcedar than for Douglas-fir (Figure 1b).

Only 4 of 117 (3%) of infected western redcedar trees had progressive lesions at the root collar compared to 136 of 752 (18%) of the Douglas-fir trees. The proportion of Douglas-firs with one or more progressive lesions increased with increasing tree dbh. However, tree dbh had no effect on response of western redcedar (Figure 1c). Examinations on Douglas-fir stem discs cut from the base of infected trees indicate continuous formation and breaching of necrophylactic periderm (NP) in the bark and barrier zones formed by the uninjured cambium to compartmentalize the infection in subsequent years as *A. ostoyae* colonizes progressively more tissue (Figure S1). In several cases, basal resinosis occurred around the entire circumference of the Douglas-fir root collar, yet trees lacked distinctive crown symptoms indicative of root disease (i.e. foliar chlorosis, thinning crowns with shorter and fewer needles, growth reduction of current year's leader), suggesting that crown symptoms are not always reliable indicators of root disease presence, at least on Douglas-fir, especially in cases where *A. ostoyae* advances quickly in the root system, such as during the dormant season. Progressive lesions at the root collar indicate an increased risk of future tree mortality. The lower frequency of progressive lesions at the root collar on western redcedar

relative to Douglas-fir suggests that fewer western redcedar trees are at risk of being killed by *A. ostoyae*.

### 3.2 | Comparison among Douglas fir, western hemlock and western redcedar

Comparisons among Douglas-fir, western hemlock and western redcedar were done using a data set comprised of 10 sites in which western hemlock represented at least 10% of the stand (Table S1). All species differed significantly from each other ( $\chi^2$ ,  $p < 0.001$ ) and are ranked in decreasing incidence of mortality: Douglas-fir (19%,  $n = 900$ ), western hemlock (10%,  $n = 1075$ ) and western redcedar (1%,  $n = 1072$ ). In general, mortality decreased with increasing dbh for all species. For Douglas-fir and western hemlock, the rate of decrease was similar across diameter classes (Figure S2), although there was more mortality of Douglas-fir in larger classes. Western redcedar mortality was low overall and associated with only the smallest diameter classes.

The frequency of compartmentalizing and callusing in western redcedar was significantly higher than western hemlock and Douglas-fir ( $\chi^2$ ,  $p < 0.001$ ). In addition, compartmentalization and callusing of basal lesions were significantly higher in western hemlock (17%,  $n = 222$ ) than in Douglas-fir (3%,  $n = 243$ ) ( $\chi^2$ ,  $p < 0.001$ ). Although both western redcedar and western hemlock showed a marked increase in the frequency of callused lesions with increasing tree size, this increase occurred much sooner on western redcedar than on western hemlock (Figure S2). Tree size did not appear to influence the frequency of callused lesions in Douglas-fir. The proportion of trees with progressive lesions at the root collar was higher in western hemlock (33%,  $n = 222$ ) than Douglas-fir (27%,  $n = 244$ ), though not significant. Progressive lesions on Douglas-fir generally increased with tree dbh, but the same trend was not evident in western hemlock.

Given similar incidence of infection, the frequency of *A. ostoyae*-caused mortality of a particular host species is a direct measure of its resistance and ability to survive in the presence of *A. ostoyae* inoculum. On western redcedar, *A. ostoyae* infections resulted in callused lesions at the root collar, but few progressive lesions and little mortality. These observations are consistent with results from field studies of similarly aged trees showing a higher frequency of successful host reactions to contain the infection in western redcedar than in western hemlock and Douglas-fir (Cleary et al., 2012). Western redcedar frequently forms a NP barrier and induced rhizodome formation proximally and distally to the primary lesion, which is eventually sloughed. Observations of lesion formation at root contacts between naturally infected Douglas-fir suggest that the frequency of *A. ostoyae* mycelial transfer is much lower between Douglas-fir and western redcedar than between Douglas-fir and western hemlock (Cleary, unpublished data), which further suggests that western redcedar can serve as a barrier to *A. ostoyae* spread between roots of susceptible hosts. When *A. ostoyae* infections advance in lateral roots of western redcedar, the infections are frequently contained

within a polyphenolic-rich barrier zone formed by the uninjured cambium that, unlike the barrier zone formed in Douglas-fir, is not readily breached (Figure S1). Such effective resistance responses in western redcedar at the root level probably contribute to low mortality in western redcedar compared to other common conifers when growing in mixed stands. In a 20-year-old species trial in the ICH southern interior, Vyse et al. (2013) reported mortality in Douglas-fir and western larch was 7 and 10 times greater, respectively, than in western redcedar. Furthermore, results from a long-term stumping trial showed mortality in western redcedar to be significantly lower than other planted conifers such as Douglas-fir and western larch (Cleary et al., 2013; Cruickshank et al., 2018; Morrison et al., 2014). Together, these findings suggest that western redcedar has higher resistance/tolerance to *A. ostoyae* relative to other conifers.

In the majority of Douglas-fir plantations in the ICH, western redcedar and western hemlock regenerate naturally, so that these naturally regenerated, shade tolerant trees are typically younger and smaller than the planted trees in young stands, which might suggest that mortality in the planted Douglas-fir has been happening for at least a few years longer than the other tree species. Nonetheless, reduced mortality rates exhibited in even the intermediate diameter classes and the higher frequency of callusing observed in the smallest diameter class indicates that western redcedar is more resistant to infection by *A. ostoyae* and that this resistance occurs much earlier than in the other conifers.

Rapid regeneration following harvesting of mature stands in the ICH increases the likelihood that young conifers are exposed to *A. ostoyae* inoculum when it is at or near its peak potential, which can result in considerable mortality or growth repression in trees that sustain non-lethal infections. So long as a continuous supply of *A. ostoyae* inoculum is maintained and inoculum transmission occurs between infected and healthy crop trees, timber productivity will fall below expectations. In the southern interior ICH, management of second-growth stands without addressing *Armillaria* root disease may result in serious losses at early stages of stand development (e.g. after the free-growing declaration). For example, approximately one-third of the crop trees had already been killed by *A. ostoyae* by age 15–16 years at Mabel Lake\_2 and Trinity Valley sites. The results of this study provide more certainty that western redcedar will not be significantly harmed by *A. ostoyae*. When faced with planting a new clearing with unknown *A. ostoyae* inoculum density, which is a common situation in the ICH zone in the southern interior, and where stump removal is not feasible, a reasonable approach would be planting a uniform mixture of Douglas-fir (or other susceptible species) and western redcedar. Where *A. ostoyae* inoculum turns out to be low, the Douglas-fir will outcompete the western redcedar to generate a healthy, mainly Douglas-fir stand. Where *A. ostoyae* inoculum is high, most of the Douglas-fir will die, but the western redcedar will form a full-canopy stand with a good yield, even if not as desirable as Douglas-fir. However, Cruickshank et al. (2018) suggest that basal lesions on western redcedar may serve as a precursor for other butt decay-fungi to become established.

In forest succession within the ICH, seral species like Douglas-fir are replaced by western redcedar and western hemlock, the climax species of this zone. Morrison and Pellow (1994) reported that expanding root disease centres in juvenile, Douglas-fir stands in the ICH had filled in with naturally regenerated western hemlock and western redcedar. Thus, *A. ostoyae* likely plays a large role in accelerating species succession in this zone by selectively removing susceptible host species and creating gaps in the stand that are filled in by tree species that are more resistant to *Armillaria* root disease. While the ingrowth of western redcedar or western hemlock can provide some compensation for losses of desired crop trees, this change is often not anticipated nor has it been traditionally monitored beyond the free-growing declaration, which can lead to large underestimates in the expected timber yields at rotation, and thus, managers need to account for any yield adjustments caused by a major change in the leading species. In conclusion, the inclusion of western redcedar in higher proportions when planting infested sites may reduce the overall impact of *Armillaria* root disease. Further investigation into disease epidemiology in mixed conifer stands with higher proportions of western redcedar is warranted.

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#### PEER REVIEW

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#### DATA AVAILABILITY STATEMENT

Data available in article supplementary material.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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