# Control of laminated and Armillaria root diseases by stump removal and tree species mixtures: amount and cause of mortality and impact on yield after 40 years.

D.J. Morrison, [1]M.G. Cruickshank and A. Lalumière, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Road, Victoria, BC Canada V8Z 1M5

[1] Corresponding author tel.: 1-250-298-2546, email: mcruicks@nrcan.gc.ca

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**Abstract**

In 1968 a trial was established near Salmon Arm in the southern interior of British Columbia to determine if whole tree logging and root raking would reduce mortality in the next rotation on a site infested by *Phellinus sulphurascens*, cause of laminated root disease. In stumped and not stumped blocks, seedlings of Douglas-fir, lodgepole pine, western redcedar and paper birch were planted alone and in all combinations of two species in three 0.04 ha plots per block; western larch and Engelmann spruce were planted on one plot in each block. Tree mortality was recorded periodically by cause over 40 years. Dominant height, diameter, and basal area were measured every five years after 20 years. The highest survival after 40 years occurred in plots where stumps were removed, especially in those of Douglas-fir alone or in mixture or of spruce or larch. Mortality averaged over all species at age 40 was on average 14% lower in plots stumped (0.47) than in those not stumped (0.61). Principal causes of mortality in both blocks to year 40 were planting failure, root diseases (mainly *Armillaria ostoyae*), abiotics, thinning, and for lodgepole pine, mountain pine beetle. Stump removal and root raking improved planting survival and reduced root disease mortality caused by *P. sulphurascens* and *A. ostoyae*. For all species except pine ($p>0.34$), spruce ($p=0.14$), and redcedar ($p>0.24$) and with the exception Douglas-fir with redcedar ($p=0.005$), yield in plots stumped showed positive effects on basal area by age 40 compared to plots not stumped, especially for western larch (60, 40 $m^2$/ha, respectively) or Douglas-fir (56, 40 $m^2$/ha, respectively). By age 40, height growth was also greater (average 70 cm) in plots stumped for most species. Quadratic mean diameter (QMD) of the 10 largest trees by age 40 was not different between stump treatments despite the greater density of the plots stumped. QMD of all trees and the 10 largest trees per plots was most affected by the tree species, where plots of larch and Douglas-fir had the largest trees. Admixing of tree species usually lowered overall combined basal area and had varying effects on tree height and diameter compared to monocultures. Admixing of resistant and susceptible tree species provided little benefit on reducing disease impact in the susceptible species. Disease impact might be lowered longer-term by disease-tolerant tree species, like cedar, having low impact from both root diseases and shade tolerance, which are then positioned to take advantage of canopy gaps created by disease and insects. Admixing is affected by functional traits that alter the combining ability of the tree species and their interaction with pests.

## 1. Introduction

Pathogenic root inhabiting fungi (*sensu* Garrett 1960) are a taxonomically diverse group of Basidiomycota that cause economically important root diseases of woody plants, worldwide. These fungi infect and frequently kill their hosts during the parasitic phase of their life cycle and then utilize host tissues as a food base during the saprophytic part. Both parts of the life cycle may be from a few years to a few decades in duration, depending on characteristics of host and pathogen and influence of environmental factors. Spread of the fungi from a food base to a susceptible host is usually by mycelial transfer at points of root contact because most of them are incapable of growth through soil. Fungal inoculum in a food base is long-lived and much of it is belowground. Hence, susceptible hosts may be exposed to inoculum for a long time.

Measures that have been researched for reducing losses to root diseases in plantations include fallow, palliative, crop rotation and mixed species planting and inoculum reduction. Greig and Low (1975) reported a reduction in mortality by *Fomes annosus* (Fr.) Bref. (*Heterobasidion annosum sensu lato*) with increasing length of the planting delay (fallow). Palliative measures were manual removal of epiphytic rhizomorphs and infected roots (Napper 1940) and fertilization of diseased trees (Rykowski 1981, Thies and Westlind 2005, Wallis and Reynolds 1974). The former was effective and the latter was not in reducing host mortality.

Crop rotation is widely used in agriculture to reduce losses from disease and species mixtures have been advocated to reduce spread and impact for many pests (Pimm 1984). These measures are often difficult to apply in forests because of the longevity of inoculum and crop and silvics of tree species. However, lists of tree species susceptibility to infection or killing are available for some important root diseases in certain ecosystems (Cleary et al. 2008, 2011, Greig 1979, Thies and Sturrock 1995)

Measures to reduce the amount and longevity of inoculum of root disease fungi include ring-barking, tree or stump poisoning, fumigation, stump inoculation with saprophytic fungi, and mechanical removal. The objective of ring-barking or poisoning or both was to kill the root system of a susceptible host as quickly as possible, facilitating colonization of its roots by saprophytic fungi and halting further spread in already infected roots or those in contact with inoculum (Garrett 1970). The method was successful in East Africa (Leach 1939) and Malaysia (Napper 1940, Fox 1965). However, Swift (1970) concluded that spread of an *Armillaria* sp. from pre-existing lesions was not inhibited and was probably enhanced. In temperate regions, ring-barking and stump poisoning were ineffective in reducing colonization of root systems by *Armillaria* spp. (Redfern 1968, Sokolov 1964), killing of young trees or number of *Armillaria* sp. basidiomes (Punter 1963).

Various fumigants reduced or eradicated root disease fungi in root systems (Bliss 1951, Filip and Roth 1977, Thies and Nelson 1982). Use of fumigants is usually considered practicable only on a small scale or in high-value crops.

Proposed and developed by Rishbeth (1951, 1963), inoculation of stumps with *Phlebiopsis* (*Peniophora*) *gigantea* (Fr.) Jülich to reduce their colonization by *Heterobasidion annosum* (*sensu lato*) is the only successful, practical biological control for a root disease. Experimental work suggested that cord forming species of *Hypholoma* may limit colonization of stumps by *Armillaria* spp. (Chapman and Xiao 2000, Rayner 1977, Pearce and Malajczuk 1990).

Removal of stumps and roots from the soil to reduce the inoculum of pathogenic root inhabiting fungi was advocated first by Hartig (1874) and frequently since then (see review by Vasaitis et al. 2008). *Phellinus sulphurascens* Pilát and *Armillaria ostoyae* (Romagn.) Herink) are common in coniferous forests of the northwestern United States and southern British Columbia (Thies and Sturrock 1995). Studies in BC, Alberta, Washington and Oregon revealed substantial impacts on survival (Morrison 2011) and growth (Cruickshank 2010, 2011, Goheen and Hansen 1993, Mallett and Volney 1999, Thies 1983) by laminated or Armillaria or both root diseases in managed stands. At eight stump removal trials, survival of conifers in areas where stumps were not removed ranged from 97.1% (16 years) to 81.6% (30 years, average of 92.4 % after 20 years) of that in areas where stumps were removed (Sturrock 2000). The 35-year-old trial in Washington State to control Armillaria root disease in ponderosa pine showed that stump removal promoted height but not diameter growth, and reduced the areas containing high mortality, but only for the most extensive treatment (Shaw et al. 2012). Data, especially for volume or basal area yield in most tree species challenged with root disease are not available.

The trial at Skimikin was established in 1968 by L.C. Weir to determine (1) the efficacy of inoculum removal for control of *Poria* weirii Murr. (later, *Phellinus weirii* (Murr.) Gilbn. and now *P. sulphurascens*), (2) to evaluate the resistance to killing of several tree species and (3) to observe the effect on disease spread of alternating rows of susceptible and less susceptible or immune species (Weir and Johnson 1970). Progress reports published in 1988 (Morrison et al.) and 1998 (Morrison) showed that Armillaria root disease (*A. ostoyae)* was the biotic agent killing most trees in the trial. This paper reports the incidence and causes of mortality and their spatial and temporal distributions. In addition, the trial yielded data on the productivity of tree species in monocultures and mixtures and their interactions with disease, stump removal and time. There are potentially four effects that may alter productivity in this study, (1) growth reduction due to non-lethal infections, (2) differences in survival, (3) the stump removal treatment itself, and (4) interactions between tree species and pests; these are discussed. The proportion of surviving trees is not always a reliable indicator of belowground infection for root disease (Cruickshank et al. 2011), so that none of these effects on yields can be easily separated from the other effects in this study without destructive sampling.

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## 2. Materials and methods

2.1 Location, design, establishment and maintenance of the trial

The trial is located at Skimikin (50° 48’ N, 119° 26’ W) near Salmon Arm, British Columbia. The site is in the mw2 subzone of the Interior Cedar Hemlock (ICH) biogeoclimatic zone (Lloyd et al. 1990) at an elevation of 750 m with a south aspect and slope of about 5%. Mean annual precipitation is 625 mm, 40% of which falls between May and September and 30% as snow. The soil is an utric brunisol occurring on a glacial fluvial deposit. The mature stand in which the trial was established consisted of 75% Douglas-fir [*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco] and 25% lodgepole pine (pine) [*Pinus contorta* Dougl. *et* Loud. var. *latifolia* Engelm. *ex* S. Wats.] with an understory composed of small numbers of western redcedar (redcedar) [*Thuja plicata* Donn *ex* D. Don] and Pacific yew [*Taxus brevifolia* Nutt.]. The overstory trees were about 80 years old. Openings in the stand caused by *P. sulphurascens* contained paper birch (birch) [*Betula papyrifera* Marsh] and trembling aspen [*Populus tremuloides* Michx.].

Two adjacent 80 m by 160 m blocks were laid out in the stand across the slope. All trees within the blocks were tallied with respect to species, diameter, condition (living or dead) and location. About 20% of the Douglas-fir and pine had been killed by *P. sulphurascens* and the cut surface of 60-70% of stumps had decay or stain typical of the fungus (Weir and Johnson 1970. In the block designated for stump removal (stumped), trees were pushed over by a bulldozer and were yarded to the landing with roots attached; following tree removal, this block was root raked to a depth of 45 cm using a bulldozer fitted with a toothed land clearing blade. In the not stumped block, trees were felled and skidded to the landing in the conventional manner. A 10 m wide strip around the blocks was push-felled and root raked to reduce the chance of root disease entering the blocks from the surrounding stand. Each block was divided into 32, 20 m by 20 m plots.

To determine the effect of push-falling and root raking on the number, size and distribution of residual roots, pits were excavated near locations of stumps infected by *P. sulphurascens* in the push-felled surround area prior to root raking and in the not stumped area. Tree roots were collected from depths of 0-30 and 31-60 cm, taken to the laboratory and examined for colonization by fungi. The number, diameter and length of roots and the identity of fungi colonizing them (*P. sulphurascens*, *Armillaria* sp. or other) were determined for each depth class and treatment (Weir and Johnson 1970).

All commercial conifer species within the range of *P. sulphurascens* are susceptible to infection (Buckland et al. 1954, Childs 1970). Douglas-fir, pine, redcedar, and birch, which are highly susceptible, tolerant, resistant, and immune to *P. sulphurascens*, respectively (Cleary et al. 2011), were selected for planting. All study tree species are susceptible to infection by *A. ostoyae*, but susceptibility to killing is high for Douglas-fir, moderate for spruce and pine, and low for larch, cedar and birch (Cleary et al. 2008). Seedlings were planted at 1.5 m by 1.5 m spacing, usually with 13 rows of 13 trees in each plot. Three plots in each block were randomly selected for planting with each species alone and all combinations of two species. One of the remaining two plots in each block was planted with western larch (larch) (*Larix occidentalis* Nutt.) and the other with Engelmann spruce (spruce) (*Picea engelmannii* Parry). Seedlings were nursery-grown, 2+0, bare root stock, except for cedar and birch which were wildlings from the vicinity of the trial. Seedlings were planted early in November 1968. In 1969 and 1970, dead seedlings were replaced using similar planting stock.

Competition for light is strong for the shade-intolerant species lodgepole pine, paper birch, and western larch, spruce and Douglas-fir are more tolerant, and western redcedar is the most shade-tolerant (Burns and Honkala 1990). Fast early growth is linked to those species that are shade-intolerant and vice versa. While competition for light occurs at any age, drought is a common first year seedling problem affecting survival in most of the conifers. Tree species also differ in longevity with lodgepole pine and paper birch being short-lived (50-80 years), Douglas-fir and western larch are moderately long-lived, and western redcedar and Engelmann spruce often live the longest (Burns and Honkala 1990).

Seedling survival was assessed in 1973. No mortality due to root disease was observed, however in some plots numerous seedlings had failed to become established. A stem map was prepared for each plot. The number of living trees in each plot in 1973 was taken as the starting point for subsequent calculations of percent mortality. Assessments of tree condition were made in 1977, 1981 and 1983 and cause and year of mortality were recorded on the stem maps. In both blocks in 1987, birch or cedar was cut in one or two of the three, 2-species plots with Douglas-fir or pine where their numbers were small (Table 1). In addition, one or two plots in each block containing one species were thinned (Table 1) to increase inter-tree distance and to address practitioners questions about causing an increase in root disease incidence among residuals when infected trees are cut. The remaining trees were tagged, their diameter at breast height (1.3m) over bark (dbh) was measured and the height of four dominant or co-dominant trees (except redcedar and birch) per plot was measured. Tree condition was assessed, dbh and height were measured and the data file was updated in 1992, 1997, 2002 and 2007. For each species in Figure 1, the percentage of trees killed by *Armillaria ostoyae* (Romagn.) Herink or *P. sulphurascens* was calculated for six time periods between 1973 and 2007 by dividing the number of trees killed during a period by the number living at the beginning of the period.

The purpose of planting alternate rows of susceptible, resistant or immune species was to observe the effect on root disease spread; this is of most interest in the not stumped block. In 1987, the number of root disease centers with two or more trees killed by *A. ostoyae* was tallied in plots of Douglas-fir, pine and Douglas-fir - pine and in plots of those species alternating with rows of redcedar or birch (Morrison et al. 1988). We tested again for an effect using 30$^{th}$-year data for all root disease mortality from the same plots. (Thirtieth-year data was used to avoid the confounding effect of later mountain pine beetle mortality.) Each 20-m-square plot was divided into 5mx5m square boxes to give 16 boxes per plot. For monocultures, every second row was deleted in order that boxes in plots would be similar to those in mixed species plots with susceptible trees every second row. The number of root disease-killed trees was tallied in each box. Fewer dead trees in clumps, indicating less secondary spread, would show as a greater proportion of boxes with fewer dead trees. Spacing had no effect (p=0.77) on the proportion of observation in categories of 1-7 dead trees per box. We then tested if species mixes had any effect on the proportion of boxes with dead trees per box with Chi-square test using exact p values.

Tree health status was recorded for each tree at each assessment, and if it was alive or dead. Tree status values were: did not establish (dead by 1973), *Armillaria ostoyae, Phellinus sulphurascens, Phaeolus schweinitzii* (Fr.) Pat., *Ophiostoma wageneri* (Goheen & F.W. Cobb) T.C. Harr., *Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka, *Dendroctonus ponderosae* Hopkins, suppression, breakage, snowpress, windthrow, animal, cut, other (undiagnosed) and missing. Fungi causing mortality were identified by their signs or by culturing or both; insects were identified by entomologists at Pacific Forestry Centre.

All summary data for tables and all statistical analyses were done using SAS System v9.2 (SAS Institute).

## 2.2 Statistical models

### 2.2.1Survival/hazard analysis

We first investigated the use of parametric regression models (proc GLIMMIX, mixed model categorical regression) and semi parametric models (proc PHREG, Cox's proportional hazard model), but found poor fit for both types of models. Survival within and between mixtures and stump treatments were non-proportionally related and the shapes of the survival curves varied dramatically across mixes and species often with sharp transitions between time periods. Nonparametric analysis of survival (proc LIFETEST) was used. This calculates survival for any time period as:

$$S(t) = \prod_{j=1}^{i-1} (1 - q_i) \qquad [1]$$

where S(t) is survival at time interval *i* and $q_i$ is the conditional probability of failure. Survival at any interval is therefore derived by one minus the product probability of failure for that interval times all the probability of all other intervals preceding it. Failure is the number of trees that failed during the interval in question divided by the number of trees potentially at risk at the beginning of that interval.

Thinned and missing trees (Table 2) were censored. At each interval, dead trees and trees that had been censored are removed from the trees at risk for the next time interval. The survival time for trees that were censored represents their minimum survival time. All other causes of mortality were considered in the analyses as uncensored until the end of the study unless noted.

The effect of stump removal and thinning on tree survival was tested using Wilcoxon rank statistics, while stratifying on tree species mixture. In some plots (Table 1), smaller trees were thinned at age 20 and this could have affected mortality of residual trees thereafter. To test for an effect, we used survival data for ages 21-40 where an effect may have occurred. There was no evidence of an effect of thinning (p=0.66) when species mixture and stump treatment were considered. We concluded that thinning did not affect survival in residual trees and did not include thinning in subsequent analyses. Tests for the effect of stump treatment on survival over time given in the figures were done separately for each mixture and species within mixture using the same tests as described for Eq. 1.

### 2.2.2 Tree growth parameters

*Model fitting*

Mixed models were fitted using maximum likelihood and model terms were included based on likelihood ratio tests and Akaike's information criteria. Residuals were checked for homoscedasticity against predicted and explanatory variables and for normality. Mixed models (Proc MIXED) were used to analyse continuous response variables which incorporated a polynomial term for time into the model along with the categorical effects of tree species, tree mixture and stump treatment. Time was centered to remove correlation between time and time$^2$. A first order autoregressive correlation structure was assumed for the residuals since repeated observations were made on the trees. This structure implies that the correlation between observations on trees within plots for basal area or tree species nested in plots for quadratic mean diameter (QMD) and height measured at any adjacent time interval *i* is $\rho$ , where $|\rho| < 1$. Plots were treated as random subjects and tested for inclusion of plot intercepts and plot slope over time.

We tested the time related effect of stand thinning completed at age 20 in some plots for all the models, but found this to be an insignificant factor affecting basal area, QMD or height based on likelihood ratio tests (p>0.05), and therefore not included in the models.

*Site index*

Site index (age 50) was calculated using tree height and age from the site tools program (Ver. 3.3) produced by the BC Ministry of Forests and Range. Heights for tree species were pooled for both stump treatments within their species monoculture or mixture to get enough trees for the calculations, and therefore contain some disease effect likely reducing the index. For larch and spruce this was four trees each from two 20-x 20- m plots, for other conifer species this was four trees each over six plots. Site index was calculated using height data at 35 years because mountain pine beetle mortality removed many of the pine trees with repeated height measures after this age.

*Plot basal area*

Plot basal area is the sum of the cross-sectional areas (cm$^2$) of trees calculated from dbh in a plot beginning at stand age 20 according to,

$$Y_{ij} = \beta_0 + \beta_1 \text{time}_{ij} + \beta_2 (\text{time})^2{}_{ij} + \beta_3 \text{stumping}_{ij} + \beta_4 \text{mix}_{ij} + a_{1ij} + a_{2ij} + \varepsilon_{ij} \qquad [2]$$

where, $Y_{ij}$ is the mean plot basal area at time *i* in random plot *j* given the fixed growing conditions $\beta_3$ and $\beta_4$ and random conditions $a_1$ and $a_2$; $\beta_0$ is the overall mean, $\beta_1$ is the continuous fixed linear effect of time *i* in plot *j*; $\beta_2$ is the continuous fixed quadratic effect time *i* plot *j*; $\beta_3$ is the effect of stump removal at time *i* in plot *j*; $\beta_4$ is the fixed effect of the species mixture at time *i* in plot *j*; $a_{1ij}$ is the random effect of plot *j* at time *i*; $a_{2ij}$ is the random effect of plot *j* at time$^2$ *i*; $\varepsilon_{ij}$ is the residual error. Tests for differences between stump treatment within each mixture given in the figures were determined at age 40 using the difference of least squares means tests within proc MIXED. Difference between the coefficients for stump treatment within a mixture over time was not tested since these differences were small compared to the intercept (age 20). Differences by age 40 account for both the intercept and slope over time.

*Quadratic mean diameter (QMD)*

QMD is calculated as the corresponding diameter at 1.3 m (cm) of the average tree basal area in a plot, which gives greater weight to larger trees. QMD is equal to or greater than the arithmetic mean depending on the diameter variance. The mean QMD was modeled beginning at stand age 20 in the form,

$$Y_{ij} = \beta_0 + \beta_1 \text{time}_{ij} + \beta_2 (\text{time})^2{}_{ij} + \beta_3 \text{stumping}_{ij} + \beta_4 \text{mix}_{ij} + \beta_5 \text{sp(mix)}_{ij} + a_{1j} + a_{2ij} + \varepsilon_{ij} \qquad [3]$$

where, $Y_{ij}$ is the mean QMD at time *i* in random plot *j* given the fixed growing conditions $\beta_3$ and $\beta_5$ and random conditions $a_1$ and $a_2$; $\beta_0$ is the overall mean, $\beta_1$ is the continuous fixed linear effect of time *i* in plot *j*; $\beta_2$ is the continuous fixed quadratic effect time *i* plot *j*; $\beta_3$ is the effect of stump removal at time *i* in plot *j*; $\beta_4$ is the fixed effect of the species mixture at time *i* in plot *j*; $\beta_5$ is the fixed effect of the tree species nested in mixture at time *i* in plot *j*; $a_{1j}$ is the random effect of the intercept for plot *j*; $a_{2ij}$ is the random effect of plot *j* at time *i*; $\varepsilon_{ij}$ is the residual error.

*Mean height of dominant trees*

The model for mean tree height (cm) followed the model in equation 2 except that $Y_{ij}$ is the mean height in cm of the four co-dominant trees per 20 x 20 m plot established for repeated measures. P-values given in figures are similar to those described in Eq. 2 at age 40.

## 3. Results

### 3.1 Efficacy of inoculum removal

Stump removal and root raking to a depth of 45 cm altered the size and distribution of roots in the upper 60 cm of soil by removing most roots >1 cm dia. and apparently raising roots <1 cm dia. from the 31-60 cm depth class into the 0-30 cm class (Weir and Johnson 1970). Roots colonized by *P. sulphurascens* or *A. ostoyae*, the cause of Armillaria root disease of conifers in BC (Morrison et al. 1985), were found in both stump treatments. The treatment removed almost all roots >2 cm dia. colonized by these fungi and the only colonized roots in the 31-60 cm class were <1 cm in dia.

### 3.2 Causes and frequencies of mortality from planting to 2007

#### 3.2.1 Planting failure

Seedling survival after the first year in the stumped plots averaged 85% for species other than redcedar, of which only 23% were living. In contrast only about 4% of redcedar seedlings and 42% of those of other species survived in the not stumped plots due to competition from herbs and shrubs, the dry site, south aspect and lack of shade (Weir and Johnson 1970). Replacing seedlings that died in 1969 and 1970 increased the percentage of planting spots occupied by established seedlings for all species by 1973. Percent establishment by 1973 was higher in the stumped block than the not stumped for all species except redcedar and was highest for pine in both treatments (Table 2). Prior to 1973 no seedlings were killed by root disease.

### 3.2.2 Root disease

Four root disease fungi, *A. ostoyae, P. sulphurascens, O. wageneri* and *P. schweinitzii* killed trees between 1973 and 2007 (Table 2). *Ophiostoma wageneri* and *P. schweinitzii* killed three and two Douglas-fir, respectively in the block stumped. *Armillaria ostoyae* killed trees of all species in both blocks, except for redcedar and birch in the block stumped. Between 1973 and 1977, trees in the stumped block that were killed by *A. ostoyae* and *P. sulphurascens* were excavated to determine the source of inoculum. In all cases, a seedling root had contacted a small piece of root colonized by one of the fungi. Between 1973 and 2007, less than 5% of established Douglas-fir, larch, pine and spruce were killed by *A. ostoyae* in the block stumped compared to 22-38% in the block not stumped (Table 2), a reduction of 80 to 100% depending on species. In both blocks, the annual rate of mortality by *A. ostoyae* declined after 1987 for Douglas-fir (Fig. 1a) and larch (Fig. 1d). For redcedar, *A. ostoyae* mortality declined after 1992 in the block not stumped (Fig. 1c). In contrast, the percentage of pines killed annually by *A. ostoyae* increased during each time period after 1992 in both blocks, although the rate in the block stumped is about 10% of that in the block not stumped (Fig.1b). Spruce mortality due to *A. ostoyae* increased over time in the block not stumped, especially in the most recent period; moreover, in the block stumped, none was recorded after 1981 until the last period (Fig.1f). Eight birches were killed in the block not stumped (Fig. 1e).

Only Douglas-fir was killed by *P. sulphurascens* in both blocks; two trees were killed in the block stumped, compared to 170 in the not stumped, a 99% reduction (Table 2). There has been no *P. sulphurascens*-caused mortality in the block stumped for 20 years, whereas the annual incidence of mortality in that not stumped has increased in each time period since 1987 (Fig.1a).

*Armillaria ostoyae* killed trees in 20 of 32 plots in the block stumped; 11 of 12 plots without mortality contained redcedar, birch or both. In the block not stumped, 31 of 32 plots contained trees killed by *A. ostoyae*; a birch plot was disease-free. *Phellinus sulphurascens* killed trees in 2 of 12 plots and 6 of 12 plots containing Douglas-fir in the blocks stumped and not stumped, respectively. In six plots not stumped with mortality attributed to both fungi, *P. sulphurascens* was dominant, killing four times as many trees as *A. ostoyae* between 1973 and 2007.

In 1988 Morrison *et al*. reported that in the block not stumped, plots of Douglas-fir, pine and Douglas-fir - pine had more disease centers with two or more *A. ostoyae*-killed trees than plots where those species alternate with rows of redcedar or birch, which have low susceptibility to killing. Most disease centers in plots of fir or pine alternating with redcedar or birch were confined to rows of Douglas-fir or pine. The effect on root disease spread was examined again with 30$^{th}$-year data. Douglas-fir mixtures significantly affected the proportion of 5m x 5 m boxes with dead trees (Fig. 2a, p=0.03). Monoculture Douglas-fir had fewer dead trees per box compared to when it was grown with pine. For pine (Fig 2b), there were also significant differences in the proportion of boxes with one or more dead trees (p=0.0001). Pine with redcedar or birch had fewer dead trees per box than monoculture pine or pine with Douglas-fir.

### 3.2.3 Stem disease

Western gall rust [*E. harknessii*] killed 1-2% of pines (Table 2, Fig. 3)). There was a moderate, non-lethal incidence of Atropellis canker [*Atropellis piniphila* (Weir) Loman & Cash] on pine prior to 2007; since then mortality has been observed.

3.2.4 Insects

In 1987 Douglas-fir, pine, larch and spruce were defoliated to varying degrees by western spruce budworm, *Choristoneura occidentalis* Freeman. Sequoia pitch moth, *Synanthedon sequoiae* Hy. Edw., killed 0.5% of pines between 1973 and 1987. Between 2002 and 2007, mountain pine beetle killed 21-22% of established pines (Table 2, Fig. 3).

3.2.5 Other agents

Suppression was a major cause of mortality in well-stocked plots of shade intolerant species, especially pine in both blocks and Douglas-fir in the block stumped (Fig. 3a); this mainly occurred after age 30. Other abiotic causes of mortality were stem breakage, snow press and windthrow; their occurrence was associated with falls of wet snow followed by wind (Fig. 3a, b). Incidence of mortality due to abiotic agents was highest for pine in both blocks and for Douglas-fir in the block stumped. Prior to 1987, squirrels feeding on bark and deer rubbing antlers killed small numbers of pine and Douglas-fir.

Most trees recorded as missing in the missing/undiagnosed column of Table 2 were present in 1973 but could not be found in a post-1973 assessment. Cause of death of some trees, mostly pines, could not be determined.

3.3 Main effects of species mixture and stump treatment on survival

We first tested for differences in mortality among species mixtures, finding a significant effect on survival ($p<0.0001$), as expected. Next we tested for the effect of stump removal when species mixtures were considered and found that stump removal reduced mortality ($p<0.0001$). Mortality averaged over all species at age 40 was on average 14% lower in plots stumped (0.47) than in those not stumped (0.61). We were also interested in testing survival within pine and Douglas-fir monocultures and mixtures separately when stump removal was not possible, i.e. in plots not stumped. To do this we removed trees that had died due to planting failure, since all other causes of mortality were of most interest. There were no differences in survival between Douglas-fir in monoculture and mixtures in plots not stumped ($p=0.49$), but there were differences for pine ($p<0.0001$). Pine survived better in plots not stumped when mixed with redcedar or birch and worst when mixed with Douglas-fir or in monoculture. Planting mortality for redcedar and birch was high regardless of mixture, and this was the greatest effect on these species; therefore, we did not test for mortality differences within mixtures of plots not stumped of birch and redcedar. The effects of stump treatment and causes of mortality are described in detail in section 3.4.

3.4 Main effects of stump treatment and species mixtures on basal area, quadratic mean diameter (QMD) and dominant height.

*3.4.1 Plot basal area*

The basal area of the study plots between age 20 and 40 was affected by tree species mixture and stump treatment over time (Table 3). Averaged over all tree mixtures, stump removal increased the plot basal area by 1.6 times by stand age 20 and 1.3 times by age 40 compared to not removing the stumps; this change over time results in the significant time by stump treatment interaction in the model (Table 3). This interaction is discussed more fully in section 3.5; but briefly, it shows that by stand age 40, and averaged over stump treatment, larch and Douglas-fir monocultures produced the highest basal area (50 and 48 $m^2$/ha, respectively). Furthermore, all plots with pine except pine with Douglas-fir had the lowest yields (8-14 $m^2$/ha) (all least-squares [LS] (marginal) means). Interestingly, by age 20, pine monocultures had the next highest basal area after the larch and Douglas-fir plots, and pine mixtures ranked midway or higher in basal area; consequently, there was a large drop in pine basal area between age 20 and 40. The significant interaction between species mixture, time, and stump treatment in the model indicate significant effects on basal area for these factors, and which are discussed more fully in section 3.5.

Random variation for plot basal area (Table 3) was greatest for plot trajectory over time (slope), and lower for the shape of the trajectory ($time^2$-curvature). The correlation between the plot basal area trajectory and its shape (time and $time^2$) was significant indicating that plots with higher slope also had greater upwards curvature (Cov. a1, a2). Random variation for plot intercepts could not be included in the model indicating that variation between plots at age 20 was not significant after the fixed effects were considered.

*3.4.2 Quadratic mean diameter (QMD)*

There were significant differences between the mean diameters of trees in the mixtures ($p<0.0001$, Table 4) with larch and Douglas-fir grown with pine the largest (21.9 and 22.4 cm respectively) and redcedar the smallest (13.9) by age 40; however, there were also significant differences in the QMD change over time indicated by the significant interaction of time with mixture and species within mixture over time (Table 4). These interactions are explained more fully in section 3.5 below for each mixture. No stump treatment term could be added to the model according to a likelihood ratio test (p=0.48).

Random variation in plot intercepts (age 20) and plot trajectories over time were significant (Table 4) indicating that there were differences in QMD at the plot level after the fixed effects were considered. Plot intercepts and slopes were positively correlated (Cov. $a_1$ and $a_2$) indicating that plots with larger mean diameter initially (age 20) also tended to remain larger over time.

We also compared the QMD of the 10 largest trees per plot (not shown) using the model for QMD above. The largest trees in stands are typically the least affected by stand density. The analysis for the 10 largest trees per plot was nearly identical to that previously described for QMD for all trees except that stump treatment significantly affected QMD (p=0.02), and the difference decreased over time (p=0.002). QMD was greater in plots stumped than in plots not stumped by age 20 (11.0 vs. 9.4 cm respectively), but the QMD was the same by age 40 (20.8 vs. 20.7 cm, respectively). The rankings of QMD for the top 10 trees for all mixtures were very similar to the results of the QMD for all trees (Table 5) with minor exceptions, and this is discussed in the section 3.5 below for each mixture. One difference between the QMD models was that the model for the 10 largest trees could not incorporate a random plot intercept indicating that plot-level differences were not great after the fixed effects were considered.

*3.4.3 Dominant height growth*

Four dominant or co-dominant trees were designated at age 20 and measured over time in plots containing Douglas-fir, pine, larch, and spruce. Averaged over all treatments, mean height in plots stumped was significantly greater (p=0.0009, Table 6) than in plots not stumped. Average tree height in plots stumped was 70 cm taller by age 40 than in plots not stumped (17.1 m vs. 16.5 m respectively, LS means). There were also significant differences in height amongst the tree species ($p<0.0001$, Table 6). By age 40 averaged over stump treatment, larch was the tallest (21.4 m), followed by Douglas-fir in monoculture and mixtures (FD/PL-19.6m, FD-18.8, FD/EP-18.2, FD/CWR-17.8), spruce (14.9 m), and pine in monocultures and mixes (PL/FD-14.9, PL/EP-14.8 m, PL-14.2, PL/CWR-14.1) (all LS means). The effect of stump removal on height growth over time also interacted with species mixtures (Table 6), and this is discussed for each species more fully in section 3.5.

Random variation in height was greatest at the plot intercept level (Table 6) and much smaller for plot height over time (slope). Plots with greater initial growth at age 20 also tended to have greater height growth over time (Cov. $a_1$, $a_2$, Table 6).

3.5 Interactions between time, stump treatment, and tree species mixtures for survival, basal area, QMD, and dominant height

3.5.1 Douglas-fir

Planting mortality to age 5 lowered survival by about 20% in plots not stumped and by about 10% in plots stumped (Fig. 4a). There are three Douglas-fir monoculture plots in each stump treatment. To age 25, Armillaria root disease killed a small number of trees (17) in two stumped plots and 74 trees in three not stumped plots. Laminated root disease was not recorded in stumped plots; in contrast, in two of three not stumped plots, 55 of the 259 trees (22%) established in 1973 were killed from age 5 to 40 years. Stumped plots had mortality after age 25 from competition and breakage.

By age 20, plots stumped contained proportionately more mid-sized and larger trees and fewer small-diameter trees than in plots not stumped (Fig.5a). By age 40 in plots stumped, there were more trees in most diameter classes than in plots not stumped, despite the greater density in plots stumped (Fig. 6a). Diameter class distribution in the monoculture was similar to Douglas-fir in its mixtures (Fig. 6 a-d) except for greater proportion of mid-size Douglas-fir stems by age 40 in the monoculture. There were no major differences between QMD of monoculture Douglas-fir and QMD in any of its species mixtures with respect to the 10 largest trees (Table 5); however by age 40, QMD for all Douglas-fir trees grown with pine were the largest because of reduced proportion of smaller-sized trees (Table 5, Fig. 6d). In contrast by age 40, monoculture Douglas-fir had lower QMD for all trees because of the greater proportion of small- to mid-sized trees, and not because it had fewer large trees (Table 5). Basal area of Douglas-fir was greater in plots stumped than in plots not stumped, and increased over time (Fig. 7a). It is not clear how laminated and Armillaria root diseases present in the plots differ in effect on basal area. One of the plots not stumped had Armillaria root disease only, and this plot ranked in the middle of basal area yield by age 40, while the highest and lowest yield plots had both root diseases (Fig. 7a). Dominant height tended to be greater in the plots stumped than in plots not stumped (Fig. 8a) and similar to that observed in other Douglas-fir mixtures except tending to lower height when mixed with redcedar and greater when mixed with pine.

3.5.2 Douglas-fir and redcedar

About 95% of Douglas-fir in plots stumped survived to age five compared to 70% in not stumped plots and 50% for redcedar in both treatments (Fig. 4b). In plots stumped, no redcedar died from root disease and Armillaria and laminated root diseases killed three and one Douglas-fir, respectively, before age 20; thereafter, a few Douglas-fir died from suppression and breakage. Plots not stumped showed decreasing survival of Douglas-fir after age five due to the combined effects of Armillaria root disease early on and laminated root disease later. *Armillaria ostoyae* killed 29 of 176 trees (16%) in three plots and *P. sulphurascens* 60 of 120 trees (50%) in two plots. After age five, Armillaria root disease killed 15 of 77 (19%) established redcedar trees in two plots.

There was more Douglas-fir by age 20 in the mid and larger diameter classes in plots stumped, and unlike in plots not stumped, all of these survived over the next 20 years (Fig.5b). By age 40 for Douglas-fir, plots stumped contained more stems in all mid-diameter classes and larger (Fig. 6b). Redcedar occupied the lower diameter classes in these plots by age 20 in both stump treatments (Fig.5b). The lower survival of Douglas-fir in all diameter classes in plots not stumped between ages 20-40 (Fig. 5b) allowed some redcedar into the larger diameter classes by age 40 (Fig. 6b). Plot basal area was always greater over time in plots stumped than in plots not stumped (Fig. 7b). Douglas-fir average dominant height growth tended to be at least 1 m greater over time in plots stumped than in plots not stumped (Fig. 8b).

3.5.3 Douglas-fir and birch

Douglas-fir survival to age five was more than 90% in plots stumped and about 70% in plots not stumped compared to 50% and 20% for birch, respectively (Fig. 4c). From age 5 to 20 in plots stumped, Douglas-fir mortality in two plots was mainly from Armillaria root disease (5% of 252 trees), and animal damage; one tree was killed by laminated root disease. After age 30, suppression mortality occurred for both species. In plots not stumped, survival of Douglas-fir was reduced by *A. ostoyae* which killed 33 of 162 trees (20%) in three plots, and by laminated root disease which killed 55 of 98 trees (56%) in two plots, with most *P. sulphurascens* mortality occurring after age 20. After age 20, thinning removed birch from two plots stumped (Table 1).

There were more large Douglas-fir and birch trees by age 20 in plots stumped, birch occupied the lower diameter classes in both treatments, and more of the larger-sized trees of both species survived over the next 20 years in the plots stumped (Fig.5c). By age 40, there were proportionally more Douglas-fir trees in most diameter classes in plots stumped mainly through lower root disease mortality, and birch continued to occupy the lower diameter classes (Fig. 6c). Douglas-fir and birch combined plot basal area remained higher and was increasing over time in the plots stumped compared with that in plots not stumped (Fig. 7c). Douglas-fir-birch plots not stumped had the lowest yield of all Douglas-fir mixtures, with one plot especially low (Fig. 7c). Douglas-fir average dominant height in the plots stumped remained over 1 m taller at all times than in plots not stumped and was similar to that observed in monoculture Douglas-fir, but the results were not statistically significant (Fig. 8c).

3.5.4 Douglas-fir and pine

In plots stumped, post-planting mortality was about 10% for both species compared to 15% for pine and 25% for Douglas-fir in plots not stumped (Fig. 4d). From age 5 to 20 in stumped plots, Armillaria root disease killed up to five Douglas-fir in two plots and five pine in three plots; thereafter mortality in both species was caused by suppression, windthrow, and snow press and in pine by gall rust. In plots not stumped, Armillaria root disease killed 36% of 192 established Douglas-firs and 51% of 193 pines in three plots to age 40. Mountain pine beetle was the greatest hazard for pine in both stump treatments after age 35. At age 40, pine in both treatments in this mixture had the lowest survival in the study, about 10%.

There were more large-diameter Douglas-fir and pine trees by age 20 in plots stumped than in plots not stumped, and more large Douglas-fir trees survived over the next 20 years in the plots stumped (Fig.5d). Douglas-fir and pine both occupied similar diameter classes by age 20; however, only mid-sized pine trees survived till age 40 mainly due to mountain pine beetle and a number of other disease agents. By age 40, Douglas-fir diameter class distributions were similar between stump treatments, and pine occupied the lower classes in both stump treatments (Fig. 6d). The QMD of all Douglas-fir trees was larger in this mixture than in monoculture or any of its other mixtures by age 40, but was the smallest at age 20 (Table 5). For the 10 largest-sized trees, Douglas-fir mixtures and monoculture had similar QMD (Table 3), but for all trees, Douglas-fir grown with pine had proportionately fewer mid-sized trees by age 40 (Fig. 6d) which increased the QMD within this mixture. At all ages, QMD of pine grown with Douglas-fir was among the smallest observed for pine, whether grown in monoculture or any mixture (Table 5). Douglas-fir and pine combined plot basal area was slightly greater initially in the plots stumped (Fig. 7d), but yield in both stump treatments slowed over time due to pine mortality. Pine-Douglas-fir plots had the highest yield of any pine plots whether grown in monoculture or mixture simply because the Douglas-fir trees were able to increase in height and diameter over time and dominate the basal area by age 40 (Fig 7d). The Douglas-fir-pine mixture had the lowest yield of any stumped Douglas-fir mixture presumably because pine competed with the Douglas-fir and pine mortality yielded no advantage to the Douglas-fir, at least so far. Dominant height of Douglas-fir was similar between stump treatments by age 40, but this mixture produced the tallest Douglas-fir trees (Fig. 8d). In contrast, pine was taller in plots stumped (Fig. 8e).

3.5.5 Pine

Planting survival in pine plots was higher than 90% at age 5 in both treatments (Fig. 4e). From age 5-35, most mortality in three plots stumped was attributed to suppression with small numbers of trees killed by stem and Armillaria root diseases. In plots not stumped, Armillaria root disease was the principal cause of mortality, killing 37% of 459 established trees in three plots. After age 35, mountain pine beetle was the major hazard in both treatments and survival of pine at age 40 was similar in monoculture and mixed species plots.

Diameter class distribution by age 20 was similar between stump treatments, but with a few more larger trees in plots stumped (Fig.5e). Over the next 20 years, only the mid-sized trees survived the combined effects of disease, suppression, and beetle (Fig.5e). Better growth and survival by age 40 in plots stumped resulted in more trees in most diameter classes (Fig. 6e). The 10 largest pine trees had similar QMD in monoculture and mixture, except when grown with Douglas-fir where QMD was smaller (Table 5). Comparing QMD for all trees to the 10 largest trees by age 40, shows that pine grown in monoculture had more smaller- and mid-sized stems than pine grown in mixtures (Table 5, Fig. 6d-g). Initially, plot basal area was greater in plots stumped than in plots not stumped, but both treatments had decreasing and converging trends by age 30 (Fig. 7e). Basal area growth slowed over time in both stump treatments due to multiple disease impacts, and to pine beetle after age 35. Mean height of dominant trees was greater in plots stumped (Fig. 8f), but death of the pine trees designated for height remeasurement makes these estimates unreliable for any pine after age 35.

3.5.6 Pine and redcedar

In both treatments, planting survival for pine at age 5 was greater than 90%, whereas it was about 40% for redcedar (Fig. 4f). After age 5, redcedar had low mortality in both treatments, except for a few undiagnosed deaths by age 15 in the plots stumped. Pine survival between ages 5-35 was mainly decreased by suppression and Armillaria root disease (2.5% of established trees killed) in three plots stumped. In three plots not stumped Armillaria root disease killed 22% of 202 established trees. After age 35, mountain pine beetle was the main hazard in both treatments.

Pine occupied the larger diameter classes exclusively by age 20 in both stump treatments (Fig. 5f), but most would die over the next 20 years making way for redcedar into some of the larger classes (Fig. 6f). By age 40, the QMD of all trees in the plots for either species were larger than in any of their mixtures, except that the redcedar had proportionately fewer small trees when grown with pine (Table 3, Fig. 6f). Combined basal area for both species was in decline by age 30 due to poor growth of the pine which initially dominated the plots (Fig. 7f). There were two plots stumped that had higher than average basal area yield by age 40 due to increasing contribution from redcedar trees since age 25 (Fig. 7f). Redcedar in pine plots was unable to make up for the loss of pine basal area, unlike redcedar in Douglas-fir (Fig. 7b and

7f). Pine dominant height was initially greater in plots stumped than in plots not stumped but this difference decreased over time (Fig. 8g).

### 3.5.7 Pine and birch

Planting survival at five years was 90% for pine but was about 40% for birch in plots in both treatments (Fig. 4g). Between ages five and 35, the main hazard agents for pine in stumped plots were Armillaria root disease (5% of trees in two plots); western gall rust and abiotic causes (snow press, breakage). In contrast, Armillaria root disease was the main hazard in three plots not stumped, killing 23% of 224 trees. After age 35, mortality from mountain pine beetle caused convergence of survival curves for pine in both stump treatments. Birch survival was good after age five although all birch in two plots in both treatments were removed by thinning at age 20 (Table 1).

The diameter class distribution of pine by age 20 was similar in both stump treatments, and only mid-sized pine trees at age 20 survived till age 40 (Fig.5g). Birch occupied the lower diameter classes in both stump treatments by age 20, but with more stems in the plots stumped (Fig. 5g). By age 40, pine had similar diameter class distribution between the two stump treatments, but with more mid- to large-size pine in plots stumped (Fig. 6g). Birch in both stump treatments was able to occupy the larger diameter classes by age 40 (Fig. 6g). Birch grown with pine had among the smallest QMD of its mixtures (Table 5). Pine showed the opposite effect to birch where it had among the largest QMD of any of its mixtures at all stand ages (Table 5). Combined basal area of both species was greater in plots stumped initially, but both stump treatments had decreasing yields over time due to poor pine survival to all agents; this was not compensated for by the birch (Fig. 7g). Although the birch made up between 2-7% of the basal area initially, it composed 25-37% of the total basal area by age 40. Height growth of pine dominants was greater in plots stumped (Fig. 8h).

### 3.5.8 Redcedar

In both treatments, about 40% of redcedar seedlings failed to establish (Fig 4h). Thereafter, a few trees died following snow press and from undiagnosed causes in plots stumped; in three plots not stumped, Armillaria root disease killed about 4% of established trees.

There were more trees in larger diameter classes in plots stumped by age 20, and only a few of the smallest trees died over the next 20 years in both treatments (Fig. 5h) than in plots not stumped. The diameter class distributions between stump treatments were similar by age 40, but there were still a few more trees in larger diameter classes in plots stumped (Fig. 6h). The average QMD for all redcedar trees and for the 10 largest trees by age 40 showed that redcedar had larger diameter trees when grown in monoculture than in mixture (Table 5). Basal area of redcedar plots was similar between stump treatments and showed a non-linear increasing yield over time (Fig. 7h).

### 3.5.9 Birch

Planting failure was the principal hazard in birch plots: almost 60% and 80% in the plots stumped and not stumped, respectively (Fig. 4i). Hazard was low in both treatments after age 5, with a few trees in plots stumped killed by suppression, and in plots not stumped by Armillaria root disease (one tree), stem breakage and suppression.

There were more trees overall and more frequent large stems in the plots stumped than in plots not stumped by age 20, and most trees of all diameters survived over the next 20 years in both stump treatments (Fig.5i). By age 40, diameter class distributions were similar between the stump treatments except that there were more trees in most diameter classes in plots stumped (Fig. 6i). Birch in monoculture or grown with redcedar produced the largest QMD birch in the study at any age (Table 5). Birch basal area was greater in the plots stumped mainly due to more, but not smaller, diameter stems, and the difference between stump treatments increased over time (Fig 7i).

3.5.10 Redcedar and birch

Planting survival of redcedar and birch was low in both treatments, lower for birch in plots not stumped and redcedar in the plots stumped (Fig. 4j). After age 5, redcedar in plots stumped had a few undiagnosed deaths while in plots not stumped hazards were Armillaria root disease (12% of trees in three plots), stem breakage and snow press. For birch, hazards after age 5 were suppression and stem breakage in both treatments. After age 20, mortality of both species was low.

The diameter class distribution for birch was similar in both stumps treatments except that plots stumped contained more trees in most size classes by age 20 (Fig.5j). Redcedar occupied the smaller classes in both stump treatments. Trees in most of these diameter classes survived well over the next 20 years, except for a few small redcedar killed by Armillaria root disease in plots not stumped (Fig.5j). By age 40, the birch diameter class distribution was similar to that described for age 20 (Fig. 6j). While the bulk of the redcedar remained in the smaller classes at age 40, some redcedar stems occupied the largest diameter classes (Fig. 6j). Diameter class distributions in redcedar-birch mixtures were similar to those in the redcedar monocultures except that there were more smaller redcedar stems in the monoculture (Fig. 6h, 6j).The basal area yield of both stump treatments was similar over time, but with only 32% of the basal area from birch in plots not stumped compared to 56% from birch in plots stumped (Fig. 7j). The yield from the redcedar-birch mixture is close to that of redcedar alone but greater than birch alone (Fig. 6h-6j). Redcedar-birch in mixture shows upwards increasing yield over time, but less than redcedar alone and more than birch alone (Fig. 6h-6j).

3.5.11 Larch

Larch was represented by only one plot in each block (Table 1). Larch survival at age five was 80% or more in both plots (Fig. 4k) and was similar to that of pine or fir (Table 2). In the plot stumped, *A. ostoyae* killed 3% of established trees between years 5 and 20; thereafter, there was minor suppression mortality. In plots not stumped, the primary hazard until age 25 was Armillaria root disease, killing about one-third of trees. There were some snow pressed trees after age 30

The larch plot stumped had more trees in mid-diameter classes by age 20 compared to the plot not stumped, and only small trees died in both treatments over the next 20 years (Fig. 5k). More trees survived Armillaria root disease after age 20 in the plot stumped than in the plot not stumped. By age 40, the diameter class distribution was unchanged from age 20 (Fig. 6k). Larch trees had among the largest QMD in the study (Table 5). Basal area at age 20 was greater in the plot stumped than in the plot not stumped, and the differences increased linearly over time (Fig. 7k). Larch had similar basal area to monoculture Douglas-fir in either stump treatment by age 40 (Fig. 7a and 7k), and both species had a similar number of surviving trees (Fig. 6a and 6k). Dominant larch in plots stumped were initially taller, but height growth converged between stump treatments by age 40 (Fig. 8i). The larch trees were about 2m taller than the next tallest species, Douglas-fir, and with some of the largest diameter trees in the study, the larch probably have the greatest volume/ha.

3.5.12 Spruce

Spruce was also represented by one plot per block in the study (Table 1). Planting survival of spruce in the plot stumped at age 5 was 76%, nearly double that in the plot not stumped (Fig. 4l). After age 5, the main hazards in the stumped plot were windthrow and snow press; 3% of established trees were killed by Armillaria root disease. In contrast, hazard in the plot not stumped was mainly due to Armillaria root disease which killed one-third of trees.

There were more trees in mid and greater diameter classes by age 20 in the plot stumped than in the plot not stumped. Fewer of the age-20 mid-sized trees survived Armillaria root disease over the next 20 years in plots not stumped (Fig.5l). By age 40 there were more trees in almost all diameter classes in the plot stumped than in the plot not stumped (Fig. 6l). Plot basal area was greater in the plot stumped than in the plot not stumped, and continued to diverge over time, but differences were not statistically different at age 40 (Fig. 7l). Though not significantly different, spruce was the only species that showed taller dominant trees by age 40 in the plot not stumped than in the plot stumped (Fig. 8j), possibly because long-term density in the plot not stumped was the lowest of all the conifers.

## 4. Discussion

The Skimikin trial was designed to answer three questions about root disease epidemiology: 1) could the incidence of mortality caused by *P. sulphurascens* in the next rotation be reduced by stump removal and root raking, 2) what tree species or mixtures thereof would yield a stocked stand on similar sites where stump removal could not be applied and 3) would alternating rows of susceptible and tolerant species reduce spread of root disease? In addition to answering these questions, the trial provided data on effects of the stumping treatment on planting survival, incidence of other biotic and abiotic causes of tree mortality, productivity of tree species and mixtures, foliage nutrient content (Whiting 1993) and soil characteristics (Curran 2001). Whiting (1993) found little difference in foliar macronutrient levels among Douglas-fir, pine and redcedar in the two blocks at age 25. Curran (2001) measured selected soil properties in both blocks, finding no significant difference in bulk density at 2-4 cm ($p=0.06$) or 6-8 cm ($p=0.84$) depth and a significant reduction of 4.6% ($p=0.049$) in total porosity in the stumped block at 2-4 cm but none at 6-8 cm depth.

The trial site was selected because there was a moderate incidence of trees killed and infected by *P. sulphurascens*. Although Armillaria root disease was detected during site assessment, it was not considered during trial design because, at the time, *Armillaria mellea sensu lato* was considered a secondary pathogen of little significance. An inter-tree planting distance of 1.5 m was selected to maximize the probability of trees contacting inoculum. Mortality caused by *A. ostoyae* was recorded in 31 of 32 plots in the block not stumped and 20 of 32 plots in the block stumped compared to 6 of 32 and 2 of 32, respectively for *P. sulphurascens*, which occurred in each block only in plots containing Douglas-fir. All plots with *P. sulphurascens* mortality also had *A. ostoyae* mortality; laminated root disease was the dominant cause in these plots not stumped. In the southern interior of BC, trees in mature stands in the ICH zone have a high incidence of infection by *A. ostoyae* (Morrison et al. 2001). After harvest, the fungus emerges from existing root lesions, rapidly colonizes stumps and root systems and begins to produce rhizomorphs (Morrison et al. 2001); most infections on young trees are initiated by rhizomorphs (Morrison 2011). Clearly, there was more *A. ostoyae* on site than pre-establishment surveys suggested. For transfer to occur from a colonized stump to a susceptible host, *P. sulphurascens* mycelium must be on the bark surface of the stump root (Wallis and Reynolds 1965). The process whereby *P. sulphurascens* in root wood grows to the root surface and initiates infection on a susceptible root has not been observed (Thies and Sturrock 1995). Probably, *A. ostoyae* was able to colonize more of stumps and root systems than *P. sulphurascens* in the block not stumped. In addition, rhizomorphs in soil give *A. ostoyae* an advantage in time and position because tree roots must grow to contact *P. sulphurascens* mycelium. These differences in fungus biology are reflected in the greater incidence of mortality from *A. ostoyae* in both blocks resulting from colonization of harvested stumps.

### 4.1 Survival of species in monoculture and mixtures

#### 4.1.1 Treatments

Over all species, stump removal reduced mortality significantly. Mortality from planting failure and root disease was lower in the block stumped, from suppression it was lower in the block not stumped and from abiotic/animal causes, mountain pine beetle and missing it was similar in the blocks.

Soil disturbance and consequent reduction in forb and shrub competition enhanced, to varying degrees, survival of seedlings of Douglas-fir, spruce and birch in the block stumped, but not that of pine and larch which was high or redcedar which was low in both blocks. Unlike the other species, redcedar usually regenerates under a canopy in the ICH, and that may account for its poor survival. Birch survival was less than 50% in both blocks; Newsome et al. (2005) attributed poor survival of planted birch to dry site conditions and competition from other vegetation. Survival five years post planting for birch and pine was within the range found by Newsome et al. (2005).

Some plots were thinned in year 20. If there were asymptomatic, *A. ostoyae*-infected trees, cutting them could result in a flush of fruiting and infection or mortality of adjacent suscepts. Neither was observed, suggesting a low level of disease in residual trees in the block stumped.

#### 4.1.2 Species susceptibility to killing by root disease

The tree species selected for the trial vary in susceptibility to killing by *P. sulphurascens* from high to moderate, resistant, tolerant and immune (Cleary et al. 2011, Thies and Sturrock 1995). Accordingly, Douglas-fir was highly susceptible to killing and mortality of moderately susceptible larch and spruce and tolerant pine could be expected. However, only two of 23 plots stumped and six of 23 plots not stumped containing one or two of these species had mortality caused by *P. sulphurascens*. The facts that only Douglas-fir was killed, and that fir was the only highly susceptible species but not the only susceptible species, suggest limited occurrence of inoculum with enough potential to kill species with lower susceptibility than Douglas-fir. Susceptibility of redcedar to *P. sulphurascens* could be assessed only in two mixed plots with Douglas-fir; no redcedar, which appeared tolerant in this study, were killed.

Fortuitously, the tree species selected also show a range of susceptibility to killing by *A. ostoyae* (Cleary et al. 2008). In the not stumped block, species were exposed to inoculum in all plots but one birch plot, thereby providing an assessment of their susceptibility. All coniferous species are susceptible to killing by *A. ostoyae*, especially when less than 15-20 years old. Thereafter, the effectiveness of host response to infection varies among species. For example, over time, larch (Robinson and Morrison 2001) and redcedar (Cleary et al. 2012) become more resistant. After peaking in year 20, mortality in larch declined and none was recorded in the last 10 years (Fig. 1d) in keeping with its reported low long-term susceptibility. The rapid juvenile growth of larch, resulting in early contact with inoculum and combined with its susceptibility, is responsible for its high early mortality. Rapid early growth after planting was also one of the largest factors positively associated with how quickly primary inoculum transferred to the surrounding Douglas-fir crop trees (Cruickshank et al. 2011). In this study, all conifers with a high initial growth rate also had the greatest mortality due to *A. ostoyae*. Mortality in cedar has been low since 1973, due initially to its slow growth and later, possibly to disease tolerance. Declining mortality in Douglas-fir after the peak at 20 years has been observed in other plantations and can be attributed to a more effective host response with increased age (Robinson and Morrison 2001) and to the longer time required to kill larger trees (Morrison 2011). The incidence of mortality from root disease in pine did not decline with age as its moderate susceptibility to *A. ostoyae* suggests it should (Cleary et al. 2008). Pine seedlings were grown at a nursery near Prince George and could be of a provenance unsuited to the site. Spruce mortality continued with age, which is in keeping with its reported moderate to high susceptibility; however, the study site is probably on the dry side for this species resulting in continued mortality long-term.

Residual inoculum of *P. sulphurascens* and *A. ostoyae* in root fragments in the block stumped and in roots and stumps in the block not stumped was responsible for mortality of established seedlings after age five. In the block stumped, more than half of the trees killed to age 20 were solitary and the rest were pairs with the second dying one to six years after the first. This suggests that there was little or no root contact between adjacent trees and consequently little or no spread from infected or killed trees to their neighbours. By age 20, killing of Douglas-fir by *P. sulphurascens* and of larch and redcedar by *A. ostoyae* had ceased in plots in the block stumped. The small numbers of Douglas-fir and spruce trees killed by *A. ostoyae* after 1987 probably were infected by tree to tree spread or were infected before age 20 and took many years to kill. Probably, contagion provides most of the inoculum after 1987 in pine in the block stumped and of all species in the block not stumped.

4.1.3 Alternating rows of susceptible and tolerant or immune species

Where stumping is not possible, species mixtures might slow root to root transfer between species susceptible to *P. sulphurascens* or *A. ostoyae* or both by placing a row of a second species with greater resistance or immunity between them. Results from 1987 (Morrison et al.1988) suggested that the number of disease centers with two or more *A. ostoyae*-killed trees was lower in mixed species plots than in those of monoculture Douglas-fir or pine. Clumping of dead trees suggests secondary spread (tree to tree). However, that was not the case by year 30 when *A. ostoyae* or *P. sulphurascens* or both were killing trees. With only 1.5 m between rows, roots of Douglas-fir had grown across rows of cedar or birch to contact those of trees in the next row of Douglas-fir permitting spread of the fungi across the row of barrier trees. There was no effect on root disease mortality in Douglas-fir in plots not stumped when it was grown in monoculture or with redcedar or birch; but Douglas-fir showed increased clumping of mortality when grown with pine, as evidenced by a greater proportion of boxes with dead trees. Pine alone or grown with Douglas-fir also had greater clumping of dead trees in the boxes compared to pine grown with cedar or birch. Cedar or birch may have helped slow the spread of root disease between pines, but it is more likely that cedar or birch competed less with pine especially given their poor initial survival. Greater competition affecting disease mortality is also suggested when the two fast early growth species, pine and fir, are grown together. If this is true, then the results suggest that interspecies competitive exclusion can interact with disease mortality, depending on the species combination.

4.2 *Productivity* of species in monocultures and mixtures

*4.2.1 Basal area*

After 40 years, basal area was 1.3 times greater in plots stumped than in plots not stumped. Douglas-fir and larch monocultures had the highest basal area growth and also the greatest absolute difference in basal area between plots stumped and not stumped. Redcedar and pine alone and in mixture were the only species that did not appear to benefit significantly from stump removal. Redcedar appeared to be tolerant of both root diseases, and although tolerance was not formally investigated, our results suggest a change in its previous designation as resistant. Basal area curves for pine in monoculture and mixtures, except Douglas-fir-pine, showed no increase by age 30, then a moderate to strong decrease thereafter. The declining basal area of pine monoculture and mixtures occurred through a combination of disease and insect agents, and this was consistent in magnitude for all mixtures and stump treatments except when grown with Douglas-fir. The basal area yield trajectories were identical for redcedar monoculture and redcedar-birch mixture or pine monoculture and any of its mixtures, but these are the only cases where this occurred. In most cases, mixtures yielded less combined basal area than monocultures except for birch, pine, or red cedar mixed with Douglas-fir which had greater combined yield in mixture. This is in part due to the higher initial density of the Douglas-fir compared to the other species in mixture except pine; however, pine with Douglas-fir did not yield better than Douglas-fir alone. The largest factors affecting combined basal area yield in mixture were dictated by the survival of the potentially fastest growing species, its interaction with disease, and the impact of disturbance from the stump treatment itself. Basal area was mainly reduced by disease, resulting in fewer trees in plots not stumped, but these trees did not have larger diameter than in plots stumped. The effect of disease on diameter and future basal area could increase if more of trees become infected and larger trees die.

*4.2.2 Quadratic mean diameter (QMD)*

QMD for all trees in plots was not affected by stump treatment, but was affected by the species mixture. QMD for the 10 largest trees per plot for each species was always greater at age 20 in plots stumped than in plots not stumped, but this was not significantly different by stand age 40. The 10 largest trees in plots not stumped apparently had slower diameter growth till age 20, but then were able to close this gap by age 40 compared to the largest trees in plots not stumped. A few more large-diameter trees were killed in plots not stumped than in plots stumped, but these were not the largest trees in the plots and did not affect QMD. Furthermore, plots not stumped generally had lower stem density than plots stumped because of lower survival; however, most trees were unable to effectively utilize the freed space or resourced for diameter growth by age 40. Greater conifer diameter is assumed with lower plot densities (Sjolte-Jørgensen 1967). A separate study showed that juvenile planted Douglas-fir was unable to take advantage of lower tree density common in plots with root disease because many living infected trees are asymptomatic (Cruickshank et al. 2009, Cruickshank et al. 2011).

The QMD of the 10 largest trees occurred in monoculture or was at least as large as the next best admixture, and tended to follow the trend for QMD of all trees, but not exactly depending on the species. The largest QMD for Douglas-fir at age 40 occurred in combination with pine. The QMD of the 10 largest Douglas-firs in mixture or monoculture were nearly identical, suggesting that Douglas-fir was able to compete in any of these mixtures at least until mid-rotation. Redcedar, Douglas-fir, and birch grown with pine had among the lowest QMD at age 20, but this had reversed by age 40 only for Douglas-fir and redcedar compared to monocultures or other mixtures. For redcedar or Douglas-fir with pine the reversal in QMD was through lower proportion of small- to mid-sized trees. Birch is shade-intolerant and it was likely not able to compete with the pine. The age of birch and its unfavorable canopy position probably reduced its ability to adjust to pine mortality near the end of this study even though it has been shown to release (Burns and Honkala 1990). The largest QMD for redcedar occurred in monoculture, but the apparent tolerance of redcedar to both root diseases and its increasing growth rate with time make it a good candidate for long-term growth in mixed stands. Redcedar had the smallest QMD in the study; however, this gap was closing with time, and some redcedar approached the size of the largest Douglas-fir. Although few pine survived till age 40, the largest diameters at any age occurred when it was grown with birch or redcedar, and in keeping with its shade-intolerance, these mixtures were among the lowest density plots.

*4.2.3 Mean dominant height*

Generally, by age 20 most plots stumped had taller co-dominant trees than in plots not stumped, except for spruce. Generally, at the species mixture level, only pine showed a statistically significant difference; however, more importantly this trend was consistent for all species measured regardless of mixture, except spruce. Larch was the tallest species in the study. Similarly, larch was found to be the tallest conifer in the Northern Rockies in the first century, matched only by pine in the first 50 years (Burns and Honkala 1990). Greater height for most species in plots stumped is likely due to greater productivity, since height growth is largely thought to be insensitive to density (Lanner 1985). Douglas-fir infected with Armillaria root disease were shorter in relation to their diameter than disease-free trees (Cruickshank and Filipescu 2012), indicating that height growth is potentially sensitive to root disease. Furthermore, stump removal promoted height growth for ponderosa pine in a Washington trial (Shaw et al. 2012). In terms of height, pine appeared to be the species most favourably affected by stump removal and larch the least. Admixing appeared to affect dominant height very little although we had no height data for redcedar or birch.

4.3 Competition and facilitation

Ecological facilitation occurs when one species benefits from the presence of another and the other species is at least unaffected. We found no clear indications to suggest that facilitation occurred when QMD of the largest 10 trees per plot were compared between monocultures and mixtures. QMD of the largest 10 trees per plot are least affected by density and therefore best represent other stand effects. Birch, redcedar, pine, and Douglas-fir in monoculture produced the highest or at least similar QMD of the largest 10 trees per plot compared to their mixtures. In a similar ecosystem, abundance of broadleaf trees was associated with larger diameter redcedar and thought to be related to the greater nutritional input from the broadleaf (Simard et al. 2004). The largest 10 redcedar trees occurred in monoculture compared to redcedar grown with birch or other conifers. Admixing birch with any of the other conifers also did not suggest any clear facilitation effects in this study based on the QMD of the largest 10 trees or that of all trees in the plots. Conifers grown with redcedar performed as well as, or outperformed other conifer-birch mixtures presumably because redcedar competes less with the other conifers. Similarly, the 10 largest birches per plot grown with redcedar performed better than birch grown with pine or Douglas-fir presumably because of lower competition. None of the mortality agents appeared to affect QMD greatly to date, and the dominant effect of admixtures on QMD appeared to be competition.

4.4 Mixed species and disturbance

Results concerning productivity in mixed stands range from positive to neutral and negative outcomes (Knoke et al. 2008, Man and Leiffers 1999, Frivold and Frank 2002). These effects vary based on the combining ability of species (Luis and Monteiro 1998) which depend on differences in size or shade-tolerance or both (Luo and Chen 2011), nutrition (Binkley 2003, Simard et al. 2004), density (Simard et al. 2004), stand age (Binkley 2003), disturbance such as fire, disease, insects, and storms (Hély et al. 2000, Knoke et al. 2008), successional and phenological timing (Man and Lieffers 1999), and soil and light resource utilization (Man and Lieffers 1999). Prior to establishment of the Skimikin study, Peace (1957) suggested that forest pathogen impact in mixed stands depended on the pathogen host range, with lower impacts in mixed stands only if the other species were resistant or immune, and not that lower impact in the susceptible species alone could be assumed. This agrees with the survival of Douglas-fir in plots not stumped, where survival was similar in admixture and monoculture; furthermore, this occurred for birch and cedar. We found higher survival when pine was grown with cedar or birch, probably because pine has low competitive ability and these admixtures had the lowest density. More important than survival rate, there was no increase in combined basal area for either species mixture compared to monoculture, and yields were usually less in admixtures. This could change with time, especially in plots of redcedar with pine or if root disease continues to kill Douglas-fir, which is likely.

Functional trait diversity (Tilman et al. 1997) might help to explain the interaction of pathogen and tree species diversity more completely. Functional traits are attributes affecting survival, growth, reproduction, and ultimately, fitness (Ackerly 2003) and are closely related to life history. Functional traits that combine a range of shade- and disease-tolerance might complement each other. The rate of successional change to climax stands of natural redcedar in this ecosystem is probably strongly affected by these traits. In this study, a planted susceptible but fast-growing overstory combined with a shade- and disease-tolerant understory, like cedar, appeared to be potentially beneficial longer-term. We found weak or no evidence that spread of root disease or beetle between susceptible species in mixed plots was affected where the second species was resistant, immune, or tolerant to the agent. Adding a second species could reduce the stand-level risk but only because of the immune, resistant, or tolerant species themselves.

This study also suggests that it should not be assumed that increasing diversity would lower disease risk. Asymmetric competition may apply more strongly between certain species (Luo and Chen 2011), for example for shade-tolerant/intolerant species, and this could interact with disease. Density could also interact with disease as fungal disease impacts can be greater at higher host plant densities (Burdon and Chilvers 1982), probably because of competition among plants and possibly higher transmission rates.

Species diversity might reduce the amount of damage in some cases, but this effect might not be consistent over time and space; furthermore, the effect of adding new tree species to stands seems to depend on the characteristics of the species concerned rather than on increased species diversity (Koricheva et al. 2006). In mixed species plots in this study, a favourable effect on basal area occurred mostly when one of the species was unaffected or only partially affected; mixing species did not lower the impact in the susceptible species. This is best exemplified by the Douglas-fir-pine mixture, which produced greater basal area than monoculture pine because disease and insects killed pines. Mixed species stands usually have lower density of susceptible species, particularly if one or more species are immune, but this also likely occurs when resistant or tolerant species are present. Boreal conifer-hardwood mixtures planted in alternating rows at higher density than this study (0.25-0.5 m) showed higher conifer survival to Armillaria root disease in admixtures two years after planting (Gerlach et al. 1997). This was probably due to lower density of conifers in mixture which limited the number of roots exposed to primary inoculum in the stumps rather than slowing conifer to conifer (secondary) spread. Two years post planting is probably not enough time for the fungus to contact a seedling, kill it, and then spread secondarily. The current study is much older and clearly showed fungal bridging between roots of susceptible trees across root systems of barrier trees. Barriers may be more effective if the species changed every two or three rows or possibly through clumped plantings (Cruickshank et al. 2009); however, barriers will not prevent spread within rows or clumps. In addition, greater quantity of fungal inoculum left in the plots not stumped was able to kill trees of a larger diameter equally in monoculture and mixtures alike despite barrier trees, compared to plots stumped. Furthermore, height and basal area were increased more strongly by stump removal than by admixing.

One further consideration on the use of mixed species to reduce disease impact is that admixtures are not favourable against polyphagous pests (Jactel et al. 2008), such as *A. ostoyae*, whose host range includes all of the study species. This occurs because most species are affected by the disease. In this case, another option to control disease spread is the use of multiple genetic lines within a tree species, each containing a genotype differing in susceptibility (Peacock et al. 2001) or possibly tolerance (Cruickshank et al. 2009). Admixing might play a role insuring against catastrophic failure of one species where disturbance agents affect specific hosts, and against market fluctuations or growing stock needs for certain species. The results of our study may change as the stands age but given the current trajectory of the yield curves, these trends look to be continuing long term.

## 5 Prescriptions for diseased sites

In the southern interior of BC, the Douglas-fir (IDF) and cedar–hemlock biogeoclimatic zones are the most productive. Both *A. ostoyae* and *P. sulphurascens* are widely distributed in the zones (Hodge 2012). *Armillaria ostoyae* was observed in 60–80% of stumps on numerous sites (Woods 1994, Morrison et al. 2000) and *P. sulphurascens* was found in 65% of stumps on the Skimikin site (Weir and Johnson 1970). In plantations of 19-34-year-old Douglas-fir on such sites, mortality caused by *A. ostoyae* is common and incidence of trees with belowground infection ranges between 22 and 59% (Morrison et al. 2000, Morrison 2011, Cruickshank et al. 2011); similar losses to age 40 are recorded for *P. sulphurascens* (Mounce et al. 1940, Bloomberg and Reynolds 1985, Thies and Westlind 2005).

Recent revisions to susceptibility lists for *P. sulphurascens* and *A. ostoyae* (Cleary et al. 2008, 2011) provide guidance when selecting species to plant in the IDF and ICH zones. The lists do not show large differences between the fungi in susceptibility of a given species to killing. However, distribution and abundance of the fungi differ in the zones and among their subzones. Hence, it is important to know the occurrence and abundance of the fungi on a site being regenerated.

### 5.1 Sites not stumped

Slope and soil characteristics may preclude stumping on a site. Also, sites of low potential productivity or low value tree species may not be suitable candidates for stump removal based strictly on financial considerations (Shaw et al. 2012). Sites with other limiting factors are also not good candidates for stump removal to control root disease unless those factors are also dealt with. On such sites, choice of species must reflect the amount of root disease inoculum. Given its high susceptibility to killing, Douglas-fir should not be the principal species planted where either fungus is present. Instead, species that show tolerance and low to moderate susceptibility after age 20 should be selected. These include redcedar (probably tolerant), ponderosa (*Pinus ponderosa* Laws.), and white pines (*Pinus monticola* Douglas ex D. Don) and larch. Birch, aspen (*Populus tremuloides* Michx.) and cottonwood (*P. trichocarpa* Torr. & A. Gray) regenerate naturally and are immune to *P. sulphurascens* and have low susceptibility to *A. ostoyae* (Cleary et al. 2008, 2011). While both resistance and tolerance allow better survival to disease, only tolerance is defined as having better growth for a given level of disease.

In this study, productivity of lodgepole pine was poor. The species is host to the largest number of pest species compared to the other conifers, and although it showed rapid early growth, its performance longer-term was severely diminished. Birch mortality from competition and Armillaria began about age 30 when it was overtopped by conifers. Birch also produces high quality *A. ostoyae* inoculum after death. Redcedar's tolerance of shade and the root diseases, and its high timber value make it an attractive species to be planted or encouraged naturally. In interior zones, redcedar is overtopped until overstory disturbance caused by insects, disease, or senescence release them; for example, this occurred in this study in plots where redcedar was grown with Douglas-fir or pine. Redcedar is preferred as a companion species over birch where *A. ostoyae* or *P. sulphurascens* is present, unless very short rotations are used where birch remains under low competition.

5.2 Sites stumped

Stump removal techniques have evolved since trials using mechanical removal began in the 1960s (Vasaitis et al. 2008). Initially, a bulldozer, usually with a straight blade pushed stumps from the soil, with or without ripping to fragment roots left in the soil, exposing them to colonization by soil fungi. Without further removal of root pieces (Shaw et al. 2012), this treatment did not significantly reduce mortality from root disease in planted trees (Kellas et al. 1997). Bulldozers often caused extensive soil displacement and compaction (Smith and Wass 1991). Later, excavators fitted with one or more tines or with a bucket and thumb efficiently removed stumps while having less impact on soil properties (Vasaitis et al. 2008). Results from equipment trials suggest that a large excavator is more effective than a bulldozer at removing stumps and roots (Bloomberg and Reynolds 1988) and would facilitate their use as biomass (Vasaitis et al. 2008).

Even with thorough removal of stumps and roots, colonized root fragments will remain and there will be mortality of juvenile trees for 5-15 years after planting, and possibly thereafter. In the IDF and ICH zones, Douglas-fir and larch, the most productive species, should be planted alone or mixed; they also may be mixed with rust resistant white pine in both zones. Given the lower productivity of lodgepole pine and redcedar, they should not be a major component of the stand on stumped sites such as Skimikin.

A volume analysis would likely show greater effect of stump removal on productivity than on basal area, QMD, or height alone because it accounts for height and taper together. Douglas-fir trees infected by *A. ostoyae* are shorter than disease-free trees (Cruickshank and Filipescu 2012) and have less height for a given diameter (likely more taper), both of which reduce lumber product recovery per stem. Knots downgrade the value of lumber products (Shmulsky and Jones 2011) according to their size, frequency, and distribution. The higher and more uniform stocking of the plots stumped combined with taller trees should result in greater crown lift and smaller branch diameters. If heights were measured for all trees, timber product yield and financial analysis could be performed with software such as SYLVER (Mitchell 1988). To date, no wood product value considerations have been included in the design or analysis of stump removal trials, including this one.

## 6 Conclusions

Pathogenic root inhabiting fungi cause economically important root diseases of woody plants, worldwide. There are few effective economical methods for reducing potential losses incurred by the diseases they cause when establishing plantations. Two of these are mechanical inoculum reduction and crop rotation, with crop rotation having the lowest upfront cost. In this study, push falling and root raking improved seedling survival, reduced root disease mortality by removing inoculum, and improved tree yields for all species except pine and redcedar, while having no negative effects. There are likely benefits from inoculum removal for future rotations given the near absence of mortality from both root diseases for the last 20 years. The study also showed that the tree species selected for the trial differed in their response to the root diseases and soil disturbance, and that disease affected the interaction between two tree species depending on their functional traits, allowing them to cope with both disease and competition. Financial costs/benefits were not considered; however, high value species like Douglas-fir and larch appeared to benefit the most from stump removal and crop rotation. Planting a high value species like redcedar on sites with root disease may also provide some gain where stumps cannot be removed. Other financial considerations such as wood quality were not determined but likely have some effect on benefit from stump removal for some species.

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Table 1. Summary statistics by stumping treatment for tree species in monocultures and mixtures, numbers of plots, number of plots thinned and of trees cut, and estimated site indices for Douglas-fir, lodgepole pine, western Larch and Engelmann spruce.

| Stumping | Species/ mixture[1] | Species[1] | # plots | #plots thinned after 1987 (#trees cut) | Site index age 50 (m) |
|---|---|---|---|---|---|
| Stumped | Cw | Cw | 3 | 1(25) | Not calculated |
| Not stumped | Cw | Cw | 3 | 0 | |
| Stumped | Cw/Ep | Cw | 3 | 2(12,35) | |
| Not stumped | Cw/Ep | Cw | 3 | 0 | |
| Stumped | Cw/Ep | Ep | 3 | 2(10,21) | |
| Not stumped | Cw/Ep | Ep | 3 | 0 | |
| Stumped | Ep | Ep | 3 | 1(37) | |
| Not stumped | Ep | Ep | 3 | 1(18) | |
| Stumped | Fd | Fd | 3 | 2(41,49) | 25.0 |
| Not stumped | Fd | Fd | 3 | 1(37) | |
| Stumped | Fd/Cw | Cw | 3 | 2(26,42) | Not calculated |
| Not stumped | Fd/Cw | Cw | 3 | 0 | |
| Stumped | Fd/Cw | Fd | 3 | 1 (14) | 23.9 |
| Not stumped | Fd/Cw | Fd | 3 | 0 | |
| Stumped | Fd/Ep | Ep | 3 | 2 (all cut) | Not calculated |
| Not stumped | Fd/Ep | Ep | 3 | 0 | |
| Stumped | Fd/Ep | Fd | 3 | 2(12,16) | 24.4 |
| Not stumped | Fd/Ep | Fd | 3 | 0 | |
| Stumped | Fd/Pl | Fd | 3 | 2(14,23) | 25.5 |
| Not stumped | Fd/Pl | Fd | 3 | 0 | |
| Stumped | Fd/Pl | Pl | 3 | 2(28,44) | 18.1 |
| Not stumped | Fd/Pl | Pl | 3 | 0 | |
| Stumped | Lw | Lw | 1 | 1(36) | 27.7 |
| Not stumped | Lw | Lw | 1 | 1(40) | |
| Stumped | Pl | Pl | 3 | 2(53,61) | 17.8 |
| Not stumped | Pl | Pl | 3 | 2(24,45) | |
| Stumped | Pl/Cw | Cw | 3 | 2(18,24) | Not calculated |
| Not stumped | Pl/Cw | Cw | 3 | 1(11) | |
| Stumped | Pl/Cw | Pl | 3 | 2(14,20) | 17.9 |
| Not stumped | Pl/Cw | Pl | 3 | 0 | |
| Stumped | Pl/Ep | Ep | 3 | 2(all cut) | Not calculated |
| Not stumped | Pl/Ep | Ep | 3 | 2(all cut) | |
| Stumped | Pl/Ep | Pl | 3 | 1 (13) | 18.5 |
| Not stumped | Pl/Ep | Pl | 3 | 0 | |
| Stumped | Se | Se | 1 | 1(33) | 21.5 |
| Not stumped | Se | Se | 1 | 0 | |

[1]Cw=western redcedar; Ep=paper birch; Fd=Douglas-fir; Pl=lodgepole pine; Lw=western larch; Se=Engelmann spruce

Table 2. Number of seedlings of species planted (1968 -1970) and established (1973) and trees surviving in 2007 in the stumped and not stumped blocks of the Skimikin inoculum reduction and species trial. The number and percentages of established trees killed by agents between 1973 and 2007 are shown.

| | | | | Cause of mortality | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment | Tree species [1] | Seedlings planted 1968-70 # | Seedlings established 1973 # (%) | *Armillaria ostoyae* # (%) | *Phellinus sulphu-rascens* # (%) | *Ophiostoma wageneri* # (%) | *Phaeolus schweinitzii* # (%) | *Endocronartium harknessii* # (%) | *Dendroctonus ponderosae* # (%) | Suppressed # (%) | Abiotic / Animal [2] # (%) | Missing / Undiag-nosed [3] # (%) | Cut [4] 1987 # (%) | Surviving 2007 # (%) |
| Stumped | Cw | 1264 | 642 (50.8) | | | | | | | | 5 (1.1) | 77 (17.0) | 190 (29.6) | 370 (81.9) |
| | Ep | 1237 | 555 (44.9) | | | | | | | 22 (6.0) | 2 (0.5) | 67 (18.2) | 187 (33.7) | 277 (75.3) |
| | Fd | 1270 | 1153 (90.8) | 45 (4.6) | 2 (0.2) | 3 (0.3) | 2 (0.2) | | | 55 (5.6) | 40 (4.1) | 93 (9.5) | 178 (15.4) | 735 (75.4) |
| | Lw | 169 | 143 (84.6) | 3 (2.8) | | | | | | 1 (0.9) | | 27 (25.2) | 36 (25.2) | 76 (71.0) |
| | Pl | 1289 | 1181 (91.6) | 42 (4.5) | | | | 17 (1.8) | 204 (21.8) | 262 (28.0) | 76 (8.1) | 94 (10.1) | 246 (20.8) | 239 (25.6) |
| | Se | 171 | 130 (76.0) | 3 (3.1) | | | | | | | 3 (3.1) | 6 (6.2) | 33 (26.8) | 85 (87.6) |
| Not stumped | Cw | 1284 | 682 (53.1) | 43 (6.4) | | | | | | 4 (0.6) | 4 (0.6) | 57 (8.5) | 15 (2.2) | 559 (83.8) |
| | Ep | 1222 | 302 (24.7) | 8 (3.9) | | | | | | 4 (1.9) | 3 (1.4) | 67 (32.4) | 95 (31.5) | 125 (60.4) |
| | Fd | 1366 | 997 (73.0) | 213 (22.6) | 170 (18.1) | | | | | 9 (1.0) | 9 (1.0) | 73 (7.8) | 56 (5.6) | 467 (49.6) |
| | Lw | 169 | 135 (79.9) | 36 (37.9) | | | | | | | 2 (2.1) | 6 (6.3) | 40 (29.6) | 51 (53.7) |
| | Pl | 1276 | 1132 (88.7) | 366 (34.9) | | | | 12 (1.1) | 221 (21.1) | 103 (9.8) | 65 (6.2) | 87 (8.4) | 84 (7.4) | 194 (18.5) |
| | Se | 169 | 75 (44.4) | 26 (34.7) | | | | | | | | 10 (13.3) | | 39 (52.0) |

[1] Tree species: Cw, *Thuja plicata* Donn ex D. Don; Ep, *Betula papyrifera* Marsh; Fd, *Pseudotsuga menziesii* (Mirb.) Franco; Lw, *Larix occidentalis* Nutt.; Pl, *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex S. Wats.; Se, *Picea engelmanni* Parry.

[2] Abiotic / Animal includes breakage, windthrow, snowpress and animal damage.

[3] Trees present in 1973 that could not be found later were recorded as missing. The cause of death of "undiagnosed" could not be determined.

[4] Cut trees are not included in denominator for percent calculations except for %cut where they are included.

Table 3. Analysis of variance table for the effects of stump treatment, tree species mixture, and time on plot basal area over 40 years.

| **Effect** | **Num DF** | **Den DF** | **F Value** | **Pr > F** |
|---|---|---|---|---|
| **A) Fixed effects** | | | | |
| 1) Time | 1 | 44.2 | 364.16 | <0.0001 |
| 2) $(\text{Time})^2$ | 1 | 68.8 | 37.28 | <0.0001 |
| 3) Stumping | 1 | 80.5 | 44.52 | <0.0001 |
| 4) Tree species mix | 11 | 83.7 | 18.68 | <0.0001 |
| 6) Time*species mix | 11 | 44.2 | 19.81 | <0.0001 |
| 7) $(\text{Time})^2$*species mix | 11 | 68.8 | 16.29 | <0.0001 |
| 8) Time*stumping | 1 | 92.4 | 5.76 | 0.0184 |
| 9) Time* stumping*species mix | 11 | 92.4 | 2.69 | 0.0047 |
| | | | | |
| **B) Random effects** | | | | |
| **Subject/parameter** | **variance** | **std. error** | **PR>Z** | |
| 1) Plot by time ($a_1$) | 7664.79 | 4004.20 | 0.0278 | |
| 2) Plot by $(\text{time})^2$ ($a_2$) | 31.5672 | 28.1946 | 0.1314 | |
| 3) Covariance plot time*( time)$^2$ ($a_1$, $a_2$) | 1353.87 | 295.63 | <0.0001 | |
| 4) Correlation among repeated measures | 0.7442 | 0.03099 | <0.0001 | |
| 5) Error | 2986222 | 427113 | <0.0001 | |

Akaike information criterion = 4711.4

Table 4. Analysis of variance table for the effects of stump treatment, tree species within mixture, species mixture and time on quadratic mean diameter over 40 years.

| **Effect** | **Num DF** | **Den DF** | **F Value** | **Pr > F** |
|---|---|---|---|---|
| **A) Fixed effects** | | | | |
| 1) Time | 1 | 94.6 | 798.06 | <0.0001 |
| 2) $(\text{Time})^2$ | 1 | 542 | 17.00 | <0.0001 |
| 3) Tree mix | 11 | 60.5 | 16.63 | <0.0001 |
| 4) Tree species within mix | 6 | 403 | 103.48 | <0.0001 |
| 5) Time*tree mix | 1 | 70.3 | 3.74 | <0.0001 |
| 6) Time*tree species within mix | 6 | 649 | 16.31 | <0.0001 |

| **B) Random effects** | | | |
|---|---|---|---|
| **Subject/parameter** | **variance** | **std. error** | **PR>Z** |
| 1) Plot intercept | 1.0357 | 0.2743 | <0.0001 |
| 2) Plot by time | 0.0043 | 0.0021 | 0.0191 |
| 3) Covariance plot intercept*time | 0.0043 | 0.0193 | 0.0015 |
| 4) Correlation among repeated measures | 0.0050 | 0.0315 | <0.8518 |
| 5) Error | 5.7394 | 0.2385 | <0.0001 |

Akaike information criterion = 1472.6

Table 5. Least squares (marginal) quadratic mean diameter for each tree species and mixture.

| Species and mixture | All trees | | | Largest 10 trees/ plot | |
|---|---|---|---|---|---|
| | age 40 | age 20 | mean age 20-40 | mean age 20-40 | age 40 |
| redcedar in Douglas-fir | 12.3 | 2.1 | 7.3 | 11.1 | 17.0 |
| redcedar in birch | 13.7 | 2.3 | 8.0 | 12.4 | 19.1 |
| redcedar | 13.9 | 3.5 | 8.7 | 14.5 | 21.1 |
| redcedar in pine | 14.0 | 2.4 | 8.2 | 11.9 | 19.3 |
| birch in pine | 15.1 | 5.8 | 10.5 | 12.7 | 17.1 |
| birch in Douglas-fir | 16.2 | 6.1 | 11.3 | 12.4 | 16.7 |
| birch | 17.2 | 7.0 | 12.2 | 15.7 | 21.1 |
| birch in redcedar | 18.2 | 7.3 | 12.8 | 15.0 | 20.3 |
| Douglas-fir | 20.2 | 11.0 | 15.7 | 20.5 | 25.9 |
| Douglas-fir in redcedar | 21.0 | 11.1 | 16.2 | 19.9 | 25.4 |
| Douglas-fir in birch | 21.8 | 11.3 | 16.6 | 20.5 | 26.1 |
| Douglas-fir in pine | 22.4 | 10.4 | 16.4 | 19.8 | 25.8 |
| larch | 21.9 | 13.7 | 17.9 | 22.4 | 27.7 |
| pine in Douglas-fir | 14.2 | 10.1 | 12.4 | 13.0 | 14.0 |
| pine | 14.7 | 10.1 | 12.6 | 14.4 | 15.4 |
| pine in birch | 15.6 | 10.9 | 13.5 | 14.5 | 14.6 |
| pine in redcedar | 15.7 | 11.1 | 13.6 | 14.7 | 15.4 |
| spruce | 17.9 | 7.0 | 12.5 | 16.0 | 22.0 |

Table 6. Analysis of variance table for the effects of stump treatment, tree species within mixture, species mixture, and time on mean height of dominant trees.

| **Effect** | **Num DF** | **Den DF** | **F Value** | **Pr > F** |
|---|---|---|---|---|
| **A) Fixed effects** | | | | |
| 1) Time | 1 | 27.2 | 1640.03 | <0.0001 |
| 2) $(\text{Time})^2$ | 1 | 360 | 39.60 | <0.0001 |
| 3) Stumping | 1 | 26.5 | 13.94 | 0.0009 |
| 4) Tree species mix | 8 | 27.3 | 20.07 | <0.0001 |
| 5) Tree species within mix | 1 | 261 | 277.89 | <0.0001 |
| 5) Time*species mix | 8 | 27.4 | 5.51 | 0.0003 |
| 6) Time*stumping | 1 | 308 | 46.44 | <0.0001 |
| 7) Tree species mix*species within mix | 9 | 30.1 | 3.88 | 0.0024 |
| 8) Time*stumping*species within mix | 9 | 30.4 | 2.31 | 0.0407 |

| **B) Random effects** | | | |
|---|---|---|---|
| **Subject/parameter** | **variance** | **std. error** | **Pr > Z** |
| 1) Plot by intercept | 5901.73 | 1827.83 | 0.0006 |
| 2) Plot by time | 25.5797 | 11.7134 | 0.0211 |
| 3) Covariance plot intercept*time | 415.78 | 135.22 | 0.00231 |
| 4) Correlation among repeated measures | -0.0526 | 0.0377 | 0.1623 |
| 5) Error | 16232 | 799.81 | <0.0001 |

Akaike information criterion = 11186.5

# Figures

Fig. 1. Periodic rates of mortality of Douglas-fir, lodgepole pine, western redcedar, Engelmann spruce, western larch and paper birch caused by *Armillaria ostoyae* or *Phellinus sulphurascens* in plots of the blocks stumped and not stumped in the Skimikin trial. Calculations are conditional on the number of living trees at the beginning of each time period and represent mortality in the mixtures and monocultures.

Fig. 2. Percentage of 5mx5m square boxes within 20m square plots having 0-7 dead Douglas-fir (a) or Lodgepole pine (b) trees by age 30 in plots with stumps left in place.

Fig. 3. Proportion of all trees killed for each five-year period after age 5 by cause and stand age.

Fig. 4. Survival probability of species in monocultures and mixtures from planting to age 40. P-values given in the figures resulted from testing for a difference in hazard between stump treatments over time within a mixture and species.

Fig. 5. Diameter class distribution for mixtures at age 20 and 40. Total bar height represents the mean frequency of living trees at age 20, and grey portions of bars represent trees that would survive till age 40.

Fig. 6. Diameter class distribution for each tree species in monoculture or mixture by age 40.

Fig. 7. Combined species basal area growth for each mixture over time. Proportions above lines in each mixture represent the proportion of total basal area for Douglas-fir, pine, or redcedar in that order with plots stumped always on top. P-values given in the figures resulted from testing for a difference in mean basal area (Table 3) between stump treatments at age 40.

Fig. 8. Mean dominant height growth over time for all species except redcedar and birch. P-values given in the figures resulted from testing for a difference in mean height of dominants (Table 6) at age 40.

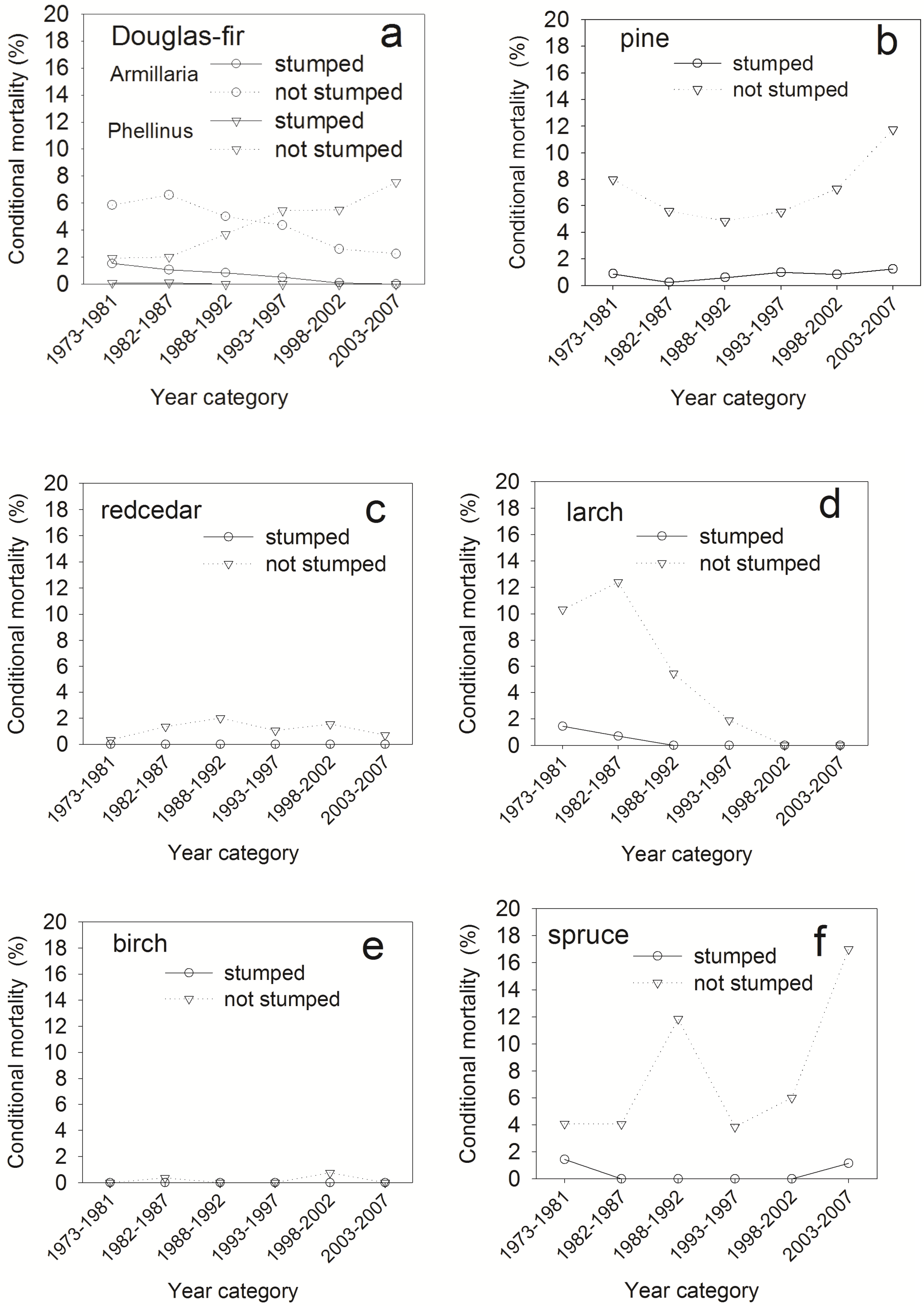
Douglas-fir
a
Armillaria
stumped
not stumped
Phellinus
stumped
not stumped
Conditional mortality (%)
Year category
pine
b
redcedar
c
larch
d
birch
e
spruce
f
1973-1981
1982-1987
1988-1992
1993-1997
1998-2002
2003-2007

Fig. 1

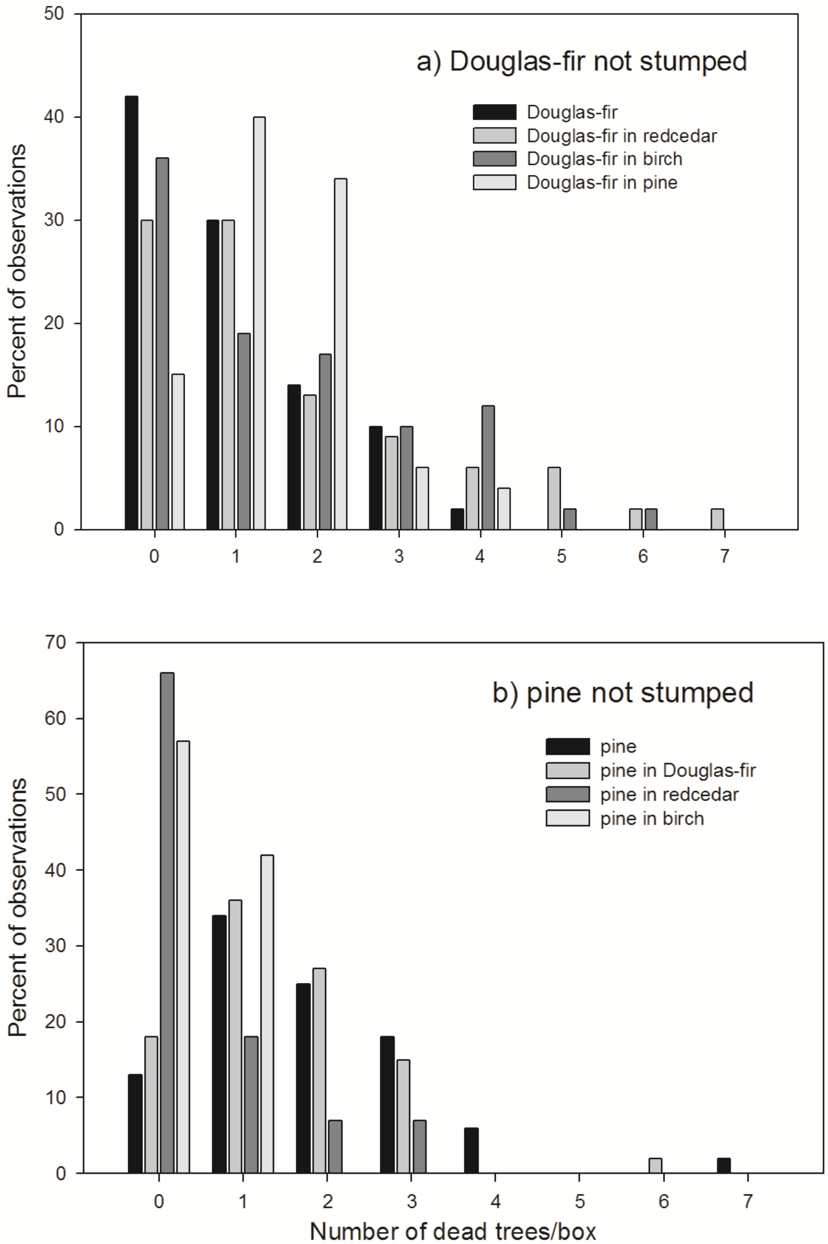
a) Douglas-fir not stumped
Douglas-fir
Douglas-fir in redcedar
Douglas-fir in birch
Douglas-fir in pine
Percent of observations
0
10
20
30
40
50
0
1
2
3
4
5
6
7
b) pine not stumped
pine
pine in Douglas-fir
pine in redcedar
pine in birch
Percent of observations
0
10
20
30
40
50
60
70
0
1
2
3
4
5
6
7
Number of dead trees/box

Fig. 2

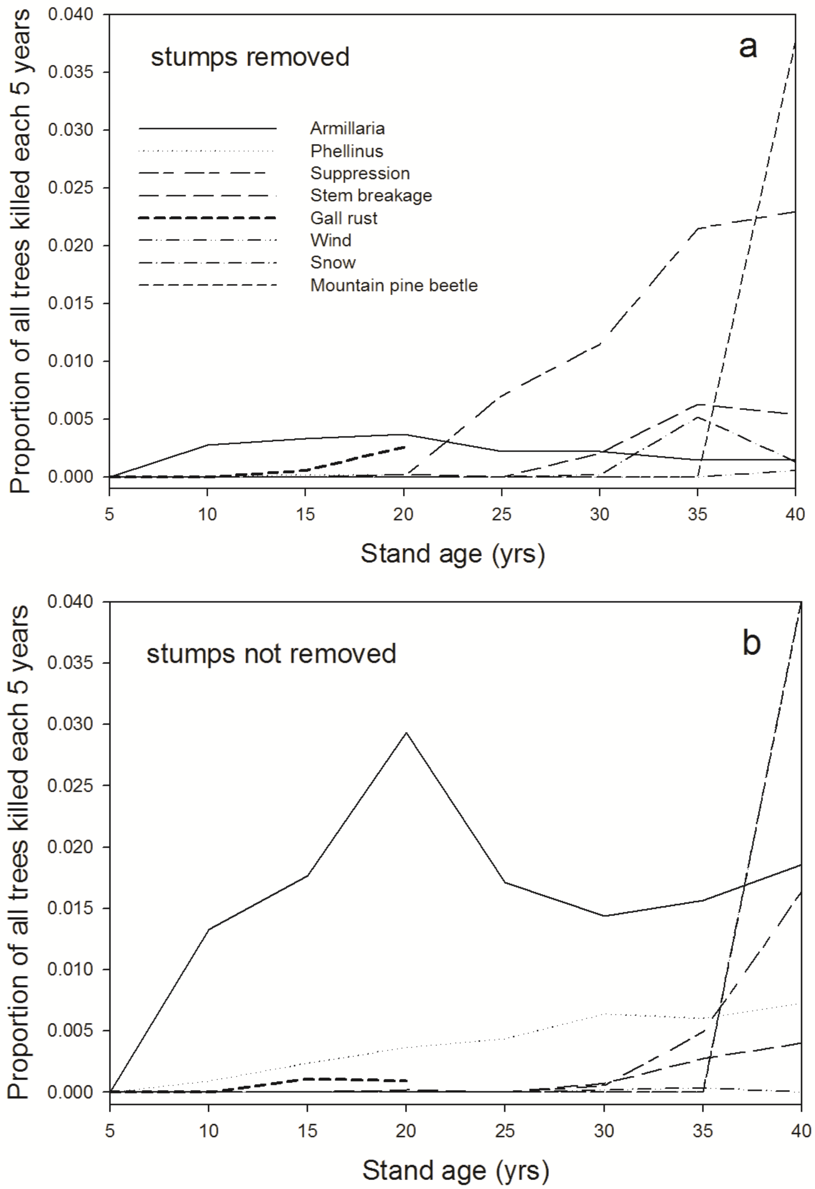
a
stumps removed
Armillaria
Phellinus
Suppression
Stem breakage
Gall rust
Wind
Snow
Mountain pine beetle
Proportion of all trees killed each 5 years
0.000
0.005
0.010
0.015
0.020
0.025
0.030
0.035
0.040
5
10
15
20
25
30
35
40
Stand age (yrs)
b
stumps not removed
Proportion of all trees killed each 5 years
Stand age (yrs)

Fig. 3

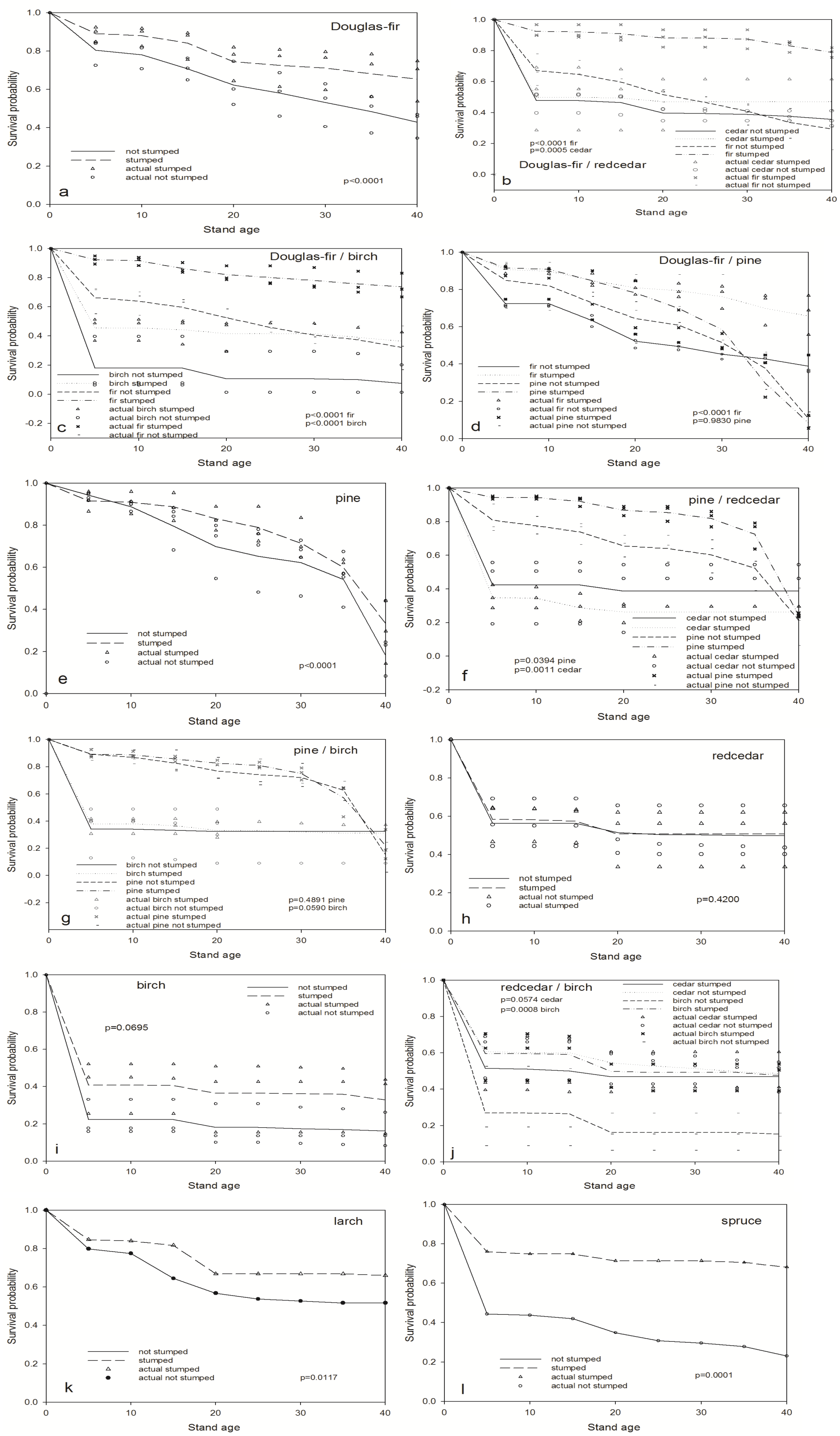
Survival probability
Stand age
a
Douglas-fir
not stumped
stumped
actual stumped
actual not stumped
p<0.0001
b
Douglas-fir / redcedar
cedar not stumped
cedar stumped
fir not stumped
fir stumped
actual cedar stumped
actual cedar not stumped
actual fir stumped
actual fir not stumped
p<0.0001 fir
p=0.0005 cedar
c
Douglas-fir / birch
birch not stumped
birch stumped
fir not stumped
fir stumped
actual birch stumped
actual birch not stumped
actual fir stumped
actual fir not stumped
p<0.0001 fir
p<0.0001 birch
d
Douglas-fir / pine
fir not stumped
fir stumped
pine not stumped
pine stumped
actual fir stumped
actual fir not stumped
actual pine stumped
actual pine not stumped
p<0.0001 fir
p=0.9830 pine
e
pine
not stumped
stumped
actual stumped
actual not stumped
p<0.0001
f
pine / redcedar
cedar not stumped
cedar stumped
pine not stumped
pine stumped
actual cedar stumped
actual cedar not stumped
actual pine stumped
actual pine not stumped
p=0.0394 pine
p=0.0011 cedar
g
pine / birch
birch not stumped
birch stumped
pine not stumped
pine stumped
actual birch stumped
actual birch not stumped
actual pine stumped
actual pine not stumped
p=0.4891 pine
p=0.0590 birch
h
redcedar
not stumped
stumped
actual not stumped
actual stumped
p=0.4200
i
birch
not stumped
stumped
actual stumped
actual not stumped
p=0.0695
j
redcedar / birch
p=0.0574 cedar
p=0.0008 birch
cedar stumped
cedar not stumped
birch not stumped
birch stumped
actual cedar stumped
actual cedar not stumped
actual birch stumped
actual birch not stumped
k
larch
not stumped
stumped
actual stumped
actual not stumped
p=0.0117
l
spruce
not stumped
stumped
actual stumped
actual not stumped
p=0.0001

Fig. 4

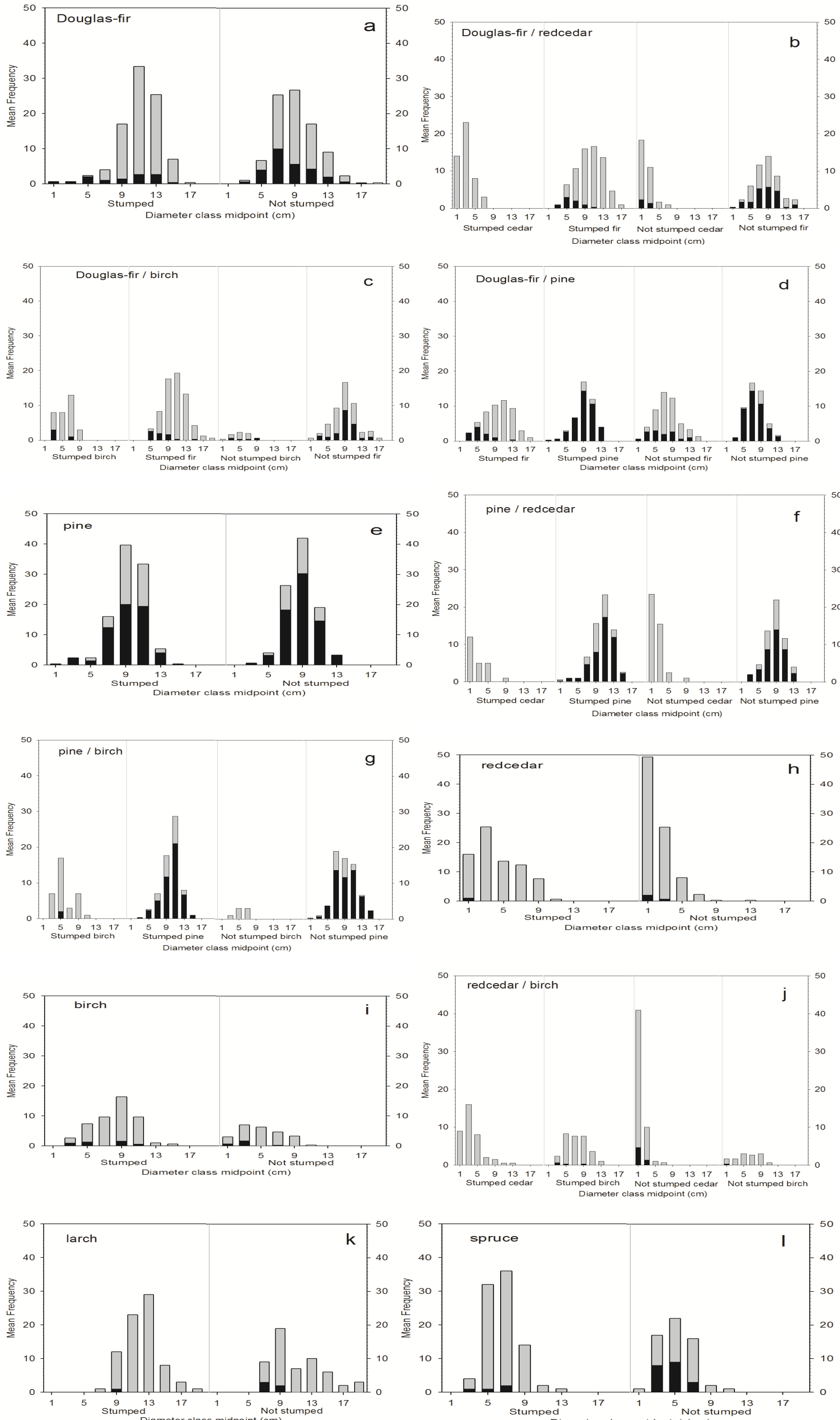
Douglas-fir
a
Douglas-fir / redcedar
b
Douglas-fir / birch
c
Douglas-fir / pine
d
pine
e
pine / redcedar
f
pine / birch
g
redcedar
h
birch
i
redcedar / birch
j
larch
k
spruce
l
Mean Frequency
Stumped
Not stumped
Stumped cedar
Stumped fir
Not stumped cedar
Not stumped fir
Stumped birch
Not stumped birch
Stumped pine
Not stumped pine
Diameter class midpoint (cm)

Fig. 5

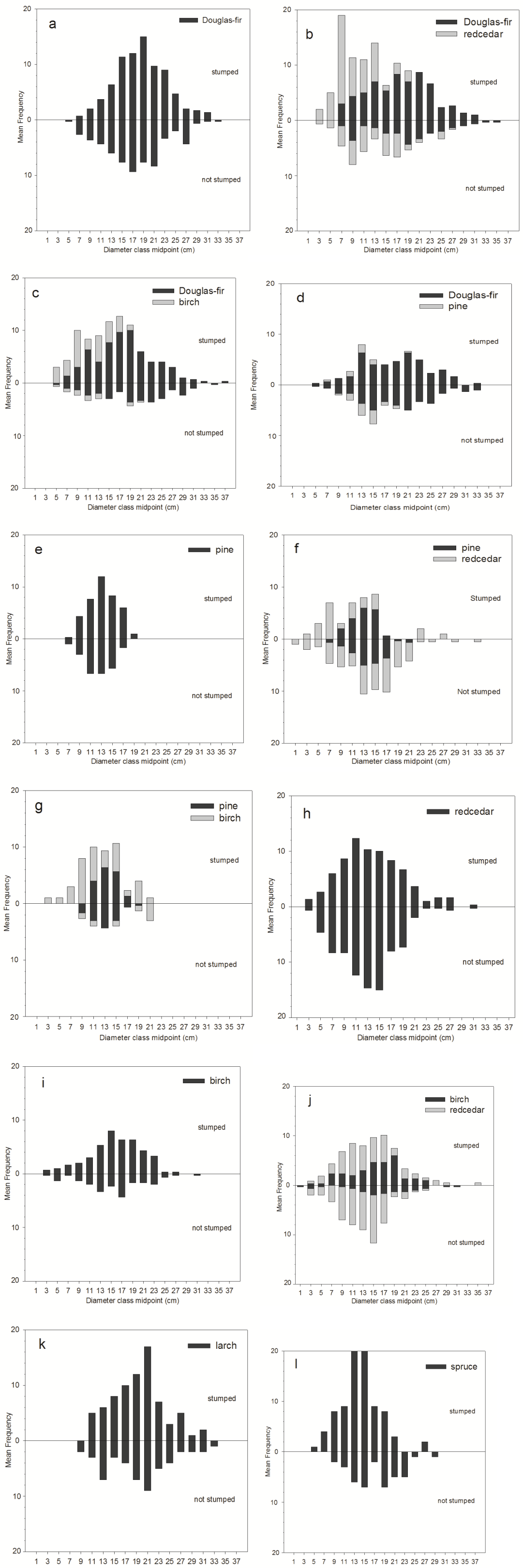
a
Douglas-fir
b
Douglas-fir
redcedar
c
Douglas-fir
birch
d
Douglas-fir
pine
e
pine
f
pine
redcedar
g
pine
birch
h
redcedar
i
birch
j
birch
redcedar
k
larch
l
spruce
stumped
not stumped
Mean Frequency
Diameter class midpoint (cm)

Fig 6.

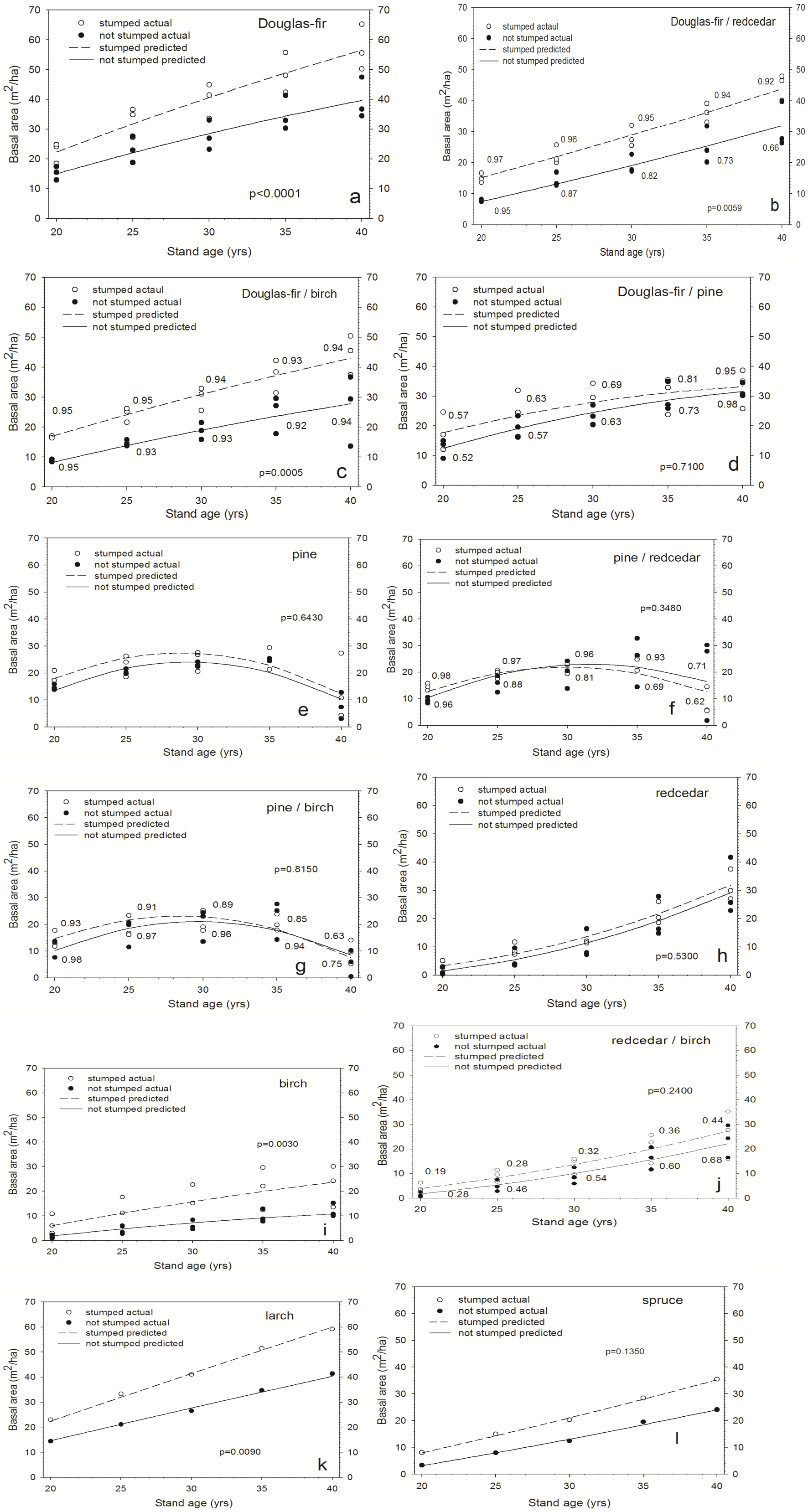
Douglas-fir
Douglas-fir / redcedar
Douglas-fir / birch
Douglas-fir / pine
pine
pine / redcedar
pine / birch
redcedar
birch
redcedar / birch
larch
spruce
stumped actual
not stumped actual
stumped predicted
not stumped predicted
Basal area (m2/ha)
Stand age (yrs)
p<0.0001
p=0.0059
p=0.0005
p=0.7100
p=0.6430
p=0.3480
p=0.8150
p=0.5300
p=0.0030
p=0.2400
p=0.0090
p=0.1350

Fig 7.

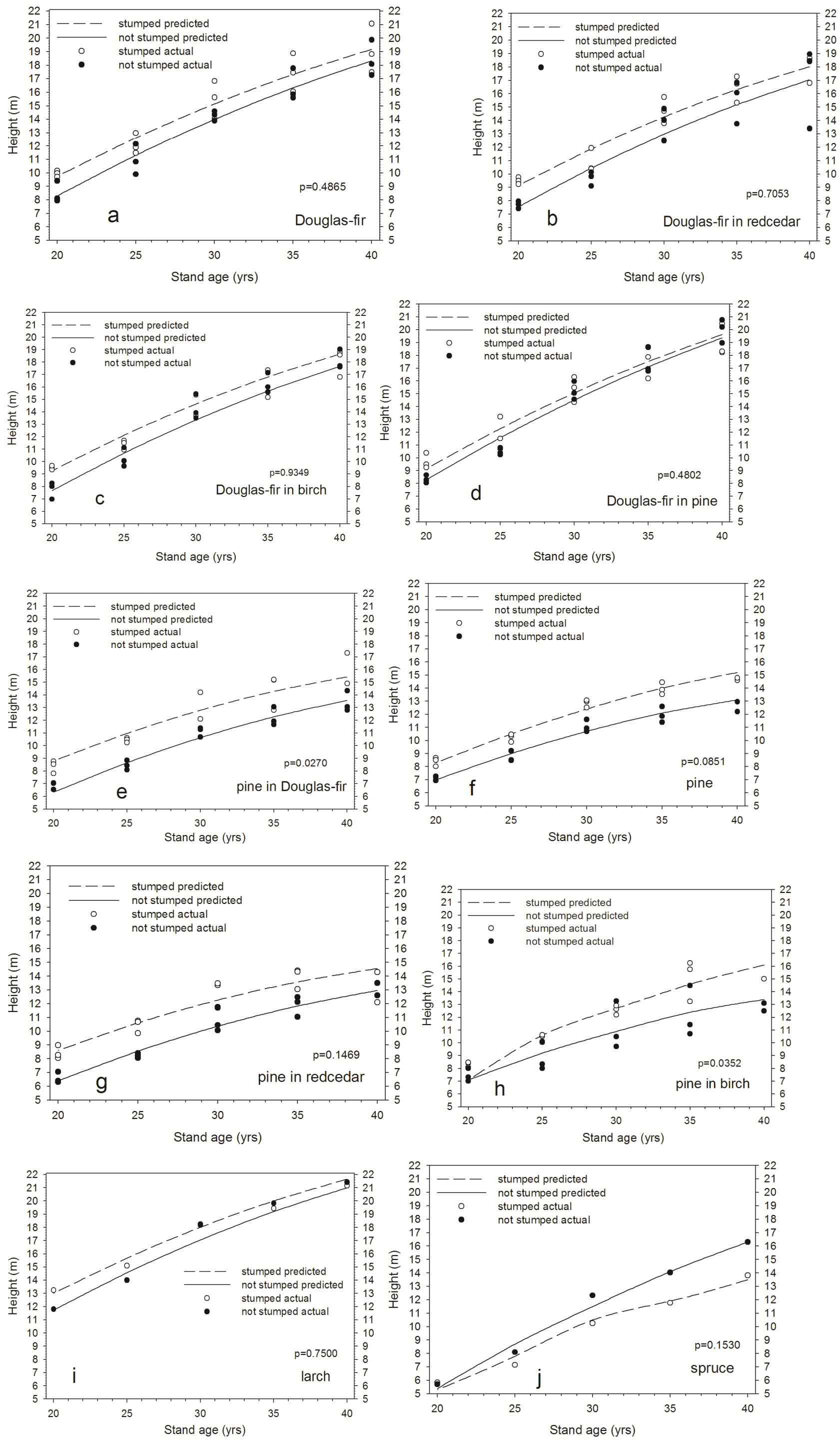
a
Douglas-fir
p=0.4865
b
Douglas-fir in redcedar
p=0.7053
c
Douglas-fir in birch
p=0.9349
d
Douglas-fir in pine
p=0.4802
e
pine in Douglas-fir
p=0.0270
f
pine
p=0.0851
g
pine in redcedar
p=0.1469
h
pine in birch
p=0.0352
i
larch
p=0.7500
j
spruce
p=0.1530
stumped predicted
not stumped predicted
stumped actual
not stumped actual
Height (m)
Stand age (yrs)

Fig. 8