MEMORIES OF NATURAL DISTURBANCES IN PONDEROSA PINE – DOUGLAS-FIR AGE STRUCTURE, SOUTHWESTERN BRITISH COLUMBIA

by

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ABSTRACT

The second chapter explicitly investigates my overall objective. I use spatial and temporal patterns in tree establishment to characterize the severity of the disturbance regime over the lower Stein Valley, British Columbia. Since there is evidence that dry, mixed conifer forests in the western United States have been modified by fire suppression, I also examine whether forest dynamics have changed since aerial fire suppression began in the 1950s in British Columbia. I attempt to derive management recommendations from my results by describing the range of natural variability in age structure.

Do not burn yourselves out. Be as I am – a reluctant enthusiast – a part-time crusader, a half-hearted fanatic. Save the other half of yourselves and your lives for pleasure and adventure. It is not enough to fight for the land; it is even more important to enjoy it. While you can. While it's still here. So get out there and hunt and fish and mess around with your friends, ramble out yonder and explore the forests, encounter the grizzly, climb the mountains, bag the peaks, run the rivers, breathe deep of that yet sweet and lucid air, sit quietly for a while and contemplate the precious stillness, that lovely, mysterious and awesome space. Enjoy yourselves, keep your brain in your head and your head firmly attached to the body, the body active and alive, and I promise you this one sweet victory over our enemies, over those desk-bound people with their hearts in a safe deposit box and their eyes hypnotized by desk calculators. I promise you this: you will outlive the bastards.

Edward Abbey
(1982) *Down the River*

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Chapter 1:

Height correction of increment cores: a method for minimizing and evaluating error

ABSTRACT

Errors in estimates of tree ages from increment cores can shift the shape of age-class distributions and thus affect inferences about forest dynamics. In this paper I examine one source of error which often arises from “height corrections” of increment cores but has been inadequately evaluated in most research on forest disturbances. Researchers traditionally bore at a predetermined height above ground and then estimate the number of years trees take to reach that height. Typically, this estimate is based on destructive sampling of existing saplings, assuming that early height growth is spatially and temporally homogeneous. Here, I present a height correction method that does not rely on such assumptions of homogeneity. I extracted a pair of cores (one at breast height and one at ground level) from 24 Douglas-fir and 17 ponderosa pine trees > 5 cm dbh. I measured early radial growth and determined the years-to-breast-height as the difference in age between the ground and breast height cores. I developed a predictive nonlinear model for each species (ponderosa pine R^2 = 0.70, mean of residuals = 0.09 years, std. dev. 6.4 years, Douglas-fir R^2 = 0.31, mean of residuals = 0.09 years, std. dev. 7.9 years). Compared to three other height correction methods, my method was superior in estimating total tree age where modern saplings do not reflect the early growth of the overstory trees or where early growth varies among trees. Using Monte Carlo simulations, I examined the implications of error expected from this height correction when interpreting regeneration pulses from age-class distributions. Because error from height corrections generated spurious pulses of tree establishment, I suggest that the magnitude of this error should govern the width of age classes to scale interpretations within the confidence of age estimates.

INTRODUCTION

Estimating the dates of tree establishment is a key requirement for research in the disturbance ecology of many forests. Approximate estimates are suitable for studies not concerned with relating tree establishment with independent temporal data. However, more accurate estimates are needed for time-since-fire calculations (Johnson and Gutsell 1994) and for correlating tree establishment with climatic variability (Savage et al. 1996; Villalba and Veblen 1997a) or chronologies of disturbances (Romme and Knight 1981). Forest ecologists traditionally use peaks in static age distributions (age distributions at one point in time) to identify disturbance initiated cohorts or pulses of tree establishment (Johnson et al. 1994; Oliver and Larson 1996). Age distributions are a function of the number of trees in each age class and thus, error in dates of establishment can shift the shape of these distributions (Palik and Pregitzer 1995). The degree to which error modifies age-class distributions, depends on the magnitude of the error in conjunction with the resolution of the age classes used in the distribution. Plotting histograms with age classes that are narrower than warranted by the confidence in estimates of establishment dates may lead to reporting spurious pulses of tree establishment. Studies on forest disturbance have rarely evaluated the sensitivity of results to the degree of error in the estimates of establishment dates.

Error in estimates of tree establishment arises primarily from the nature of the method used to sample the age of individual trees (Norton and Ogden 1990). To estimate the establishment dates of trees non destructively, you would ideally sample the root-shoot boundary of every tree with an increment borer. Even with destructive sampling, however, it is difficult and laborious to identify the root/shoot boundary of trees accurately (Savage et al. 1996; DesRochers and Gagnon 1997). Studies based on increment boring typically rely on cores taken at a predetermined height, such as breast height (1.3 - 1. 4 m) or 20 - 40 cm above ground (e.g., Henry and Swan 1974; Lorimer 1980; Veblen et al. 1991; Everett et al. 1997). This is not only more efficient but also avoids problems associated with boring at the base of trees; at ground level trees are more likely to have fire scars, rot (Frelich and Reich 1995), or flare beyond the size of the borer making complete cores not possible (Stephenson and Demetry 1995).

Boring at a specified height above ground, when used to estimate dates of establishment, encounters three possible sources of error: 1) assigning calendar dates to tree rings; 2) estimating the number of years to the pith on cores which miss or fall short of the pith, and 3) estimating the number of years to grow to the height at which the tree is cored (Norton and Ogden 1990). The magnitude of error for each of these sources varies from a few years to a few decades depending on patterns of tree growth and height of coring (Norton and Ogden 1990; Palik and Pregitzer 1995). Various methods have been used to minimize error from these sources, but few studies have analyzed the adequacy of these methods. Some describe visual or computer-assisted crossdating to eliminate dating errors (Yamaguchi 1991; Grissino-Mayer and Holmes 1993). Most focus on modeling the number of missing trees, regardless of when and where they establish, have similar rates of early growth (Palik and Pregitzer 1995). When a more accurate estimate of age is necessary, one of two methods is typically used. In the first method the average difference in age between pairs of cores taken at ground level and at coring height from mature trees is added to every sample (e.g., Henry and Swan 1974). I call this the "ground method". The second, and most frequently used method of height correction involves cutting saplings at the root collar and determining a height correction from either the average basal age of saplings of the coring height ("sapling method") (e.g., Veblen et al. 1991) or a regression between sapling height and age (e.g., Mast et al. 1998). Instead of regressions, some studies defined general categories of growth and used the average age of fast growing saplings for fast growing mature trees, and the age of slow growing saplings for slow growing mature trees (e.g., Romme and Knight 1981). Any method using saplings assumes the growth conditions of current saplings are similar to those experienced by older canopy trees (Villalba and Veblen 1997a). Both the sapling and the ground methods also assume that an average of several trees accurately describes the early growth of any one tree. However, averages provide accurate height correction only when there is little variability in early tree growth (Palik and Pregitzer 1995) and this variability is normally distributed. It is unlikely that there are many forests where these two assumptions of temporal and spatial homogeneity in early growth rates are not violated. Successional stage, microhabitat, genotype, topography, changing climate, logging and changes in natural disturbance regimes can all cause the growth rates of young trees to vary.

In this paper, I develop a method to minimize the error associated with height corrections and analyze the influence of uncertainty in the dates of tree establishment on interpretations of forest dynamics. My first objective is to develop a regression method for the height correction of increment

METHODS

Study site and context

My study site is in the lower canyon of the Nlaka’pamux Stein Valley Heritage Park in the interior of British Columbia near Lytton (50^0 15’ N, 121^0 40’ W). This area is transitional between the dry hot variants of Ponderosa Pine (PPxh2) and the Interior Douglas-fir (IDFxh2) biogeoclimatic variants (Lloyd et al. 1990). I cored trees on seven flat river terraces (28 ha total) separated from each other by the Stein River, rocky ridges or ephemeral streams (Chapter 2). The seven stands vary in successional status but most saplings are suppressed in the understory. The average density of trees on the terraces was 429 trees/ha, dominated by Douglas-fir (73% of trees) and ponderosa pine (23%) with small numbers of western red cedar (*Thuja plicata*), black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) and paper birch (*Betula papyrifera*) (4% total). The mean interval between surface fires ranges from 5 to 24 years per 2 ha on the terraces (Riccius 1998).

This study is part of a larger study of forest disturbance in which I analyze dates of tree establishment and integrate data on surface fire history to infer the relative roles of disturbances of different severity in a ponderosa pine - Douglas-fir forest (Chapter 2). I will refer to the larger study as the “disturbance study” and this present study as the “height correction study”. The sampling design used in the disturbance study influenced the design of the height correction study. For the 1 Tfı˝6.23 0 TDıy..2ER f˝0.0

Four methods of height corrections

Height corrections of increment cores follow the general equation:

$$\text{age}_{\text{measured at coring height}} + h_c = \text{age}_{\text{total}}$$

I calculated height corrections (h_c) for ponderosa pine and Douglas-fir, comparing the sapling, ground and regression methods. For the sapling method I estimated hc as the average age of current saplings at ground level. The value of h_c was estimated from 15 ponderosa pine and 15 Douglas-fir saplings randomly selected over the study area of the larger disturbance study. Saplings averaged 1.3 m high; approximately half were growing in relatively open space and half in patches of small trees. I cut these saplings at ground level using a handsaw. Basal disks were sanded and dated using standard dendrochronological methods (Stokes and Smiley 1968).

For the ground and regression methods I calculated h_c from pairs of cores taken at ground level and at breast height from 17 ponderosa pine and 24 Douglas-fir trees (Figure 1). I stratified my sampling of these 41 trees according to the number of trees sampled on each terrace in the larger disturbance study. For example, 40% of the trees used for the disturbance study were from one terrace so I cored approximately 40% of the 41 trees used for the height correction on this terrace. Sampling points were placed at regular intervals along the transects previously cored in the disturbance study. At each sampling point, I cored and measured the total tree height and dbh of the 3 closest trees that met the following criteria: 1) all > 5 cm dbh, 2) one of the 3 trees was a different one at ground level (average height = 0.19 m). To core close to the ground: 1) I dug pits in the soil in which the handle of the increment borer could turn, 2) I used the handle of a 10” increment borer on a 18” borer, or 3) instead of a handle, I used a ratchet to drill in the shaft of the borer and a crescent wrench to extract the shaft. An adapter was made from two 3/8” drive sockets connected by a piece of 1/2” hex bar to join the ratchet to the borer shaft. The modified ratchet system increased the torque on the shaft of the increment borer, so extra care was needed to prevent the shaft from bending. I required that both the ground level and breast height cores intersected pith or were within what I judged to be one year of the pith. Cores were mounted, sanded and visually crossdated using standard dendrochronological methods (Stokes and Smiley 1968; Yamaguchi 1991) and existing tree-ring width chronologies (Riccius 1998). The number of years to breast height, h_c, was calculated as the absolute difference in age between each pair of ground level and breast height cores. For the ground method, the h_c for each species was simply the average of this difference (Henry and Swan 1974, Table 1).

I developed a regression from measurements of early radial growth (y), height (x) and dbh (x) using the 41 trees described above. I measured the widths of the first 15 rings of the cores taken at breast height to a precision of 0.0001 cm using a sliding-stage micrometer (Velmex-ACcuRite; Figure 1). For both ponderosa pine and Douglas-fir, I examined the strength of regressions between years-to-breast height and the following independent variables: a) cumulative radial growth in the first 5, 10, or 15 years on cores sampled at breast height, b) total tree height and c) dbh. Least squares linear, log-linear, and various nonlinear regression models (negative exponential, power and quadratic) were fit to the data (SPSS 8.0). I selected the final model based on the distribution of the residuals, the magnitude of the mean square error (MSE), and the coefficient of variation (Ratkowsky 1990).

the number of trees were at least 50% greater than the preceding date class (coarse resolution) or the preceding 4 date classes (fine resolution) (Wells et al. 1998).

RESULTS

Sapling and ground methods

Modern saplings took approximately twice as long to grow to breast height as saplings did in the past. On average, modern breast high ponderosa pine saplings were 35 years old (median = 30, std. dev. = 10) and modern Douglas-fir saplings were 37 years old (median = 39, std. dev. = 11). Generally, saplings that grew faster were not observed in sites with better substrate or light conditions. Based on the ground method, mature ponderosa pine on average, required 16 years (median = 12, std. dev. = 12) and mature Douglas-fir required 20 years (median = 20, std. dev. = 10; Figure 2) to reach breast height when they were young. On average, these ponderosa pine and Douglas-fir grew at similar rates in both height and diameter (2-sample t-test: p (2-tailed) = 0.064; p(2-tailed) = 0.21).

Regression method

The variable that best estimated the height correction of increment cores taken at breast height was cumulative radial growth in the first 5 years. The relationship between years-to-breast height (y) and cumulative radial growth during the first 5 years on the breast height core (x) was best described by a power function ($y = ax^{-b}$, where a controls the slope and b influences the shape of the curve). Other models using cumulative radial growth in the first 10 or 15 years exhibited heteroscedastic residuals. Compared to the power function, linear, loglinear, negative exponential and quadratic regressions had lower MSEs and coefficients of variation, and poorer distributions of residuals. The power model explained most of the variance in years-to-breast height for ponderosa pine ($R^2 = 0.70$) but only about a third of the variance in that for Douglas-fir ($R^2 = 0.31$; Figure 3). Weak linear relationships existed between years-to-breast height and total tree height or dbh (height: all R^2 values < 0.29, $p > 0.026$; dbh: all R^2 values < 0.156, $p > 0.112$).

Sensitivity of regression to missing pith

The regression was not significantly sensitive to measuring radial growth in time periods later than the first 5 years. The distributions of error from the regression were centered around zero for both ponderosa pine and Douglas-fir (mean error = 0.09 years; Figure 4). For Douglas-fir, using radial ground method was greater than from the regression method (-15 to +12 years). For Douglas-fir, ranges of possible error from these two methods were essentially the same (-12 to 26 years). For both species, distributions of error from the regression method were less skewed (skewness: pine: -0.176; Douglas-fir: 1.102) and more peaked (kurtosis: pine: 0.962; Douglas-fir : 2.282) than the other methods.

Error affected distributions of tree establishment

Error in establishment dates can significantly change the shape of age distributions if the resolution of analysis is too fine. This is illustrated when estimated age distributions (determined from height corrected ring counts), differ from simulated distributions (those which summarize possible scenarios if these height corrections were wrong) (Figure 6). When class widths of 20 years were used (coarse resolution) , estimated and simulated distributions of dates of establishment were not significantly different in location, dispersion and skewness (K-S test: p = 0.89; Figure 6a). However, these two distributions significantly differed when classes were 5 years wide (fine resolution) (K-S test: p = 0.031; Figure 6c). The tradeoff between error and resolution of data analysis is further emphasized in Figure 6 b and d. When histograms of fine resolution were used there was greater deviation from a perfect correlation between the estimated and simulated proportion of trees in each age class; i.e., increased scatter around the 1:1 relationship; Pearson coefficients: coarse (0.995), fine (0.954); (Figure 6b and d).

Error in establishment dates, resolution of analysis, and whether pulses were identified visually or by quantitative criteria affected the number and position of regeneration pulses that I was able to identify. Under coarse resolution analysis, estimated and simulated distributions agreed on the

DISCUSSION

When relating dates of tree establishment derived from increment cores to independent data such as chronologies of fire, insect outbreaks or El Niño events, it is important to correct estimates of age for the number of years to reach coring height. I demonstrated that ignoring height corrections and simply reporting age at breast height resulted in a different distribution of tree establishment dates from what was actually observed (Figure 5a). Assuming uniform growth rates in young trees across time may affect conclusions about stand dynamics, even if tree ages are not being related to independent temporal data.

Each method has an appropriate context

Each of the three methods of height correction considered here requires certain assumptions about the growth of young trees. The sapling method assumes temporal and spatial homogeneity in growth rates of young trees. If modern saplings are growing under conditions similar to the older overstory, then the average basal age of saplings of the coring height should provide accurate height corrections. In my case, modern saplings were suppressed relative to growth rates exhibited by older trees, which likely established under different competitive and climatic regimes. Thus the regression model corrected the ages of ponderosa pine and Douglas-fir cores substantially better than the sapling

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have been more efficient to use the ground method instead of the regression method to height correct

differential growth rates between different tree populations and microhabitats. When feasible, take complete sections (e.g., with a chain saw) at z height and close to the root-shoot boundary from recent stumps or blowdown to more accurately estimate germination dates.

2. Mount, sand and crossdate all cores. The ease of crossdating depends on the accessibility of a master chronology and the sensitivity of radial growth to climate. Measure the widths of the first 5 to 20 years on all cores.
3. Choose best fit regressions between early radial growth and the difference in years between cores taken at ground level and at z height.
4. Use these regressions to estimate the height correction for all trees. For cores that miss the pith, use any of the models in the literature (Applequist 1958; Norton et al. 1987; Duncan 1989; Stephenson and Demetry 1995; Villalba and Veblen 1997a) to estimate the number of years to pith. Monte Carlo simulations can be used to assess the implications of error from height correcting or extrapolating to pith on interpretations of age-class distributions.

Other applications

The concept of using early radial growth to estimate early height growth can be extended to slightly different sampling problems. When boring trees such as black spruce (*Picea mariana*), which have an adventitious root system and thus a root collar hidden well below ground level, it is difficult to estimate establishment dates without excavating every tree (DesRochers and Gagnon 1997). It should be possible to estimate the number of years between coring height and the root collar via regressions of radial growth on the cores. These regressions can be constructed from excavating and cross sectioning a subsample of trees at the root collar and at the coring height. My regression method may also be useful in forestry applications when timber cruisers estimate site productivity from site index. In British Columbia, site index is defined as the height of a stand when trees are age 50 at breast height and is usually estimated from height-age models (Nigh 1999). Often these models require estimating years-to-breast-height via stem analysis of saplings. If developed for each species, the regression method could offer a more accurate estimate of years-to-breast-height in the field based on one core taken at breast height.

Assessing uncertainty is key

No matter which method of height correction is chosen, I advocate formally assessing the uncertainty around estimates of dates of tree establishment. In my method of height correction, uncertainty exists around the parameters of the regression, the number of years to pith on cores missing pith, and crossdating. The magnitude of error expected from height corrections should govern the width of date/age classes to scale interpretation of histograms within the confidence in the estimates of dates/ages. I suggest quantifying error in height corrections by the range of error in estimates. Since the majority (88%) of error for Douglas-fir was between -10 to 10 years from actual ages, I was confined to the coarse resolution of 20 year widths for histogram analysis. I verified 20 years was an appropriate scale of analysis for the expected amount of error, because the estimated age distribution (determined from height corrected ring counts) did not differ from the simulated distribution (summarized possible scenarios if height corrections were wrong). If I had analyzed histograms using date classes 5 years wide, the indicated three regeneration pulses could have been misinterpreted as a forest structured by multiple, moderate-severity disturbances. In contrast, the histogram with date classes 20 years wide indicated one moderate-severity disturbance which did not kill all the old trees followed by a long 60 year period of regeneration. These two interpretations are extremely different in terms of disturbance frequency and extent and have serious management implications. If I had used the sapling method to height correct, the resulting error could have had profound management implications. Therefore it is critical to analyse the influence of error on conclusions derived from static age distributions. I recommend evaluating the influence of error from height corrections by simulating possible age distributions which include error and examining where these simulated distributions differ from distributions estimated from height corrected establishment dates. Because the number and location of regeneration pulses were also influenced by the type of method used to identify pulses, it is important to explicitly define how pulses of regeneration were identified in histograms.

ACKNOWLEDGEMENTS

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Table 1. Summary of methods used in other studies to estimate the number of years trees require to grow to coring height; h_c =correction factor added to age determined by increment cores taken at a certain height above ground.

METHOD	ASSUMPTION	e.g. STUDY	STUDY'S PURPOSE
GROUND METHOD subsample of basal and coring height cores from live trees > 5 cm dbh: h_c= average difference between the two cores	• average can describe early growth of any one tree (spatial homogeneity in growth rates)	Henry and Swan 1974, Everett et al. 1997	track forest succession over 300 years
SAPLING METHOD destructive sampling of young trees: i. h_c = average basal age of saplings of coring height	• average can describe early growth of any one tree(spatial homogeneity in growth rates) • current saplings grew in same conditions as older trees (temporal homogeneity in growth rates)	Romme and Knight 1981, Savage 1991, Veblen et al. 1991	influence of disturbances and climate on structure
ii. h_c = regression between height and age of saplings of varying heights		Huff 1995, Mast et al.1998	influence of fire and climate on age structure
iii. stem analysis; h_c = regression between height and age		Villalba and Veblen 1997 a, b Heyerdahl 1997	influence of climate on age structure date post fire cohorts
NO CORRECTION report age as that at coring height	• uniform rates of early tree growth	White 1985, Fulé et al. 1997 Frelich and Reich 1995, Veblen 1986	reconstruct historical forest successional patterns

Figure. 1. Components of the regression method for the height correction of increment cores. The

Figure 2. Summary of the parameters used to estimate the number of years to coring height: a) difference in years between ground level and breast height cores; b) cumulative radial growth in the first five years at breast height. Thick lines in boxes indicate the mean and thin lines are the median; grey and white boxes are for ponderosa pine (PP) (pbe the median;

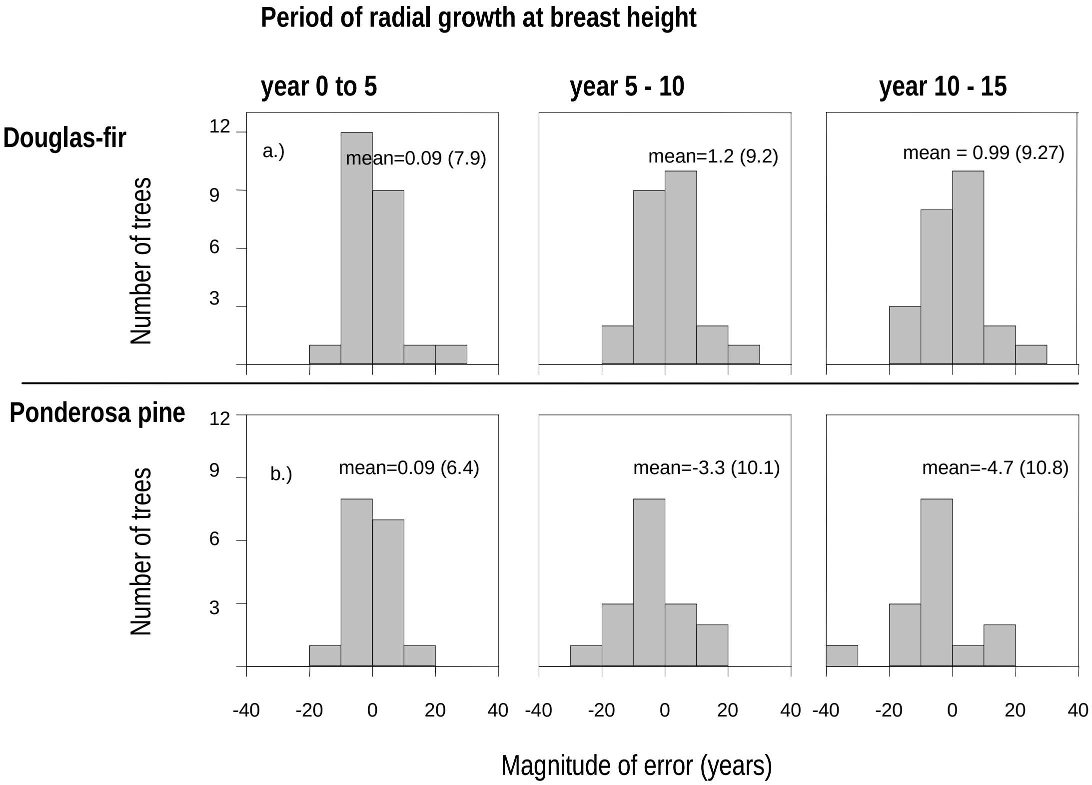
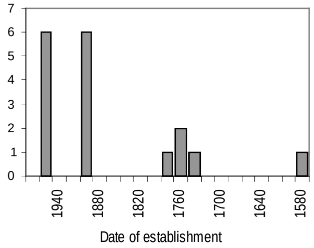


Figure 4. Comparing the distribution of error in estimates of years-to-breast-height from our regression method when cores with pith were used versus cores 10 or 15 years off pith at breast height (brackets contain standard deviation).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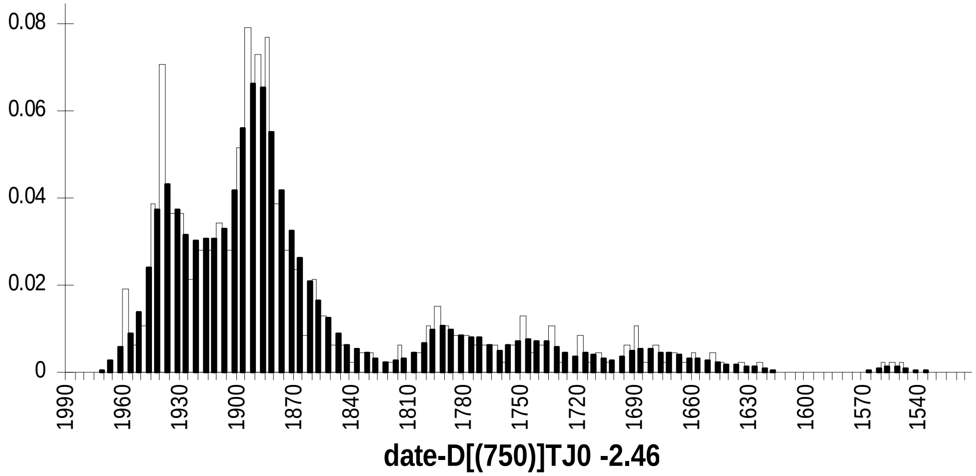
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Chapter 2:

Memories of natural disturbances in ponderosa pine - Douglas-fir age structure, southwestern British Columbia

ABSTRACT

In dry, mixed conifer forests of the inland western United States and British Columbia south of

To examine whether current forest structure has changed from historical conditions, I reconstructed age structure as it was in 1937 (year after last widespread fire) and 1900. Because the comparisons between 1937 and 1995 forest density were sensitive to assumptions about when snags and stumps died, I could not determine if forest density overall had increased between 1937 and the

INTRODUCTION

Our evolving paradigm of forest management in Canada and the United States emphasizes placing management actions within the range of natural variability of disturbance regimes (FEMAT 1993, Swanson et al. 1993, Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995). In dry, open forests of the inland western United States and British Columbia south of 52°N, such as those dominated by interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), giant sequoia (*Sequoiadendron giganteum*), or ponderosa pine (*Pinus ponderosa*), disturbances can include fires, insect outbreaks, flooding and avalaches, all of varying severity, frequency and extent (Agee 1993, Covington et al. 1994). Natural variation in disturbance severity and frequency is an important source of structural diversity in forested landscapes (Spies and Franklin 1989, Lertzman et al. 1998), yet little research has focused on quantifying the relative roles of disturbances of different severity and frequency in dry, open forests. Here, I infer the relative and historical roles of disturbances of different severity from the modern age structure of a ponderosa pine – Douglas-fir forest, British Columbia, Canada.

In dry forests where ponderosa pine dominates and is often the only conifer species, frequent, low-severity fires are considered to be the primary driver of forest structure before European settlement (Agee 1993, Covington et al. 1994). Fire exclusion, due to grazing, fire suppression or wet climatic periods, has increased forest density and shifted the age structure to younger trees of more shade tolerant species in many of these forests since around 1900 (e.g., Savage 1991, Minnich et al. 1995, Everett et al. 1997, Fulé et al. 1997, Nystrom Mast et al. 1999). This modification of forest structure has sparked substantial interest in reconstructing disturbance regimes and forest structure before European settlement as a basis for comparison with current conditions.

In dry forests, particularly mixed-conifer forests, the range of natural variability of disturbances is not necessarily limited to frequent, low-severity fires (Agee 1993, Shinneman and Baker 1997). Rather, disturbance regimes in these forests are often composed of different disturbance types of different frequency and severity. There is historical evidence of root diseases (Hessburg et al. 1994) and reoccurring insect outbreaks (e.g., western spruce budworm (*Choristoneura occidentalis*; Swetnam and Lynch 1993), Douglas-fir tussock moth (*Orgyia pseudotsugata*; Swetnam et al. 1995) and pandora moth (*Coloradia pandora*; Speer 1998). In dry, mixed conifer forests, like ponderosa pine-Douglas-fir forests in central Idaho, western Montana and eastern Oregon, Washington and British Columbia, there is additional evidence of moderate- and high-severity fire patterns (e.g., Arno et al.1995, Arno et al. 1997, Heyerdahl 1997, Taylor and Skinner 1998). Thus the natural disturbance regime is often a mixed-severity regime comprised of frequent, low-severity disturbances and infrequent, moderate- to high-severity disturbances. Because mixed-severity disturbance regimes are often hard to identify and sample (Lertzman et al. 1998), little research has quantified the relative roles of the elements within such regimes.

This lack of research is in turn reflected in the focus of management of dry, mixed conifer forests. In British Columbia, Canada, ponderosa pine-Douglas-fir forests are classified as forests maintained by frequent, low-severity fires (British Columbia Ministry of Forests 1995). Guidelines suggest silvicultural systems mimic the structural consequences of such a fire regime by creating open, multi-layered stands. Dense patches of young Douglas-fir in these forests are considered “unnatural”, non-productive and a fire risk (Robert Gray pers. com.). Managing based on a paradigm of solely frequent low-severity fires may lead to a uniform landscape of multi-aged forest. Contrastingly, a mixed-severity disturbance regime may result in large patches of open and park-like forest juxtaposed with small patches of dense, even aged trees (Arno et al. 1995, Shinneman and Baker 1997, Taylor and Skinner 1998).

In this paper, I use modern age structure and species composition to infer past patterns of tree establishment in a ponderosa pine - Douglas- fir forest in the lower Stein Valley, southwestern British Columbia. This valley has not been logged, grazed, or settled, however, aerial suppression of fires began in the 1950s. Fire-scarred trees are common, indicating that, historically, low-severity fires were frequent disturbances in the lower Stein Valley (Riccius 1998). Based on 351 crossdated fire scars from 102 trees sampled over the 28 ha study area, both coarse (e.g., regional climate) and fine (e.g., fuel loadings) scale factors influenced when and where low-severity fires occurred (Riccius 1998). Parameters of the fire regime such as seasonality, mean fire interval and extent, were similar over the study area indicating that coarse scale trends in regional climate were significant drivers of surface fire regime. The majority of fires between 1616 and 1972 burned in the late summer and fall or in the early spring, prior to new radial growth. During a defined “period of reliability” from 1876 to 1936, mean fire intervals ranged from 5 to 28 years over 2 ha units and most fires were small, burning only 2 or 4 ha. The largest recorded fire burned at least 24 ha. Although the historical fire regime was similar over the study area, fire history differed among locations within and between terraces. Fire dates were asynchronous between places in the study area, suggesting that fire location depends on fine scale variation in continuity and moisture content of fuels.

Relative to the history of low-severity fires, very little is known about other types of disturbances in the Stein Valley. I integrate temporal and spatial patterns in the past establishment of trees in 7 stands with the history of low-severity fires to infer the severity of the dominant (disturbance regime in each stand. I first ask for each of the 7 stands if regional climate primarily drove tree establishment over the last 300 years and if not, which disturbance regime (low-, moderate-, high- or mixed-severity) predominantly influenced past forest structure. By predominant, I mean dominating over 80% of the general pattern of an age-class distribution. I made a number of *a priori* hypotheses and predictions regarding the influence of regional climate and various disturbance regimes on tree establishment (Table 1). Testing these hypotheses relies on differentiating between the temporal and spatial consequences of five categories of drivers of stand age structure (Figure 1):

1. *Regional climate*: Regional trends in climate can directly induce or inhibit synchronous tree establishment over a region. For instance, periods of warm, wet springs and summers, favorable for the survival of ponderosa pine seedlings, have been associated with correlated establishment in regionally dispersed stands (Savage et al. 1996, Swetnam and Betancourt 1998). If regional climate primarily drives tree establishment in the Stein, then I expect age distributions of the 7 stands to be similar (Table 1).
2. *Frequent low-severity disturbances*: Low-severity disturbances like low-severity fires, root rot or insect attacks, tend to kill small patches of trees and are sometimes species specific (Agee 1993,

composition (Keane et al. 1990, Miller and Urban 1999), regeneration capacity, multi-agedness (Taylor and Skinner 1998), size structure (Minnich et al. 1995), and volume of dead wood (Keane et al. 1990; Table 1).

3. *Less frequent moderate-severity disturbances*: Moderate-severity disturbances, including moderate fires, insect outbreaks and windthrow, tend to be patchy without killing all trees in an area (Agee 1993). Age-class distributions of such areas have multiple cohorts with bell-shaped pulses of regeneration (distinguishable from a multi-aged distribution that has trees in almost every age class resulting from frequent, low-severity disturbances; Figure 1). Moderate-severity disturbances may also be spatially, but not temporally distinct, and without spatial analysis, resulting pulses of regeneration cannot be identified from age-class distributions (Duncan and Stewart 1991, Heyerdahl 1997). If moderate-severity disturbances predominantly influence tree establishment, then I expect the age-class distributions of the 7 stands to be multi-cohorted (Table1).
4. *Infrequent high-severity disturbances*: High-severity disturbances like crown fires, windthrow, avalanches, debris flows and catastrophic floodings, typically kill all trees in a large area leaving a wide spatial and temporal window for regeneration as a single cohort. High-severity fires typically characterize the northern boreal forests and the lodgepole pine (*Pinus contorta*) forests in the Canadian Rockies (Johnson and Wowchuck 1992), but evidence of similar fires has also been found in ponderosa pine forests (Shinneman and Baker 1997, Brown et al. 1999). Within a single high-severity fire there can be spatial variability in burn severity (e.g., Yellowstone fires of 1998, Turner et al. 1994). If high-severity disturbances drive tree establishment, then I expect the 7 stands to be characterized by single cohorts (Table 1).

5. *Mixed-severity disturbances*: Such disturbances may be one event like a fire, which is internally heterogeneous in severity or a series of events that are each a different severity. A regime of mixed-severity disturbances is some combination of low-, moderate- and high-severity disturbances with some disturbances masking the structural consequences of others (Agee 1993, Taylor and Skinner 1998). At a fine scale, the structural consequences of a mixed-severity disturbance may resemble one of any within the gradient of severity in Figure 1. However, at coarser scal at

fine scale analysis, but at a coarser scale of analysis, these effects may be masked by those from a crown fire.

Even though the Stein Valley is relatively undisturbed by humans, fire suppression either by foot by fire wardens beginning in 1912 or more effectively by aerial technology in 1958, potentially confounding the natural disturbance regime. To determine if forest structure has departed from historical conditions, I reconstructed age structure across the study area for two historical dates, 1936 (date of last widespread fire in the area) and 1900 (date before fire wardens were stationed 60 km from the Stein Valley; Parminter pers. com.). I then ask for the entire study area whether forest structure changed since 1936 and 1900? I hypothesize that because fire exclusion began later than in the western United States (date of last fire is 1936 versus 1880s), the effects of fire exclusion (a shift to more young and shade tolerant trees and increased tree density; e.g., Savage 1991, Minnich et al. 1995, Keane et al. 1990) are not as clear as elsewhere (Table 1).

METHODS

Study site

The 28 ha study site is in the lower canyon of the Nlapka’pamux Stein Valley Heritage Park in southwestern interior British Columbia near Lytton (50^{0} 15’ N, 121^{0} 40’ W) (Figure 2a,b). Forests here are open and transitional between the dry hot variants of the Ponderosa Pine (PPxh2) and the Interior Douglas-fir biogeoclimatic subzones (IDFxh2) (Table 2) (Lloyd et al. 1990). The biogeoclimatic ecosystem classification has been adopted across British Columbia to represent ecosystems capable of supporting similar plant communities under the same regional climate (Meidinger and Pojar 1991, MacKinnon et al. 1992). The study site is close to the northern extent of dry ponderosa pine-Douglas-fir forests (Agee 1993). Most of the study area is dominated by Douglas-fir (73% of canopy trees) and ponderosa pine (23%), but western redcedar (*Thuja plicata*), black cottonwood (*Populus balsamifera* spp. *trichocarpa*), and paper birch (*Betula papyrifera*) are common in riparian areas. Understory vegetation includes saskatoon (*Amelanchier alnifolia*), kinnikinnick (*Arctostaphylos uva-ursi*), soopolallie (*Shepherdia canadensis*), falsebox (*Pachistima myrsinites*), dull Oregon-grape (*Mahonia aquifolium* modified trees indicate the extent of First Nations' use of the lower valley. Burning by First Nations to encourage bulb and berry production has not been reported in the Stein Valley, but has been recorded nearby in Botanie Valley (Turner 1991). A few trappers' and gold miners' cabins were built early in the 1900s but there has been no concentrated European settlement or grazing within the unlogged and unroaded watershed. My study is one component within a large research project studying natural disturbance regimes at scales ranging from inter-stand to inter-watershed analyses in the Stein and a nearby valley, Cayoosh Valley (Fall 1998, Riccius 1998, Dorner et al. in prep., E. Heyerdahl unpublished, S. Karpuk unpublished).

Sampling stand structure

Seven distinct terraces were sampled, each bounded by the Stein River and steep slopes (Figure 2c). These terraces were created by the Stein River after the last glaciation (Ryder 1981) and are flat, littered with round boulders, and have shallow soils with little organic material. Terrace A consists of two terraces, one slightly elevated above the other (Figure 2c). In 1995, four to ten 50 x 10 m plots were sampled on each terrace along transects parallel to the Stein River (Figure 2c, Table 2). The terraces vary in size by an order of magnitude, consequently more plots were sampled on larger terraces. The northeastern corner of each plot was georeferenced using a global positioning system (GPS).

Various elements of stand structure were measured by plot. In each plot every live tree > 5 cm diameter at breast height (1.3 m) was cored and its diameter at breast height (dbh) was measured along with its height and location relative to the transect. For rotten trees (3%), the closest tree of similar size outside of the plot was sampled as a replacement. The number of seedlings and saplings

> 0.5 m in height and < 5 cm dbh in plots were recorded on 5 of the 7 terraces. The amount of dead wood in each plot was characterized by measuring the height and the diameter closest to breast height of stumps and snags and the length and diameter of both ends of downed logs.

I took several steps to minimize error in estimating establishment dates. I visually crossdated (Yamaguchi 1991) well-sanded increment cores (Stokes and Smiley 1968). Cores that could not be crossdated were excluded from further analyses (7%). For cores that did not intersect the pith (40%), I estimated the number of rings to pith using an overlay of concentric rings (mean 4 years; std. dev. 5 years; Applequist 1958). I also corrected each tree age for the number of years to reach coring height based on regressions relating early height growth to early radial growth (first 5 sampled years at breast height) developed in Chapter 1.

Analyses of age structure on terraces

I analyzed influences on the age structure of ponderosa pine and Douglas-fir at two spatial scales (terrace-level versus study area) using different analyses at each scale. For each terrace, I examined age-class distributions and box plots of age for temporal patterns indicative of specific disturbances (low-, moderate- and high-severity). For entire study area, I used a total age-class distribution plus incorporated a spatial index to evaluate spatial patterns indicative of specific disturbances regimes.

For each terrace, I constructed age-class distributions with 20 year classes as this is the degree of error expected from the height correction of increment cores (Chapter 1). Monte Carlo simulations used to simulate distributions with randomly added error in ages, revealed that any resolution of age class less than 20 years resulted in spurious peaks of tree establishment. I did not

Assessing the influence of surface fires

To examine how surfaces fires affect general forest structure, I assessed the strength of regressions between several structural characteristics of the stands and the mean fire interval (MFI) (Riccius 1998) on each terrace. Stand structure on each terrace was characterized in terms of species composition (percentage), density of saplings (< 5 cm dbh and > 0.5 m tall), average tree size (mean basal area), degree of multi-agedness, and volume of dead wood. I used the interquartile range of age (range of age between the 25th and 75th percentiles) to quantify multi-agedness on each terrace. I calculated the volume of downed wood using Smalian's equation and assuming downed logs were cylindrical (Bell et al. 1984). Since MFI is a function of study area and the terraces disturbances (Duncan and Stewart 1991, Arno et al. 1995). To identify spatially overlapping cohorts I conservatively examine the significance of each distance class. Thus tree age for a certain distance class was positively autocorrelated if $z(d)$ was > 3.15 and negatively autocorrelated if $z(d)$ was < -3.15. If $-3.15 < z(d) < 3.15$, then tree age was randomly distributed over space. A pattern of alternating points of positive and negative autocorrelation would indicate patches of similarly aged trees separated by some distance (Legendre and Fortin 1989). Distance classes were not interpreted if they contained less than 1% of the possible pairings of trees (Legendre and Fortin 1989). I also examined the spatial pattern of young (< 150 years) and old trees (> 150 years) for each species.

Moran's *I* is sensitive to the spatial layout of sampling designs (Fortin et al. 1989). I tested the sensitivity of Moran's *I* to my sampling scheme by using the same scheme to sample simulated maps of randomly distributed trees (see Appendix for details). Results from these simulations indicate that while the sampling design may influence the global significance of a correlogram, it does not cause a spurious pattern of alternating positive and negative autocorrelation. I compensated for the potential spurious influence of my sampling design on Moran's *I* by interpreting each distance class using the more conservative Bonferroni corrected level of significance.

Cluster analysis of proximity index

Once a spatial pattern in age structure was established, I proceeded with the second step of identifying spatial and temporal cohorts. I identified groups of trees of similar age and location by hierarchical agglomerative clustering of an index of proximity. Proximity in age and space for every pair of trees was calculated as (Duncan and Stewart 1991):

$$c_{ij} = d_{ij}/d_{max} + a_{ij}/a_{max}$$

where d_{ij} and a_{ij} = differences in distance and age between trees i and j

D_{max} and a_{max} = maximum differences in distance and age among all pairs of trees

Clustering using single linkage and complete linkage produced roughly consistent groupings of trees. I report clusters from complete linkage to ensure all trees within cohorts are within some maximum distance of each other (Johnson and Wichern 1998). I first identified clusters based on a level of proximity that minimized the number of clusters and the standard deviation in age within each group to approximately 50 years. I then mapped the trees in each cluster to determine if the cluster formed a patch of contiguous trees. Clusters passing these criteria were identified as spatial and temporal cohorts.

Reconstructing historical age structures

I reconstructed the age structure and forest density as it was in 1937 and 1900 by hypothesizing different scenarios about two uncertain states of nature: 1) possible causes of missing trees alive in 1937 or 1900 from the 1995 record and; 2) the death dates of dead wood recorded in 1995 (Table 3). For the first state of nature, two plausible causes of trees missing in1995 are decomposition and consumption by fire. I was confident that the evidence sampled in 1995 was missing very little of the 1937 record due to fire consumption or decomposition. The last widespread fire in our study area was in 1936 and as this ecosystem is very dry, it is also unlikely that decomposition over the 58 years can obliterate remains of large trees. For example, a trapper’s cabin in the valley built with local trees in 1953 still stands intact and Riccius (1998) crossdated a snag sampled in 1995 with outside rings dated to the 1860s. I would also expect very little of the 1900 record to be missing from the 1995 evidence due to decomposition. However, because 11 fire dates, each of which burned at least 4 ha, were recorded between 1935 and 1900 (Riccius 1998), the missing record due to fire consumption was modelled for 1900.

I hypothesized two different scenarios for the second uncertain state of nature, the death dates of snags and stumps for the 1937 reconstruction, because I did not crossdate dead wood. Downed logs were excluded because they may have been part of snags or stumps. I first assumed that all dead wood observed in 1995 was dead by 1937 and subtracted 58 years from the age of every tree in 1995. (Table 3). Trees were excluded from the 0 – 20 years age class for both 1937 and 1995 because I did not know the survival rates of modern saplings. I then assumed that all snags and stumps observed in 1995 were alive in 1937. For each snag and stump I estimated its minimum age from regressions of log transformed age at ground level and dbh from the live tree data (ponderosa pine: $R^2 = 0.637$, $p < 0.001$, $n = 142$; Douglas-fir: $R^2 = 0.608$, $p < 0.001$, $n = 465$). I assumed that the diameter measured on snags and stumps approximated dbh. This estimate represented a minimum age of snags and stumps because decay over 58 years would decrease snag and stump size. I reconstructed age structure under this second assumption by adding the age estimates of snags and stumps to the live data. I compared the age structure in 1995 with that in 1937 by examining distributions of differences between 1995 and 1937 proportions of trees in each age class. I also compared total tree density, density of young trees (< 80 years) and percentage of Douglas-fir on each terrace in 1995 and 1937 using paired t tests.

I reconstructed the age structure in 1900 using three different methods. Because no model exists for predicting the mortality of ponderosa pine due to fire from my data, I only reconstructed the 1900 age structure for Douglas-fir. Assuming that none of the 1900 record was missing from the 1995 evidence, I reconstructed 1900 using the two methods described above (see Table 3). The third method modeled the missing record - trees that were alive in 1900 but died and disappeared before 1937 because of fire consumption. I assumed each of the 11 recorded fires were low-severity and when a tree was killed, it was irrespective of location. I also assumed that a tree killed by a fire was completely obliterated. I calculated the probability of mortality from fires using a model based on bark thickness (Ryan and Reinhardt 1989). A different probability of dying was assigned to each age class instead of individual trees to avoid reconstructing historical diameters. I estimated the average bark thickness for each 20 year age class based on the average dbh for each age class (Monserud 1979). Probabilities of mortality ranged from 0.37 for 21 – 40 year old trees to 0.05 for trees older than 400 years.

I calculated the number of trees in each age class in 1900 on each terrace as:

$$N_{1900,(x-20a)} = (N_{1937,x}\,(1-P_x)^{-Fa})$$

where N = number of trees at a point in time

x = age class

P_x = probability of dying from a surface fire in age class x

Fa = number of fires within a 20 year period on terrace

a = the number of 20 year periods; here a = 2, after each 20 year period, trees were shifted down an age class.

The sensitivity of the model was tested by varying fire severity to 30% crown kill and the number of fires. I compared the Douglas-fir age structure in 1995 with that reconstructed in 1900 from the physical evidence and from modeling potential fire consumption. I did not compare forest density between 1995 and 1900 because of the uncertainties involved.

RESULTS

The forests on the seven terraces varied considerably in structure and composition (Figure 3). Trees ranged in age from 32 to 453 years. The mean age of ponderosa pine was oldest on Terrace F, whereas the mean age of Douglas-fir was oldest on Terrace A. Stands on Terraces C and D were the densest and youngest, originating around 80 to 110 years ago. Overall, ponderosa pine constituted from 8% to 75% of the composition on terraces. Terrace B was the only terrace where the density of ponderosa pine was greater than that of Douglas-fir (Table 2). Although Douglas-fir on average covered more area (15.15 m^2/ha vs. 8.03 m^2/ha), ponderosa pine trees were generally larger than Douglas-fir (average basal area: 0.096 m^2 vs. 0.074 m^2).

Assessing the influence of regional climate: different age structures on different terraces

Age structures were not the same on all terraces. Age-class distributions of ponderosa pine and Douglas-fir on Terraces C and D were significantly different from each other and every other terrace (Kolmogorov-Smirnov test: $p < 0.0001$; Figure 3). Other pairs of terraces were also significantly different as Terraces A and F differed in the distribution of Douglas-fir age, and B and E differed in the distribution of pine age.

Terraces C and D were distinct not only because they had the youngest average age of trees, but also because their pulsed age distributions indicate recent high severity disturbances. A single pulse of ponderosa pine and Douglas-fir establishment, where 50% of the ages were within a 50-year range, characterized the age distributions of Terraces C and D (Figure 3 box plots). The two terraces differed from each other as the post disturbance cohort on D originated around 1880 and on C between 1920 and 1940. Terrace D was almost all Douglas-fir (90% of trees), half of which established within a 13 year period. Terrace C was only 66% Douglas-fir, half of which established over 47 years.

All the other terraces were broadly multi-aged or had distinct multiple cohorts, as the interquartile ranges of ponderosa pine varied from 114 to 276 years and Douglas-fir from 63 to 181 years (Figure 3 box plots). Terrace E displayed evidence of 2 cohorts; one originating around 1745 and the other around 1880. Terraces F and B also seemed to have experienced a recent moderate-severity disturbance as there was a bell shaped pulse of young trees in addition to trees in many older age classes.

Assessing the influence of surface fires: a strong influence on certain structural elements

The historical frequency of low-severity fires influenced the composition of the stands on the terraces. Terraces with longer mean fire intervals had relatively less ponderosa pine and more Douglas-fir (Figure 4a, R^2=0.64). The asymptote of the negative exponential relationship suggests a minimum of about 8% ponderosa pine establishment on the terraces; i.e., there were some dry microhabitats where, regardless of fire frequency, ponderosa pine could outcompete Douglas-fir while establishing.

Spatial autocorrelation of age: spatial patterns exist

There is a spatial pattern in tree age that is specific to each species. The correlograms for both species were globally significant, with at least one distance class significant at p = 0.0017 (Figures 6 a and b). However, the overall shape of the correlogram differed between species. This was not a function of different sample sizes because a random selection of 116 ages of Douglas-fir did not affect the shape of the Douglas-fir correlogram. The correlogram of ponderosa pine fluctuated close to zero suggesting that spatial structure of ponderosa pine age was predominantly random. Pines close together (1 – 100 m and 401 – 500 m apart) were exceptions as they were significantly similar in age (Figure 6a). This may suggest patches < 100 m of even aged pines existed within 500 m of each other. However, pines 101 – 400 m apart are not significantly negatively autocorrelated, implying trees this distance apart establish independently of one another . At greater distance classes, only pines 1101 to 1200 m apart were significantly different in age from each other.

In contrast, alternating significant positive and negative values in the Douglas-fir correlogram indicated Douglas-fir had a patchy or wave-like spatial distribution of age (Figure 6b). Significant values of Moran's *I* at the first distance class suggested small patches of even-aged Douglas-fir at a scale of 100 meters. These small patches may be separated from other small patches by 400, 1001 to 1300 meters and/or 2201 to 2500 meters (Figure 6 b). This suggests a pattern of synchronous moderate-severity or low-severity disturbances.

Some patterns emerged from examining the spatial pattern of specific age groups. Young (< 100 years) and old (> 100 years) ponderosa pine were randomly distributed over the Lower Stein (Figure 7). Old Douglas-fir were also randomly spaced, but young Douglas-fir (< 100 years) were significantly spatially autocorrelated. Trees < 100 m apart were predominantly < 100 years old.

Cluster analysis of proximity index

Cluster analysis revealed three possible larger-scaled, temporal and spatial cohorts of ponderosa pine (Figure 6 c), of which one differed from those identified in the age class distribution of all combined trees (Figure 5). These cohorts were temporally distinct as the 95% confidence intervals surrounding the mean age of each cohort did not overlap (Table 4). According to the clustering, single cohorts of 22 and 23 pines established around 91 and 140 years ago in the western half of the study area (Figure 6 c). In the eastern half, the 91 year old cohort overlapped spatially with a 267 year old cohort. Each group occupied a relatively large area as the maximum distance between a pair of trees was around 1500 m. Proximate pines were similar in age, which may explain the points of positive autocorrelation at distance classes 100 and 500 m in the correlogram. The negative autocorrelation at 1000 m may reflect the spatial layout of the three cohorts.

Throughout the study area there were cohorts of Douglas-fir which overlapped spatially. Two cohorts that established around 94 and 250 years ago dominate the western end of the study area. Two cohorts that originated approximately 91 and 289 years ago characterize the eastern half (Figure 6 d). The 94, 91 and 289 cohorts were not revealed in the age-class distribution of all the combined trees. The 94 and 91 year old cohorts were clustered as spatially distinct but overlap temporally and established at approximately the same time. The positive autocorrelation at the 100, 500 and 1100 – 1300 m distance classes may reflect both the size of a cohort as well as the distance separating the two 90 year old cohorts and the two older cohorts.

Age structure differed in 1937

The reconstructed age structure in 1937 differed in significant ways from the 1995 age structure. Generally for both Douglas-fir and ponderosa pine, there are more 61 - 140 years old trees now than in 1937, but more 21 - 60 and 141 – 200 years old trees in 1937 than now; i.e., there may have been periods of tree establishment in the 1880s and the 1740s (Figure 8a, pine not shown). The comparison was slightly biased in the relative proportions of very old trees. There are relatively more very old trees (> 320 years) now than in the past because more old trees from the 1937 record were missing due to decay. Assumptions about the death date of dead wood did not result in different reconstructions.

The forest in 1995 may or may not be denser than that in 1937 depending on assumptions about the death date of dead wood. In 1995, the mean density for Douglas-fir was 308 trees/ha and

Age structure differed in 1900

The age structures reconstructed for 1900 from both the physical evidence and the modeling methods, were similar to the 1937 age structure (Figure 8a). There were relatively more mid-aged trees (141 – 180 years) in 1900 than in 1995; i.e., a period of establishment occurred around 1730. There were relatively more young trees (41 – 120 years) in 1995 than in 1900. The relative age structures of 1937 and 1900 did differ in that proportions of trees 81 – 120 years old in 1900 resembled 1995 more closely. Also the 1937 and 1900 age structures conflicted on whether more or less 41-60, 121-140 and 201 to 260 years old trees were in 1995 than in the past. Reconstructions based on physical evidence and modeling conflicted on whether there were more or less trees in 1900 than in 1995 in the 140 and 200 year age classes. The two methods also differed in the relative similarity of the proportion of 60 to 120 year old trees to 1995.

DISCUSSION

Over the past 300 years, disturbances have been heterogeneous in severity across the lower Stein Valley. Patterns in the age structures both on and across terraces indicate that forest structure was not influenced solely by frequent, low-severity fires, but also infrequent moderate- and higher-severity disturbances. While such mixed-severity disturbance regimes have been observed in other ponderosa pine-Douglas-fir forests (e.g., Arno et al.1995, Heyerdahl 1997, Taylor and Skinner 1998), it is remarkable to find such a complex pattern of disturbances expressed over such a small area of 28 ha. Heterogeneity in disturbance severity exists in this forest at scales finer than those at which these forests are typically studied and managed.

This study, along with Riccius (1998), provides the first intensive data on the historical disturbance regime and structure in forests near the northern extent of ponderosa pine in North America. Unlike pure ponderosa pine forests in the southwestern United States, the forest in the lower Stein Valley was not influenced historically by a regime solely of frequent, low-severity fires, but rather a mixed-severity disturbance regime. Similarly, in a mixed ponderosa pine - Douglas-fir forest further east in the Rocky Mountain Trench, British Columbia, there is also evidence of a mixed-severity disturbance regime (Gray et al. 1998). There, the age structures of four 0.25 ha plots placed randomly within 20 ha were either multi-aged, single or multi-cohorted. This supports the idea that fine scale heterogeneity in disturbance severity is of significance in forests at the northern extent of ponderosa pine.

Mixed-severity disturbance regime on Stein terraces

Trees did not establish synchronously across the terraces of the lower Stein Valley. Thus regional climate and large high-severity disturbances, like a large stand-replacing fire, were unlikely to have driven tree establishment in the lower Stein Valley in at least the last 300 years. Undoubtedly, periods of warm, wet springs and summers did occur across the entire study area, but such episodes of possible tree establishment at the scale of terraces were likely masked by other disturbances. Preliminary analysis of establishment patterns 10 -20 km up the Stein Valley, suggest general patterns resembled those across terraces, indicating that regional climate may be dominant in

Terraces C and D are distinct among the terraces studied because they are separated by a 400 m wide riparian area, yet they differed in the establishment dates of cohorts and in tree composition. This implies that riparian barriers can localize high-severity disturbances within terraces. Because the regeneration pulse on Terrace D began around 1880, it was not the result of the widespread fire in 1936. Even though old pine trees were available as a seed source and Terraces C and D were on the southern aspect, the regeneration on Terrace D was 90% Douglas-fir. Terrace D in 1880 may have experienced a severe flooding or debris flow event associated with the riparian drainage. This is supported by geomorphic evidence on Terrace D of a past fluvial avulsion. The event could have killed most trees (Terrace D has the highest density of snags) and made the terrace hydrologically less conducive for ponderosa pine regeneration. Terrace C had a near reverse-J-shaped age distribution of Douglas-fir, indicative of a stand with recruitment (Oliver and Larson 1996), which coupled with the lack of veteran trees and the narrow range of establishment time (47 years for 50% of the Douglas-fir) suggests a recent high severity disturbance. The peak of trees in the 41 - 60 year age class implies that the 1936 fire was especially severe on this terrace. An additional fire occurred on Terrace C in 1889 (Riccius 1998). The pulse of ponderosa pine regeneration in the 120 year age class may be correlated to this fire (Figure 3). In contrast to Terrace D, age structure on Terrace C reflects the regeneration after the 1936 fire in addition to the legacies from the 1889 fire.

Frequency of low-severity fires responsible for certain forest structure

The occurrence of moderate- and high-severity disturbances does not mean low-severity fires did not influence forest structure on the terraces. The strong empirical relationships between the mean fire interval and various structural components on the terraces indicate the importance of such fires. In other ecosystems, frequent low-severity fires can direct species composition (Keane et al. 1990, Minnich et al. 1995, Fulé et al. 1997, Miller and Urban 1999), size structure (Keane et al. 1990, Minnich et al. 1995), density of saplings (Keane et al. 1990), degree of multi-agedness (Savage 1991, Taylor and Skinner 1998), and volume of coarse woody debris (Keane et al. 1990, Covington and coarse-grained vegetation changes, while periods of high fire frequency cause fine-grained pattern. He bases his scaling rule on a negative exponential relationship between fire frequency and fire extent, inferred from the number of trees scarred by fire in five Sequoia groves over a 160km transect. He interprets this relationship to indicate that during periods of low fire frequency, fuels accumulate, resulting in more intense fires, while during periods of high fire frequency, fuels remain low, resulting in small, patchy fires. While my data were sampled on much smaller spatial scale, the negative exponential relationships I found between fire interval and species composition and multi-agedness moderate-severity disturbance regime is simply a larger scale expression of a mix of low-and higher-severity disturbances. Because the “larger” scale of analysis in the Stein is relatively small compared to other studies, this implies that other studies that have identified moderate-severity disturbances, may find a mix of distinct low- and high-severity disturbances at a smaller scale. It may be more useful to think of moderate-severity disturbances as this mix rather than ambiguously as some intermediate along the gradient between low- and high-severity disturbances. The possible intermediates along this gradient make sampling and interpreting moderate-severity disturbance regimes difficult and challenging for management (Lertzman et al. 1998).

The spatial pattern of ponderosa pine establishment across the study area supports the idea that the establishment of ponderosa pine is driven by frequent, low-severity fires (e.g., Cooper 1960, White 1985). At a small scale, ponderosa pine in the lower Stein established in small, even aged patches < 100 m wide (Figure 6 a). Other studies found ponderosa pine establishing in patches from 10 to 55 m wide (Cooper 1960, White 1985, Nystrom Mast and Veblen 1999). At a larger scale, ponderosa pine establishment in the study area is a mosaic of these small patches as indicated by the random pattern of pine at intervals > 500 m, resembling the spatial pattern of low-severity fires which were small and random in location (Riccius 1998). Pine regeneration on terraces was also strongly related to fire frequency (Figure 4). Thus indirectly, climate may drive the temporal pattern of ponderosa pine establishment through influencing fire frequency, whereas the spatial pattern may be driven by fuel structure (Riccius 1998).

Do low-severity fires also drive Douglas-fir establishment? Like ponderosa pine, Douglas-fir also established in 100 m patches. However, the similarly aged patches of Douglas-fir were separated by up to 1000 m, which was reflected in two clusters of overlapping cohorts of young and old trees in the east and west end of the study area. I suspect that the process governing the Douglas-fir pattern is specific to this species. Since the Douglas-fir pattern in the correlogram is driven by relatively young trees (< 100 years old), the difference between the two species may reflect cumulative effects of fire suppression and a mountain pine beetle outbreak (Dendroctonus ponderosae) recorded near the Stein in the 1980s (Erickson 1987). Fire suppression may have increased the survival of young Douglas-fir growing in the understory - this is supported by finding more 61 - 140 year old trees in 1995 than in 1937 and 1900. Without examining patterns in the radial growth of Douglas-fir, we cannot tell if there had been a mountain pine beetle outbreak among the pines on the terraces. If there was, there may have also been a release of the understory Douglas-fir after beetles killed the overstory ponderosa pine (Veblen et al. 1991).

The pattern of spatially overlapping cohorts of both ponderosa pine and Douglas-fir (Figure 6 c and d) can be interpreted in two ways. First, the pattern can indicate a moderate-severity disturbance regime. In this scenario, the spatial pattern results from two moderate-severity disturbances, occuring around 90 and 270 - 290 years ago. Second and more likely, the overlapping cohorts may be the large-scale expression of multi-aged structure from frequent, low-severity fires; i.e., the multi-aged structure was essentially translated into young and old trees. There is strong evidence in the multiple fire scars on single trees that low-severity fires were important on the terraces and certainly capable of producing small patches as exhibited by both species. In models of Californian forests, low-severity fires generated spatial heterogeneity in basal area, but also did not produce a regular spatial pattern detectable by spatial autocorrelation (Miller and Urban).

Interpreting patterns in age structure at multiple scales is also challenging (Lertzman and Fall 1998). A visual analysis of the combined age-class distribution for the entire study area (Figure 5) illustrates that aspatial analysis can lead to misinterpretations of forest dynamics; e.g., multiple cohorts exist uniformly across the entire study area. On the other hand, integrating spatial information into the definition of a cohort; i.e., a cohort is a group of trees proximate in space and time of origin, causes a loss of the temporal richness found in age-class distributions. Thus it is important to realize that the cluster analysis gave simply a visual summary of general patterns of establishment at a larger scale; e.g., spatial heterogeneity specific to each species, not obvious at the smaller scale, was highlighted in this larger scale analysis. Since the numbers of clusters were arbitrarily limited, the cohorts were not necessarily statistically different, nor did they indicate the date of a disturbance event. Analyses that attempt to draw conclusions about age structure over a large area should integrate information from age-class distributions (temporally rich) and cluster analysis of a spatial and from relatively more old trees to more young trees (e.g., Minnich et al. 1995). In the Stein Valley, two dates were different (e.g., the two dates conflicted on whether more or less 41-60 and 121-140 year old trees existed now or in the past).

2. “History” occurred at more than one spatial scale. Because processes occur at multiple scales, multiscaled studies are important for reconstructing ecological history across a landscape (Heyerdahl 1997, Lertzman and Fall 1998). Analysis at the larger scale of the entire study area revealed different influences on forest structure from analyses at the small scale of one terrace. For example, on terraces I found low-severity fires were an important influence, whereas the characteristic multi-aged structure was not evident at the coarser scale of analyses.

Without testing the sensitivity of the assumptions, I may have unequivocally concluded that the forest was denser now than in 1937.

Latitudinal gradient in disturbance severity

The difference in disturbance regimes between northern and southern forests containing ponderosa pine, suggests a latitudinal gradient in the severity of disturbance regime in which the occurrence of moderate- and high-severity fires increases with latitude. Forests where ponderosa pine is the sole or dominant conifer species are primarily found in the southwestern United States and are associated with a disturbance regime dominated by low-severity fires (Covington et al. 1994). With increasing northern latitudes, there are larger zones of dry, mixed, conifer forests (Agee 1993) and more evidence of moderate- and high-severity disturbances (e.g., northern California (Taylor and Skinner 1998), eastern Oregon (Heyerdahl 1997), South Dakota (Shinneman and Baker 1997), western Montana (Arno et al. 1995)). This latitudinal gradient is analogous to the elevational gradient in fire severity observed in dry, southern conifer forests (Agee 1993, Taylor and Skinner 1998). With increasing elevation in such a forest, drier stands dominated by ponderosa pine and low-severity fires disturbances within mixed-severity regimes appears less important. Roughly 24% of the area sampled in the lower Stein Valley was multi-aged, 53% was structured by multiple cohorts, and 23% by single cohorts, suggesting up to half of the lower Stein Valley was influenced by moderate-severity disturbances in the past. While more research is needed on the relative roles of various disturbances within mixed-severity regimes, a latitudinal gradient in fire severity suggests the broad influence of climate on disturbance regimes.

Defining the range of natural variability in age structure

Structural diversity associated with disturbance regimes in forests is important for maintaining biodiversity (Bunnell 1995). For example, in ponderosa pine - Douglas-fir forests of southwestern British Columbia with heavy snowfall, mule deer (*Odocoileus hemionus* ssp. *hemionus*) require relatively dense patches of mature crown closure in which to overwinter (Armleder et al. 1986). In contrast, northern spotted owls (*Strix occidentalis caurina*) prefer more open, multi-layered old ponderosa pine – Douglas-fir forests with abundant snags and coarse woody debris (Everett et al. 1997, British Columbia Spotted Owl Management Interagency Team 1997). Forest practices will increase homogeneity in forest structure if they do not reflect the natural variability in disturbance severity and frequency.

A number of authors have proposed that the natural range of variability (RNV) be used as a guide for managers in developing silvicultural systems and setting stand management targets (e.g., Swanson et al. 1993, Lertzman et al. 1997, Landres et al. 1999). There is however, no standard approach to characterize the RNV, for instance, it has been described as a simple range between naturally occurring minimum and maximum values and as a probability distribution of observing a particular state in a random sample of the landscape (Swanson et al. 1993). I summarized the age-class distributions on each terrace using 3 variables: spread in age (the interquartile range in age (IQR)), "peakiness" (the proportion of trees in the modal age class) and central tendency (median age; Figure 9). The relationships between IQR and the other two variables captures the variability in age-class distributions better than simple minimum and maximum ages.

What is a meaningful way of thinking about the RNV in terms of these relationships? One approach would be to describe RNV as the 2-D space within the 95% confidence ellipses around the modern and historical (1937) bivariate means (Figure 9). The axes of the ellipses are derived from the standard deviation of the means and the orientations reflect the Pearson correlation between the two variables. Any stands outside of the 95% confidence ellipses could be considered out of the RNV and thus might be targets for restoration. Ellipses based on different confidence intervals could be used to define different RNVs depending on management objectives.

For the Stein data, modern bivariate ellipses are different from 1937 ellipses for both species and for both relationships (IQR versus "peakiness" and IQR versus median age). The differences between the two relationships with IQR are particularly evident (Figure 9a and b vs. c and d). The historical ellipses are primarily smaller than modern ones for the relationship between spread and "peakiness" in age distributions, whereas the ellipses differ more in orientation than size for the relationship between spread of age and median age. This suggests that whichever process was affecting tree populations, the "peakiness" was influenced differently from the central tendency. If the RNV is defined as the 1937 ellipse, then the relationship between IQR and median age for Douglas-fir has moved outside of the range of natural variability substantially. The change in sign of the Pearson correlation suggests that in 1937, IQR decreased as stands got older (Figure 9d). In contrast, modern

IQR increases as stands get older. The increasing modern IQR probably reflects the shift to more young trees in modern Douglas-fir age structure which I previously attributed to fire exclusion.

These ellipses can be used to trace the temporal trajectory of age structure on individual terraces. For example, in 1995, only Terraces E was in the range of variability of Douglas-fir age structure as defined by the 95% confidence ellipse in 1937. Most terraces in 1995 have different IQRs than in 1937, but have not changed in the proportions in modal age classes. Thus, what needs to be determined is whether the different interquartile ranges in 1995 arises from missing old trees from the 1937 record (censorship of the record) or from human-caused modifications. Because some terraces have a narrower IQR and some have a wider IQR in 1995 than in 1937, such a distinction needs to be based on stand level data. For example, Terrace F has a narrower IQR and slightly more trees in the modal age classes in 1995 than in 1937. Terrace F is also the terrace with the largest and most used backcountry campsite. It is possible that fire suppression coupled with campers decreasing the amount of fuels by collecting wood for campfires has decreased the multi-agedness of this stand. To restore Terrace F back to 1937 conditions, Figure 9b and d could be used to develop management plans (about 20% of Douglas-fir should be maintained in one age class, and the remaining 80% should be distributed over enough age classes so that the interquartile range in age approximates 135 years and the median 100 years).

Using the range of natural variability is challenging to operationalize in forest management. One particular challenge is maintaining the variability within the RNV, in this case the 95% confidence ellipses. It is important to acknowledge that the actual distribution of variability within these ellipses may not be random or uniform. More data may be needed to define the distribution of occurrences within the ellipses.

heterogeneity. At the scale of terraces, the forest in the lower Stein Valley was not primarily even aged - only 23% of the area sampled was dominated by a single cohort and I suspect most of this was caused by a flooding or debris flow event. Thus, clearcutting would create large areas of unprecedented homogeneity in the structure of similar ponderosa pine - Douglas-fir forests. Variable retention (Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995, British Columbia Ministry of Forests 1999) within the range of natural variability in temporal and

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APPENDIX

Moran's *I* is sensitive to the spatial layout of sampling designs (Fortin et al. 1989). My sampling design resulted in a wide range of sampling intervals both between plots within a terrace (10m - 125m) and between terraces (200m - 1000m). Therefore, spurious spatial autocorrelation may arise from the irregular clustering of my sampling. However, it is also possible that I sampled intensively enough to capture a wide range of distance classes and there was little effect of the sampling scheme on the shape of correlograms (Fortin et al. 1989). I tested the sensitivity of Moran's *I* to my plot-based sampling scheme by using the same scheme to sample simulated maps of randomly distributed trees. I created the simulated maps to evaluate the effect of the sampling design on Moran's *I* by representing the lower Stein Valley with a 3500 m x 1400 m matrix of forest simulated in SELES (Fall and Fall 1996). A forest was simulated where trees were placed randomly in space, irrespective of terrace boundaries. 96.7% of the cells 89). I tested ng the lo. I tep.at(. 5(n)-1(a w)(e)-9)5(ng desi)5(gp
iheme on the shape of co6-9(ce)]TJı˝T*ı˝[(()6(r)6(a)-1996)˝T*ı˝-1actust ws. ervals bo6-9pond(s. osa p[(()esi)5(m)6Be

structure to age, arising simply by chance. These correlograms though, if uninfluenced by sampling design, should not share consistent points of significant autocorrelation.

Results of the simulations showed the sampling design did not influence the shape of correlograms. When n = 445, 9 of the 10 simulated correlograms were globally significant. This suggests the sampling design caused spurious spatial autocorrelation of age. However, the number and location of significant points of autocorrelation varied between the 10 correlograms, indicating that these significant points were simply random occurrences, not a spurious pattern imposed by the plot-based sampling design. In addition, within a simulated correlogram there were no two consecutive distance classes that had significant autocorrelation and certainly none which displayed the same pattern as the observed data (Figure 6). Thus, while my sampling scheme may have influenced the global significance of the correlograms, it is unlikely that it caused spurious patterns of alternating positive and negative autocorrelation.

When n = 116, only one simulated correlogram was globally significant, suggesting Moran's *I* is dependent on sample size. This implies that either sampling with smaller sampling sizes fails to find spatial structure (low power) or that random placement of 116 trees may have less chance of being spatially structured. To compare spatial pattern of establishment between species, I compensated for the difference in sample size by randomly selecting 116 ages from the actual Douglas-fir data. Correlograms created with these 116 randomly selected Douglas-fir trees were not different from correlograms created with all Douglas-fir.

Table 1. Hypotheses and predictions for two scales of analysis: on each terrace (stand) and across all terraces (study area).

Hypotheses	Predictions
STAND	
Regional climate or large disturbances primarily influence tree establishment.	Age-class distributions are the same between stands
Influence of disturbances of different severities varies with stands and overrides the influence of regional climate.	Age-class distributions differ between stands Some stands are multi-aged (low-severity influence), some are multi-cohorted (moderate-severity) and some are single cohorted (high severity).
Frequent, low-severity fires are structurally important .	Stands with higher fire frequency or most recent fire date: have more ponderosa pine have less saplings are more multi-aged have larger trees have less dead wood
STUDY AREA	
Influence of different severity disturbances varies with scale.	Patterns in age structure across study area differ from terrace-level patterns.
Fire suppression since the 1950s has not yet changed forest structure.	Compared to past forest, modern forest has: not increased in tree density not shifted to more younger trees not shifted to more shade tolerant Douglas-fir

Table 2. Characteristics of terraces sampled in the Lower Stein Valley.

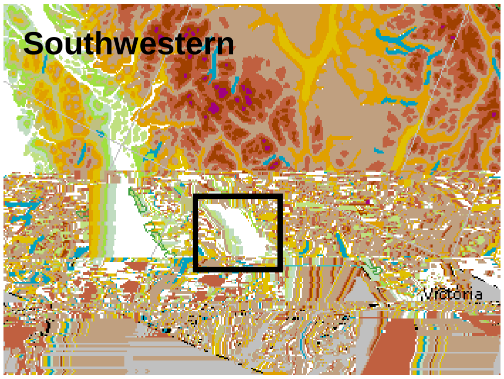
Terrace	Size (ha)	Number of plots	Sampling intensity (% of terrace area)	Mean fire interval (years)	Density of ponderosa pine (trees/ha)	Density of Douglas-fir (trees/ha)
A	1.5	4	13	10	95	165
B	1.6	4	12	9	195	65
C	5.8	3	4	14	160	340
D	0.9	5	17	28	113	907
E	15.5	10	3	15	28	312
F	1.4	4	15	12	50	295
G	1.4	4	14	12	80	75

Table 3. Assumptions about two uncertain states of nature for reconstructing 1937 and 1900 age structure from 1995 data.

State 1 (cause of missing trees from the 1995 record)	State 2 (death date of dead wood)	Calculation of age in past
1937		
1. No fire consumption or decomposition	A. Snags and stumps were dead by 1937	i. subtracted 58 yrs. from age in 1995
	B. Snag and stumps were trees alive in 1937	ii. subtracted 58 yrs. from age in 1995 and estimated minimum age of snags and stumps from age-dbh regressions
1900		
1. No fire consumption or decomposition	A. Snags and stumps were dead by 1900	i. subtracted 95 yrs. from age in 1995
	B. Snag and stumps were trees alive in 1900	ii subtracted 95 yrs. from age in 1995 and estimated minimum age of snags and stumps from age-dbh regressions
2. Fire consumption but no decomposition	A. Snags and stumps were dead by 1900	iii. used 1937 age structure to roll back to 1900, modelling the probability of mortality of trees in each age class after 11 fires
	B.. Snag and stumps were trees alive in 1900	iii. used 1937 age structure to roll back to 1900, modelling the probability of mortality of trees in each age class after 11 fires

Table 4. Characteristics of temporal and spatial cohorts identified by cluster analysis of c_{ij}.

Cohort	Number of trees	Average age	Standard error (yrs.)	Minimum age	Maximum age	Max. distance between trees (m)
Ponderosa pine						
cohort 1	70	90.4	4.1	35	173	1558
cohort 2	23	139.8	13.9	79	313	1390
cohort 3	22	267	13.2	172	409	1444
Douglas-fir						
cohort 1	161	90.7	3.8	32	229	1546
cohort 2	216	94.1	1.5	31	159	1244
cohort 3	46	249.5	7.4	178	356	1583
cohort 4	19	288.7	11.9	220	436	1079



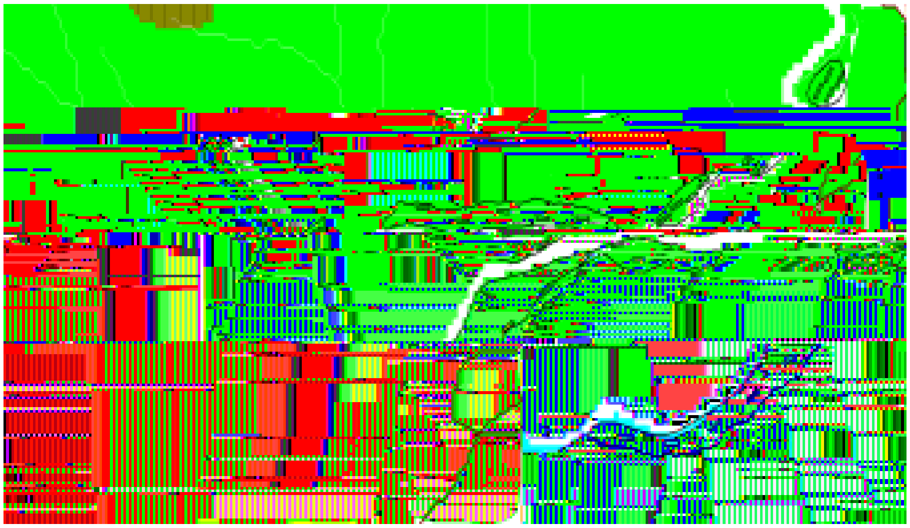


Figure 2 a). Location of the Stein Valley in British Columbia. b) The study area, the lower Stein Valley, where white denotes unforested areas. c) The layout of 50 x 10 m plots within the Terraces A - G. Terraces are separated by streams, cliffs and the Stein River. The total area of the outlined terraces is 28 ha.

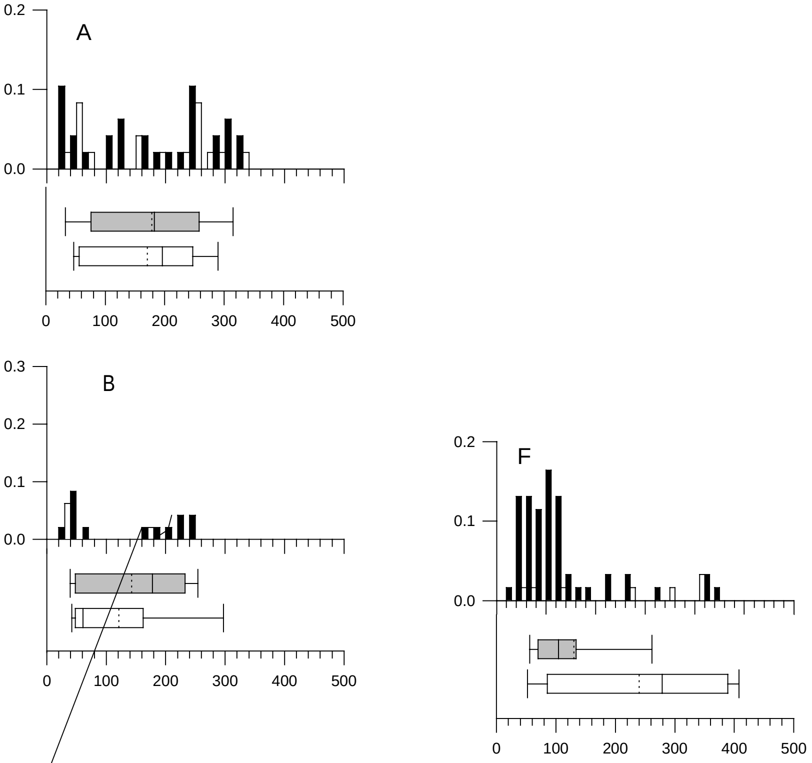


Figure 3. Age-class distributions (proportion of total trees on a terrace in each age-class) and boxplots of age for ponderosa pine (white) and Douglas-fir (black and gray) on terraces A to G. Age-classes are 20 years wide and dotted lines in boxplots indicate mean age. Rows of plots represent relative positions of terraces from east to west; left column contains terraces on the north side of the Stein River, right column contains south side terraces.

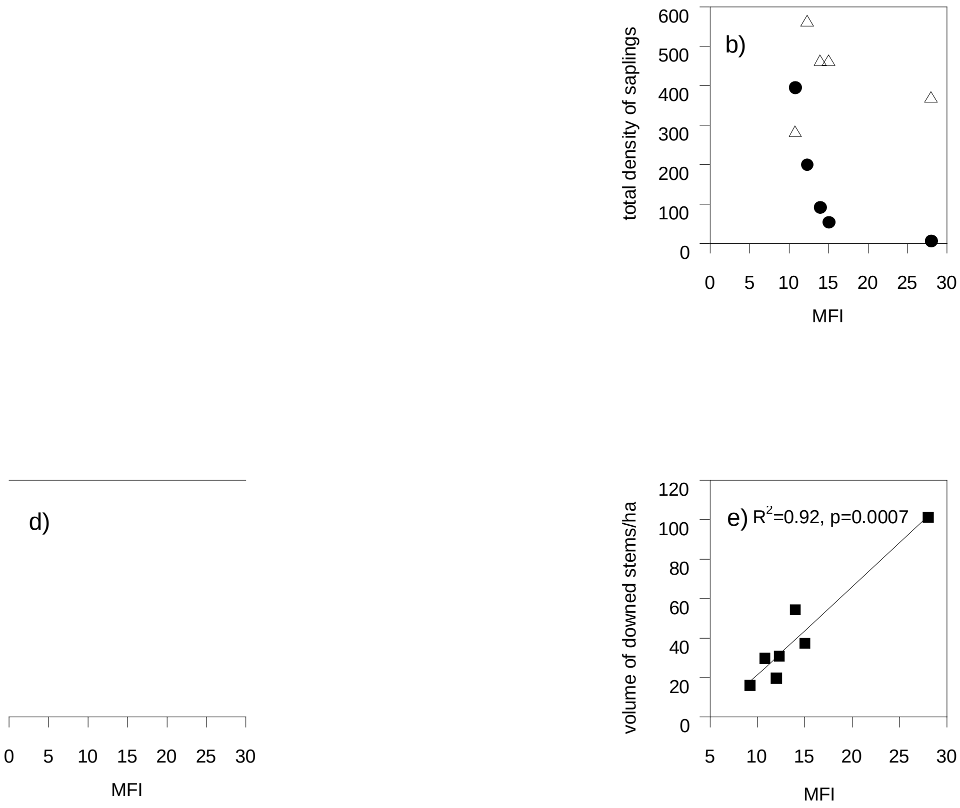


Figure 4. The influence of mean fire interval (MFI) on stand structure on terraces: a) ponderosa pine composition (Py); b) density of ponderosa pine (●) and Douglas-fir (△) seedlings and saplings; c) 25th – 75th quartile range in age for all trees (■); d) mean basal area of ponderosa pine and Douglas-fir; e) per hectare volume of downed logs.

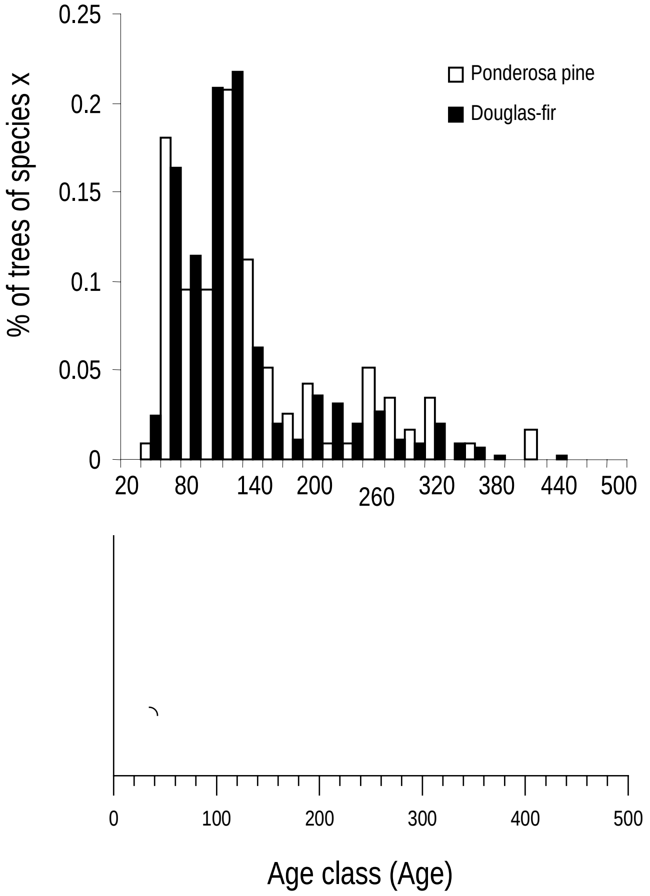
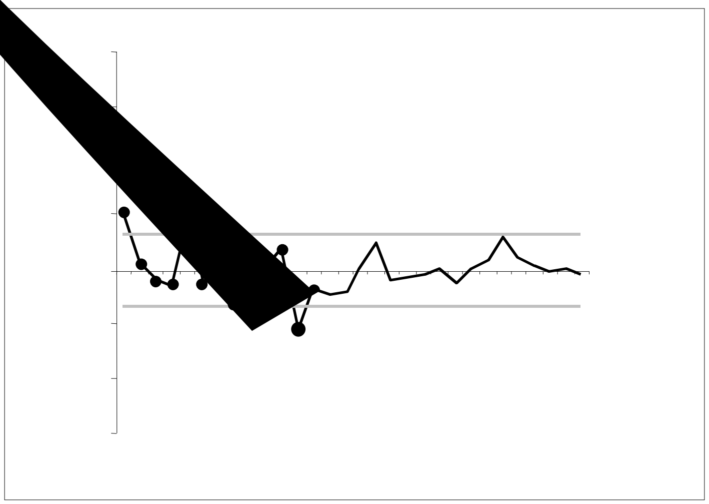


Figure 5. Age-class distribution using 20 year widths of all ponderosa pine (n = 116) and Douglas fir (n = 445) across the terraces. Arrows indicate possible pulses of establishment for ponderosa pine (Py) and Douglas-fir (Fd) where the age class contains 50% more trees than preceding age class. Below is the box plot of the ages of all ponderosa pine (white) and Douglas-fir (grey). Solid black lines in boxes indicate median age, dotted lines are the mean. Open circles are ages outside 10th and 90th percentiles.

Figure 6. Correlograms of standard deviates of Moran's *I*, (z(d)), versus distance classes of 100 m for ponderosa pine (a) and Douglas-fir (b). Gray lines are Bonferroni corrected 95% significance levels. There were less than 1% of possible pairings of trees (but >> 30 pairs) in distance classes > 2200 m. Ponderosa pine established primarily in small patches < 100 m, whereas alternating significant positive and negative z(d) in (b), suggest Douglas-fir established in patches at larger scales. Stem maps of the study area demarcate the spatial and temporal cohorts identified from cluster analysis for ponderosa pine (c) and Douglas-fir (d). Mean ages and standard error of each cohort are in the boxes. For both species there are spatially overlapping cohorts of young and old trees, which for ponderosa pine are located in the eastern end and for Douglas-fir are in two clusters in the east and west end.



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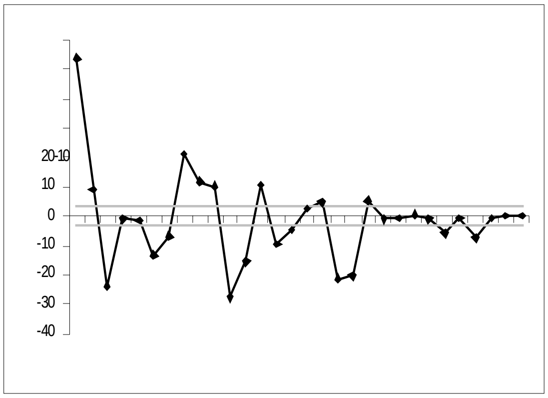

Figure 7. Correlograms of young (< 100 years) and old (>100 years) ponderosa pine (left column) and Douglas-fir (right column. Ponderosa pine and old Douglas-fir generally established randomly in space at intervals > 100 m, whereas young Douglas-fir are spatially autocorrelated at greater distances.

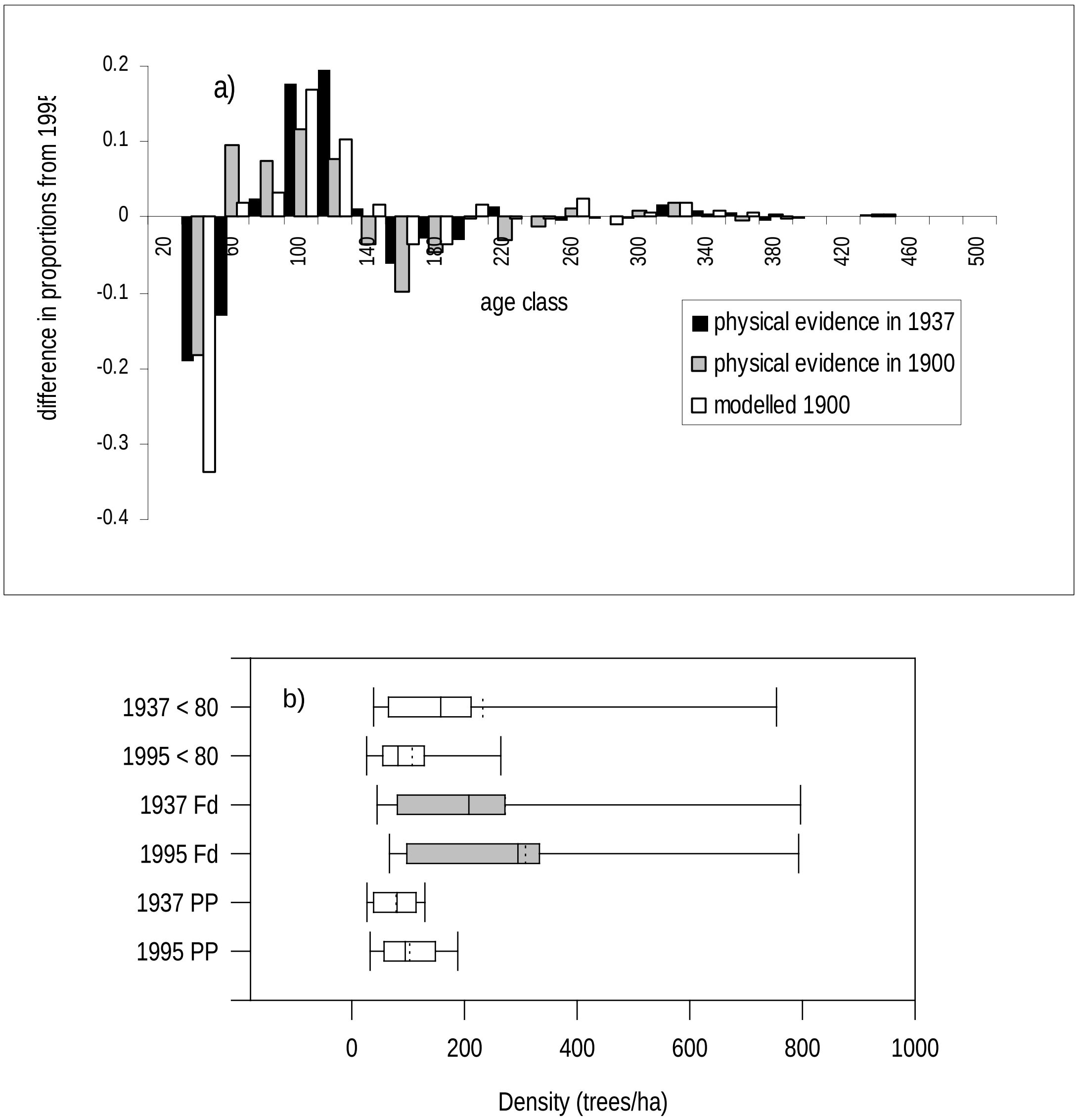

Figure 8. a) Distribution of differences between 1995, 1937 and 1900 in the proportion of Douglas-fir in each age class. Positive differences indicate more trees in a certain age class in 1995 than in the specified past. Age classes are 20 years wide; trees in class 0 – 20 have been omitted because they were a magnitude more abundant. b) Boxplots of total densities of ponderosa pine (clear boxes) and Douglas-fir (grey boxes) on each terrace in 1995 (1995PP and 1995 Fd) and in 1937 (1937 PP and 1937 Fd). Top two boxes are densities of trees < 80 years old on each terrace in 1995 (1995<80) and in 1937 (1937<80). Dotted lines are the mean densities which in some cases overlap with the median. Assuming snags and stumps were live trees in 1937, there were no significant differences between 1995 and 1937 densities of ponderosa pine, Douglas-fir or young trees (alpha = 0.05).

Ponderosa pine

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