Wildfire responses and tree longevity in old-growth ponderosa pine/Douglas-fir forests

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ABSTRACT

Mixed ponderosa pine forests are widespread in the western United States and are experiencing less frequent wildfire today than they did historically. Higher stand densities associated with lack of fire raise concerns that trees in these forests are under physiological stress due to increased competition for resources, and that current wildfires are more likely to harm trees than fires of prior centuries because of higher fuel loads today. However, little research has addressed effects of wildfire and lack of fire by comparing contemporary unburned stands to frequently burned stands in forests that have not been logged.

The main focus of this research is to understand how wildfire and lack of fire affect ponderosa pine communities and individual ponderosa pine trees in forests that were never logged or directly managed. I utilized sites in old-growth ponderosa pine/Douglas-fir forests in Montana and Idaho, each with at least two stands, one not burned for at least 70 years and one burned at approximately the historical fire frequency. I found higher overall tree densities and densities of shade-tolerant tree species (Douglas-fir and grand fir) in unburned stands, although overstory and understory community composition and structure varied from site to site. Surprisingly, there were no significant biological differences between mature ponderosa pine trees in burned versus unburned stands in a suite of physiological variables. I found a trend of increasing negative growth responses to wildfire (reduced stemwood (basal area) growth in the burned stand compared to the unburned stand) in recent fire years that had drier winters.

I was able to study very old trees that are otherwise extremely rare across landscapes. Recent investigations on “age-related” growth in trees have led to the common assumption that old trees grow slowly due to negative effects of age or height on growth. In contrast, I found that tree age and height have little effect on basal area growth, and I present evidence that slow growing trees may be more likely to reach old age. These findings highlight the potential importance of old-growth ponderosa pine/Douglas-fir forests as reservoirs and sinks for carbon in a future with novel fire regime and climate.

DEDICATION

This dissertation is dedicated to the memory of my father, Charles David Keeling.

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PREFACE

Ponderosa pine forests, widespread across western North America, experienced more frequent fire in the past. Specific historical accounts and documentary photographs of these forests often show open stands of large, widely spaced trees with understories dominated by grasses. After roughly a century of active management to control fire, many of these forests today are generally denser, with greater numbers of tree species that compete with pondersosa pine such as Douglas-fir or grand fir. High stand densities raise concerns that trees in these forests are under physiological stress due to increased competition for resources, and that contemporary wildfires will harm trees more than fires of prior centuries because of higher fuel loads today.

There has been much scientific interest in documenting changes in stand density and species composition that have occurred with lack of fire in ponderosa pine forests and determining whether these changes affect the function of individual trees. Researchers commonly employ various methods to estimate historical stand densities for a site, and then measure responses in trees when stands are returned to historical densities by experimental treatments (either through thinning or prescribed fire). However, accurate estimation of past conditions is difficult, and treatments may not realistically simulate the effects of wildfire. A potentially more accurate approach compares unburned stands to nearby reference stands that have continued to burn at approximately the historical fire frequency. The comparison of burned and unburned reference stands can provide an estimate of how lack of fire has affected the composition of forest communities without the use of reconstructions, historical descriptions, or photographs. Further, comparing growth characteristics between trees in burned and unburned stands can test hypotheses about responses to fire and lack of fire directly, without the use of treatments that may not realistically mimic effects of unmanaged wildfire.

An additional problem at many research sites is that historical logging removed large trees and may have facilitated the incursion of dense stands of smaller trees. Logging therefore presents a potential confounding influence for determining the causes of stand density increases in unburned stands. In addition, tree responses to treatments that reduce stand density in previously logged forests may not accurately reflect responses in unlogged, fire-excluded stands, because treatments are reversing the effects of both fire exclusion and higher recruitment after logging. Locating paired stands in old-growth forests (defined here as forests that have never been logged and contain trees >250 years old) controls for confounding effects of prior logging on the assessment of stand density changes and responses to stand density reductions.

The main goal of my research was to determine how wildfire and the lack of fire affect ponderosa pine/Douglas-fir forests and the individual function of old-growth ponderosa pine trees. A distinguishing feature of this work is the use of remote sites in old-growth ponderosa pine/Douglas-fir forests in Montana and Idaho. Each site included at least two stands, one not burned for at least 70 years and one burned at approximately the historical fire frequency. To my knowledge, this is the first study that utilizes this approach for mixed ponderosa pine forests in the inland Northwest. In chapter one, I test the hypothesis that, compared to burned stands, unburned stands will contain higher densities of trees, especially Douglas-fir or grand fir, and different understory plant community composition. In chapter two, I hypothesize that mature ponderosa pine trees in unburned stands will show signs of physiological stress due to increased competition for resources such as water and nitrogen. In chapter three, I test whether short- and long-term basal area growth responses to wildfires are positive (increased growth in the burned stand compared to the unburned stand) for mature ponderosa pine and ask whether growth responses to wildfires are changing over time due to climate or increased time between fires.

Although old-growth forests may be important study systems for studying the effects of fire and lack of fire, old ponderosa pine trees are a rarity and are of great scientific interest in themselves. Old trees provide long records of tree growth that may be used to better understand fundamental questions about how age affects growth rates in trees. Currently, there has been much interest in whether old trees grow slowly as a result of age *per se* (senescence) or the negative effects of increasing height. Two study sites with particularly old trees provided an opportunity to investigate an alternative hypothesis, namely that slow growth may an intrinsic feature of trees that reach old ages. In chapter four, I test this hypothesis by asking whether basal area growth in old ponderosa pine trees is related to tree age, tree height, or intrinsic differences in growth rates between old and young ponderosa pine trees.

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CHAPTER ONE

Effects of fire exclusion on forest structure and composition in unlogged ponderosa pine/Douglas-fir forests

Abstract

Research to date on effects of fire exclusion in ponderosa pine (*Pinus ponderosa*) forests has been limited by narrow geographical focus, by confounding effects due to prior logging at research sites, and by uncertainty from using reconstructions of past conditions to infer changes. I selected reference stands in unlogged ponderosa pine / Douglas-fir (*Pseudotsuga menziesii)* forests at seven sites across a broad region of Idaho and Montana. Within each site, understory and overstory community structure and composition were surveyed in 2-4 stands exposed to different numbers of fires during the 20th century. Student's t tests were used to test differences between the most fire-excluded ("unburned") and the most frequently burned ("burned") stands across the entire study. Multivariate analyses were used to characterize successional changes resulting from lack of fire. Understory community composition varied from site to site and was not related to fire exposure. However, species richness was higher in unburned stands. Overall tree densities and densities of shade-tolerant tree species increased with the absence of fire. There was a marginally significant association between xeric understories and ponderosa pine dominated overstories and mesic understories and Douglas-fir or grand-fir dominated overstories. Our multivariate analysis suggests that while general trajectories of succession in the absence of fire may be predictable, the structure and composition of ponderosa pine/Douglas-fir communities across complex landscapes may be difficult to relate to specific exposure to fire or time since fire. This study highlights the importance of natural variability and heterogeneity in ponderosa pine/Douglas-fir forests of the inland Northwest, and supports other recent research calling for cautious approaches to restoration in these forests.

Introduction

Pure and mixed ponderosa pine (*Pinus ponderosa*) forests extend across western North America from northern Mexico to southern Canada (Oliver and Ryker, 1990). Fire is likely the most important natural disturbance agent in ponderosa pine forests throughout this region. Since 1900, fires have become much less frequent across the western United States as a result of fire exclusion policies (Agee 1993, Arno et al. 1995a, Keane et al. 2002), and less indigenous burning (Barrett and Arno 1982). The accumulation of fuels during the fire exclusion period is seen as a major cause of widespread and relatively severe forest fires in recent years. Largely in response to forest structure changes attributed to fire exclusion, restoration efforts are underway in national forests to reduce stand densities by reintroducing fire, thinning stands mechanically, or by combination of both burning and thinning (Allen et al. 2002, White House 2002, Arno 1999).

Successful restoration of fire-excluded ponderosa pine forests may benefit from a clearer understanding of how changes in fire frequency affect natural forest communities. Fire exclusion is thought to increase stand densities, increase shade-tolerant species in the overstory, increase overall plant cover, decrease grasses, slow nutrient cycling, and decrease overall species diversity (Cooper 1960, Merrill et al. 1980, Covington and Moore 1994ab, Arno et al. 1995b, Fule et al. 1997, Keane et al. 2002, MacKenzie et al. 2004, DeLuca and Sala in press). However, it is increasingly recognized that fire effects in ponderosa pine forests can vary considerably in space and time (Brown et al. 1999, Schoennagel et al. 2004) and vegetation responses may reflect this variability. Recent research suggests that perspectives on fire exclusion and restoration in ponderosa pine forests must broaden to include substantial natural heterogeneity, highly dynamic ecosystems and persistent scientific uncertainty (Allen et al. 2002).

Ponderosa pine forests encompass different natural stand structures and fire regimes depending on geography and topography. Much of what is known about fire exclusion in ponderosa pine forests comes from research focused on dry, pure stands in low-elevation forests of the Southwest US (Schoennagel et al. 2004). In these forests, frequent, low-severity fires historically maintained open stands (Swetnam and Baisan 1996). However, at mid-elevations and at more northern latitudes where ponderosa pine is seral to Douglas-fir (*Pseudotsuga menziesii)* or grand fir (*Abies grandis*), stand structure may be more variable. Mid-elevation and more northern ponderosa pine forests historically experienced a mixture of low severity and high severity fires, probably at less frequent intervals (Schoennagel et al. 2004). This mixed-severity fire regime creates a mosaic of fire effects with high spatial variability in forest structure at the landscape level (Arno 1980, Schoennagel et al. 2004). Because mixed-severity fire regimes are inherently more complex than the low-severity fire regimes of the Southwest, restoration strategies adopted in the Southwest may not be applicable to ponderosa pine/Douglas-fir (PP/DF) forests of the inland Northwest. Greater insight into the range of natural variability in northwestern PP/DF forests is needed to guide future restoration strategies in these forests (Landres et al. 1999).

A limitation in our understanding of fire and fire exclusion in western forests is that much of the available data comes from forests that were logged some time in the past. In fact, it is difficult to find examples of forest conditions that are clearly a product of absence of fire alone. High stand densities commonly attributed to fire exclusion may be partially a result of previous removal of older, fire-resistant trees resulting in the incursion of dense stands of younger trees (Laudenslayer and Darr 1990, Stephens 2000, Kaufmann et al. 2000). In order to separate effects of fire exclusion from confounding effects of previous logging, there is a critical need for research in forests with no prior logging history.

An additional and inherent difficulty in studying any long-term process in forests is the uncertainty in our knowledge of past conditions. Unlogged forest stands that might serve as references to past conditions are rare, and often located in remote wilderness areas, posing considerable logistical challenges to researchers. Many studies rely solely on historical accounts or reconstructions of pre fire exclusion era stand structure rather than seeking suitable reference stands in contemporary forests. Documentary records such as photographs or written descriptions, though valuable, are often incomplete or spatially biased toward areas close to early settlements (Kaufmann et al. 2000, Swetnam et al. 1999). Reconstructions of historical forest structure using dendrochronological techniques (Covington and Moore 1994b, Arno et al. 1995b, Arno et al. 1997) or General Land Office survey data (Habeck 1994) are also subject to bias (Wright and Agee, 2004).

Dendrochronology can only make use of wood that has survived to present times and therefore will not detect trees that died and decayed before research is initiated (Stephenson 1987, Fulé et al. 1997, Allen et al. 2002). Similarly, General Land Office surveys may have failed to record the presence of smaller size-classes and certain species (Manies et al. 2001, Whitney and Decant 2001, Wright and Agee 2004). Natural reference stands in contemporary forests that have continued to experience the historical fire frequency can provide essential independent benchmarks of natural variability to verify historical data or reconstructions (Swetnam et al. 1999, Gildar et al. 2004, Laughlin et al. 2004).

Another benefit of using reference stands as opposed to reconstructions is that the understory community may be studied (Laughlin et al. 2004). Although historical understory composition in forests may be modeled or simulated (Covington and Moore 1994b), dendrochronology cannot be used to reconstruct historical understories. Uncertainty persists about the long-term effects of frequent fire versus fire exclusion on understory plant communities. Because most ponderosa pine forests usually contain only a small number of overstory species, understory plants represent a far greater contribution to biodiversity than does the overstory in these ecosystems. Reestablishment of natural understory structure and species composition is seen as a vital part of restoration of natural ecosystem processes and fire dynamics in fire-excluded forests (Allen et al. 2002). Understory responses to fire and absence of fire therefore deserve careful study alongside overstory responses.

In the work presented here, we compare forest stands exposed to different numbers of fires during the 20th century within remote sites in unlogged PP/DF forests in Idaho and Montana. These sites were used to assess the influence of recurrent fire at roughly historical frequencies versus lower fire frequencies on community structure and composition. Our use of natural reference stands provides benchmarks of forest change independent of historical accounts or reconstructions and without the confounding influence of prior logging. A total of seven sites, ranging across a broad geographical area, but within a consistent forest type (PP/DF) were selected. We surveyed both the understory and overstory. In addition, soil characteristics, nutrient cycling and tree physiology were studied and are subjects of related forthcoming papers (See DeLuca and Sala in press).

Methods

Site Selection

With the aid of a GIS database built from USFS fire maps (see Rollins et al. 2002), seven study sites were located in low- to mid-elevation ponderosa pine/Douglas-fir forests in western Montana and Idaho. Sites were chosen in areas with no previous logging history, either within or on the periphery of wilderness areas. Site locations, names, and abbreviations are shown in Figure 1. Within each site, 2-4 stands were identified, each with 0, 1, 2, or 3+ recorded fires since 1880. Sites were selected where stands shared similar physiographic (elevation, aspect, slope) characteristics. Stands were chosen so that years of 1st, 2nd and 3rd burns were relatively consistent across the entire study. Consequently, all stands of the same burn number have experienced roughly the same fire-free time interval up to the present, and effects resulting from number of fires versus time since last fire are not separated. The most recent fire at any site was more than a decade before this study was conducted; therefore documented effects are not simply short-term responses to recent fire.

Due to restrictions prohibiting the use of chain saws in wilderness areas, detailed fire scar analyses could not be conducted at every site. Instead, published USFS fire histories in the GIS maps were verified by visual reconnaissance based on the presence of charcoal and fire-scarred trees. Increment cores from fire-scarred trees were further analyzed in the laboratory (Barrett and Arno, 1988). However, at two sites (TW and MB) a detailed fire-scar analysis was conducted in 2005, subsequent to our field surveys (E. Heyerdahl and J. Riser, Fire Sciences Laboratory, USFS; unpublished data). At MB, results of this study verified the 20th century fire history in the GIS. At TW, four stands (0-, 1-, 2-, and 3-burns) were sampled in 2003. However, the fire-scar analysis conducted in 2005 found that a majority of trees within 0-, 1-, and 2-burn stands had in fact experienced two 20th century fires. Data from these three stands were averaged and analyzed as a 2-burn stand. The USFS recorded fire history was used to demarcate stands at all other sites.

For purposes of analysis, the lowest fire frequency stand at each site is referred to as "unburned" and the highest fire-frequency stand is referred to as "burned" (Table 1). At one site (MB), the unburned stand experienced one fire early in the 20th century (in 1919). At all other stands, unburned stands had not experienced fire since 1880. One site (TW) lacked an unburned stand and was not included in analyses where burned and unburned stands were compared. "Burned" stands burned 2-4 times during the 20th century. Although some physiographic differences between stands existed, on average there were no systematic physiographic differences between unburned and burned stands from each site across the entire study. While we cannot determine whether fires may have been actively suppressed even in these remote areas, the fire return intervals in our burned stands are within the historical range, which can be more than 25 years for mixed ponderosa pine forests in the northwest region (Arno and Allison-Bunnell 2002, Arno 1980).

Data Collection

Data collection was completed during June and July of 2003. In each stand, three 400m^2 plots were established at random perpendicular distances from three stratified points along an access route. Plots were located within the boundaries demarcating that stand. Each plot was defined by two 20 m transects running at right angles through a plot center. At every plot center, GPS coordinates, elevation, slope, and aspect were recorded. Table 1 lists the environmental and fire history data associated with all stands at every site.

At points every 20 cm along each transect, vegetation intersecting the transect was identified and recorded in three vertical strata: < 0.5 m, 0.5 m – 3 m, and >3 m. Species recorded in the lower two strata were considered "understory" while species recorded in the high strata were considered "overstory". Plants not identified to the species level were lumped at the generic level. Plants not positively identified but recognized across a site were recorded as "unknowns" and counted for plant functional group and species richness measures only. In addition, all trees in each plot were counted and diameters at breast height (dbh) were measured for all trees with dbh greater than 5 cm. Trees with dbh less than 5 cm were counted and recorded as seedlings.

Data analysis - understory

Cover values were calculated by counting the number of times vegetation of a given species intersected a transect point and dividing by the total number of transect points per plot. Because more than one plant could be counted at a single point, cover values can exceed 100% for a given plot. Species richness was calculated by counting the total number of unique species recorded across all plots within a stand. Plants were categorized into one of the following functional groups: grass, forb, deciduous shrub, evergreen shrub (non-ericaceous), ericaceous shrub, and tree. In addition, plant status as exotic or N-fixer was tabulated. Species richness and mean cover values for all functional groups, exotics and N-fixers were calculated for each stand. Variables which did not meet the normal distribution and homogeneity of variance assumptions for student's t-test were transformed using a square-root function. To test differences across the entire study, only the lowest burn frequency stand ("unburned") and highest burn frequency stand ("burned") were used from each site (see Table 1). T-tests were used to test for differences in plant functional groups and species diversity between burned and unburned stands across the entire study.

A multivariate approach was used to compare community structure based on species data. The goal of this approach was to determine whether plant community similarity was greater between stands grouped by fire history versus stands grouped by site. In addition to these two *a priori* grouping schemes (by fire history or by site), multivariate techniques were used to find a non-*a priori* grouping scheme that grouped stands by the highest degree of community similarity. The non-*a priori* grouping scheme (hereafter referred to as "community groups") could then be used to determine whether factors other than site or fire strongly affect the plant community.

In order to separate stands into community groups based on similarity, mean cover values for individual understory species were calculated for each stand, and these values were arranged in a multivariate data matrix (stand x species) for processing using the software program PC-ORD (McCune and Grace 2002). Understory percent cover values were not relativized or transformed. Potential grouping schemes were generated using either hierarchical cluster analysis or two-way indicator species analysis (TWINSPAN). Cluster analysis uses distance measures to generate a dendrogram that displays subgroups with high similarity nested within larger groups of decreasing similarity. A grouping scheme is then selected by choosing cut-off points along branches of the dendrogram. TWINSPAN uses "differential species" to divide the sample plots into progressively smaller groups until a final grouping scheme is produced.

Grouping schemes were evaluated using Indicator Species Analysis (Dufrene and Legendre 1997). Indicator values are calculated by multiplying relative abundance (proportion of a given species found in a specific group) by relative frequency (proportion of sample units that contain that species within a specific group). High indicator values reflect high faithfulness and even membership to stands within a group. By this method, species can be associated with specific community groups. The Monte Carlo test compares the indicator value for species in the tested grouping scheme to maximum indicator values for 1000 randomly generated grouping schemes and reports a significance value for each indicator species assigned to a tested group. A high number of significantly associated indicator species ($p \leq 0.05$) reasonably distributed among groups was used as the criterion for judging the various grouping schemes generated (McCune and Grace, 2002).

A multivariate indirect ordination scatter plot was generated using Nonmetric Multidimensional Scaling (NMS) in the PC-ORD software package (McCune and Grace 2002). Sorenson distance was used with PC-ORD's autopilot mode to select the optimal solution. Autopilot uses 40 runs with real data and 50 runs with randomized data, and chooses the highest dimensionality that yields a final stress that has stabilized and is lower than 95% of the random runs. Potential groups were overlaid with the ordination for possible further refinement of groups. Any new groups emerging from the ordination were evaluated again using Indicator Species Analysis and results were compared until optimal groups were selected. Ancillary information from the US Forest Service Plant database (www.fs.fed.us/database/feis/plants) was used to tabulate descriptions of ecological characteristics of all indicator species and these descriptions were used to characterize each group.

Multi-response permutation procedures (MRPP) in PC-ORD were used to evaluate differences in community composition between final community groups compared to differences when stands were grouped either by site or by fire history.

MRPP generates an agreement statistic, A, that describes within-group homogeneity compared to random chance, and a significance value. As with NMS, our MRPP analyses used the Sorenson distance measure.

In order to identify potential drivers of the understory community structure, the NMS ordination axes were correlated with relevant environmental data treated as independent variables. Independent variables for each stand included elevation, heat index (a transformation of aspect and slope outlined in Stage (1976), time-since-fire, species richness, % cover >3m (a surrogate for shade), and 14 soil variables (see DeLuca and Sala in press).

Data analysis - overstory

Counts of tree species were converted to trees per hectare and diameter measures were converted to basal area per hectare for all tree species. For each stand, mean densities and basal areas of the three most commonly occurring overstory species (ponderosa pine, Douglas-fir, and grand fir) were calculated. As with the understory, variables were tested for normal distribution and homogeneity of variance assumptions and transformed using a square-root function if necessary. A t-test was used to test differences in dominant overstory species density and basal area between unburned and burned stands across the entire study.

For the multivariate analysis of the overstory, counts of ponderosa pine, Douglas-fir, and grand fir for each plot were separated into 8 size classes and mean count values of each species in each size-class per hectare were calculated for every stand. Data were arranged in a multivariate data matrix (stand x spp in each size class) and log-transformed and relativized by column maximum in order to eliminate skew toward size-classes with much higher counts (i.e. seedlings). The community grouping procedure was exactly as for understory species (see above) except that overstory community groups were distinguished by indicator species in particular size-classes, rather than species alone. Size-class distributions (plotted as bar charts) of each stand were also used to evaluate the final grouping scheme and as a more precise method for comparing differences between stands.

Data analysis - overstory/understory relationships

To examine the association of overstory and understory, an NMS ordination scatter plot for all stands was produced from the tree species/size-class matrix and both overstory and understory groups were overlaid. Overstory-understory associations were tested using a chi-square test.

Results

Understory

89 understory plant species were positively identified across all sites. On average, 7 additional unidentified species per site were also recorded. There was no consistent understory plant functional group response to the number of burns (data not shown). However, species richness was significantly higher ($p \leq .05$) in the unburned stands (Figure 2).

Multi-response permutation procedures results show that grouping stands by site produced higher understory within-group homogeneity than grouping by fire history (Table 2a). An optimal community grouping scheme was produced by cluster analysis (flexible beta linkage method, Sorenson distance measure). Table 3 lists the indicator species in the understory groups generated and the associated p-values from the Monte Carlo test for each species. Three groups and a total of twenty-one species with p-values below 0.05 were found. The three groups were characterized as 1) moist, shade adapted species (mesic) 2) dry, open canopy adapted species (xeric), and 3) high elevation adapted species (high). Although this grouping scheme produced the highest number of indicator species, it failed to produce larger within-group agreement than grouping by site (Table 2a). With the exception of two sites, MB and MC, all stands within a site were classified in the same understory group. Correlations of environmental variables with the NMS ordination plot (not shown) indicated that the high elevation community group was indeed correlated with higher elevations and the mesic community group was associated with higher NH_4^+ and higher species richness than the xeric community group. There was no significant correlation with time-since-fire.

Overstory

When averaged across all sites, unburned stands had significantly higher ($p \leq .05$) total tree densities and Douglas-fir densities than burned stands (Figure 3). Total basal area and Douglas-fir basal area was also higher in unburned stands, but differences were not statistically significant (Figure 4). Grand fir was abundant in unburned stands at two sites (LC and BR) but when averaged across all sites, differences were not statistically significant.

In the multivariate analyses, grouping by site produced slightly higher within group homogeneity than grouping by fire history, but neither grouping scheme was statistically significant (Table 2b). An optimal community grouping scheme was generated by TWINSPAN. Table 4 lists indicator species/size-classes in the overstory groups generated and the associated p-values from the Monte Carlo test for each species/size-class. Four groups with a total of ten indicator species/size classes with p-values under 0.05 were found. The four groups were characterized as 1) ponderosa pine-small, 2) ponderosa pine-large, 3) mixed (ponderosa pine/Douglas-fir), and 4) grand fir. General descriptions of these groups are included in Table 4. Table 2b shows this community grouping scheme produced larger within group agreement than grouping by site or fire history.

The NMS ordination for the overstory is shown in Figure 5 with the overstory groups overlaid with boxes and the understory groups overlaid as symbols. This ordination explained 71.4% of the variation in the original overstory data. The ordination was rotated such that the x-axis correlated positively with time-since-fire ($r^2 = .206$), and thus could be used to roughly locate stands on a gradient from early to late succession. The four overstory groups show a gradual transition from stands dominated by early succession species (ponderosa pine) to stands dominated by later succession species (Douglas-fir, grand fir), with some overlap between groups. Forest floor total N also correlated positively with the x-axis ($r^2 = .319$). There were no strong y-axis correlations with any environmental or soil variable.

Figure 6 plots overstory NMS x-axis scores for all stands at every site. The NMS x-axis alone explained 51.5% of the variation in the original overstory data. Time-since-fire correlated with the NMS x-axis, and overstory community groups separated along this axis. Therefore, Figure 6 can be used to compare successional status between stands within sites, much the way successional vectors would be used in an ordination plot. Locations and relative distances along the axis in Figure 6 relate to degree of difference between stands in overstory structure with early succession characteristics (ponderosa pine) low on the axis, grading into late succession characteristics (Douglas fir, grand fir) higher on the axis. Numbers above symbols in Figure 6 refer to the number of burns associated with that stand. Filled squares are stands that were classified by TWINSPAN and Indicator Species Analysis into one of two early succession groups, while open triangles are stands classified into one of two late succession groups (see Table 4). Two stands marked with an asterix (WW3 and MC1) are stands that differed significantly in both aspect and elevation from the other stands in their respective sites (See Table 1).

Overstory/understory relationships

Figure 5 presents the relationship between overstory and understory groups. Six out of the eight stands where the understory was classified as xeric (open squares in Figure 5) were classified into one of the two early-succession overstory groups. Similarly, four out of five stands where the understory was classified as mesic (closed diamonds in Figure 5) were classified into one of the two later succession overstory groups. A chi-square test revealed these understory-overstory associations to be marginally significant (p = .057).

Discussion

We collected data over a broad geographical area in forests representative of the complex, mixed-severity fire regime in the inland Northwest for which current knowledge is limited (Schoennagel et al. 2004). Our study focused on effects due to absence of fire, ruling out effects related to prior logging, and avoiding uncertainties associated with using reconstructions of past conditions as a basis for inferring changes. We have addressed a critical need for study of long-term effects resulting from recurrent natural wildfire versus no fire, rather than short-term responses to experimental fire (van Mantgem et al. 2001).

Consistent understory community or plant functional group responses related to fire exposure were not apparent in our results. NMS ordination results for the understory (not shown) and the MRPP results (Table 2a), suggest that site-influences in general, and elevation in particular (based on NMS correlations and the understory community grouping scheme), were more powerful drivers of plant community composition than fire exposure. Significant short-term understory responses directly following fire have been documented in other ponderosa pine forests, but effects appear to be very site-specific and without a general pattern (Merrill et al. 1980, Armour et al. 1984, Bock and Bock 1984, Covington and Moore 1994ab, Metlen et al. 2004, Wienk et al. 2004, Laughlin et al. 2004). Studies of long-term effects of fire exclusion on the understory are rare (but see MacKenzie et al. 2004), however there is evidence that at greater time and spatial scales, environmental factors and spatial variability are stronger forces than fire in shaping the understory community (Gildar et al. 2004). At the scale of our study, it appears that site-to-site variation in understory community composition masked any consistent fire-related responses.

On the other hand, overall species richness was higher in unburned stands than in burned stands (Figure 2). This finding contradicts the general view that plant diversity decreases with advancing succession during periods of fire exclusion (Keane et al. 2002, Covington and Moore 1994b). However, reported decreases in diversity related to lack of fire were comparisons with short-term responses to single fires (Wienk et al. 2004). In the Southwest, measuring longer term trends in reference stands, Laughlin et al. (2004) found lower species richness in an unburned stand, but this effect was not duplicated at another nearby unburned stand (Gildar et al. 2004). Our results indicate that over long time periods the presumed general effect of increasing understory species richness with frequent fire (Covington and Moore 1994b, Keane et al. 2002) may not hold.

Higher species richness in unburned stands may be related to differences in plant available N. We found higher rates of nitrification in frequently burned stands (DeLuca and Sala in press). In addition, the mesic understory community group was associated with higher NH_4^+, higher species richness, and late succession overstory. It is possible that more uniform availability of mobile NO_3^- is providing opportunities for strongly competitive plant species to exclude other species in burned stands (Grime 1974). Alternatively, patchy availability of relatively immobile NH_4^+coupled with plant specialization for uptake of NH_4^+ and organic nitrogen may drive richness up in unburned stands (Gundale et al. 2005).

Note that very few studies have looked at understory diversity responses to fire in unlogged stands. It is possible that the disturbance of prior management may interact with the disturbance of fire to produce higher species richness by favoring colonizer plant species in managed forests that have burned. In unlogged forests, this interaction would be absent and other factors associated with lack of fire (patchy N or light availability in the understory) may increase richness by creating new niches for different species in unburned stands. Our results clearly point to the need for further study of understory plant community responses to long-term fire regime change in natural forest settings, and suggest that generalizations from short-term studies or studies in managed forests may not apply to natural forests.

There was a general pattern of xeric understory communities associated with ponderosa pine dominated overstory, and mesic understory communities associated with mixed, Douglas-fir, or grand-fir dominated stands (Figure 5). These associations may be simply correlated responses in both the overstory and understory to local environmental conditions. However, none of the environmental or soil chemistry variables measured in this study can clearly explain the association. Changes in the overstory related to absence of fire may indirectly affect the understory by increasing shade, altering soil moisture, or altering forest floor litter quality and composition (MacKenzie et al. 2004). These effects may not have been strong enough to be detected as direct understory responses related to number of burns. Although understory responses were not dramatic, the species richness response (Figure 2) and the weak association between overstory and understory (Figure 5) suggest that long-term fire frequency effects on the understory may not be entirely absent.

In the overstory, our results show increases in overall tree density and density of shade-tolerant, late succession tree species in unburned stands compared to burned stands (Figure 3). A shift in forest structure and composition to higher densities of shade-tolerant, late succession tree species is perhaps the most extensively documented effect of fire exclusion in fire-adapted forests (Keane et al. 2002). Previous studies in northwestern PP/DF forests have found densities of shade tolerant species to increase three- to five-fold with fire exclusion (Habeck 1994, and Arno et al. 1995b as cited in Keane et al. 2002). Gildar et al. (2004) reported a roughly 3-fold increase in overall tree density with fire exclusion in a study using reference stands in the Southwest. Averaged across our entire study, densities of combined shade-tolerant overstory species (Douglas-fir and grand fir) were considerably higher in unburned stands versus burned stands (Figure 3). However looking at individual sites and using the three- to five-fold increase as a standard of comparison, four sites in our study had higher increases in shade-tolerant overstory species, two sites had lower increases, and one site was within the range (data not shown). Our results confirm the general shift to higher densities of shade-tolerant tree species with absence of fire. However, the magnitude of this shift may be more variable across landscapes than what has been reported in other studies. Basal areas for total tree and shade-tolerant tree species were only moderately higher in unburned stands and differences were not statistically significant (Figure 4). The magnitudes of inferred basal area increases for total trees and for shade-tolerant species were similar to increases reported by Arno et al. (1995b, 1997) in unlogged stands using reconstructed stand structure.

While increases in densities of shade-tolerant tree species may be a predictable trajectory of succession following exclusion of fire, Figure 6 shows that sites exposed to the same number of fires had different overstory structure, and that rates of change due to lack of fire varied from site to site. These results suggest that forest structure and composition at a given moment in time may be difficult to relate to any specific fire frequency or time since fire. Outlier stands at two sites (WW3 and MC1) point to the possibility that differences in aspect or elevation may be responsible for site-specific successional responses to fire. However topographic variables in the overstory NMS ordination did not correlate with community structure along the axis relevant to succession, suggesting no consistent effect of topography on forest structure. Preexisting differences in forest structure and composition between sites, coupled with differences in the severities of 20th century fires (see Keane et al 2002), are likely factors in site-to-site variation in successional changes.

The study of recurrent wildfire versus fire exclusion presents notable statistical challenges (van Mantgem et al. 2001). Because treatments are natural wildfires rather than experimental fires, randomization and independence of plots within treatments, and replication of treatments across sites is not possible. This would normally prevent generalization of results beyond a given site. This limitation was anticipated and addressed by selecting a relatively high number of sites (7) across a broad geographical area. However, this remedy had its own costs. Namely, conducting a study of this scale at remote sites in rugged terrain necessarily precluded extensive sampling at each site. For this reason, findings of no difference in understory species composition between stands should be viewed as suggestive rather than conclusive.

The use of reference stands as chronosequences requires addressing the possibility that measured differences between stands, and variability in general may be due to inherent environmental differences between stands. Rollins et al. (2002) found that fires in the Selway-Bitterroot Wilderness were more likely to occur on dry, western and southwestern aspects between elevations of 1000 and 1700 meters elevation. This pattern raises the possibility that physiographic conditions drive fire frequency patterns across the landscape, and that these environmental differences between stands may confound plant community structure and composition differences otherwise attributable to fire. However, across our study, there were no systematic significant differences between burned and unburned stands in any physiographic variable (elevation, aspect, slope, heat-index). Therefore, measured differences in stand structure and species richness are more likely a result of lack of fire than site environmental characteristics.

Because fire history before 1880 was not available for these sites at the time of our study, we cannot be certain that disturbance history prior to 1880 was similar for all stands within a site. Older fire histories would clarify whether 20th century fire frequency differences between stands is a recent phenomenon, akin to a “treatment”, rather than a persistent historical characteristic of the site. At one site (MB) where a detailed fire-scar analysis was conducted in 2005 (E. Heyerdahl and J. Riser, Fire Sciences Laboratory, USFS; unpublished data) results showed that the unburned stand experienced much higher fire frequencies prior to the 20th century. This evidence, plus the lack of any consistent physiographic differences between stands that would create intrinsically determined fire behavior, leads us to believe that fire frequency differences during the 20th century, and not pre-1880 fire histories, are responsible for the conditions at these sites. Further investigation is needed to clarify the relationship between prior fire history and contemporary fire behavior in PP/DF forests.

This study points to the need for continued research and cautious approaches to management of northwestern ponderosa pine forests. Our findings suggest that even within the relatively consistent PP/DF forest type, fire and absence of fire produce variable effects in the understory and different rates of successional change in the overstory across varied landscapes. Further study, with greater replication and sample sizes, is needed to corroborate these general conclusions. Our study supports other recent research that cautions against specific targets for forest structure in restoration treatments (Allen et al. 2002), and underscores the importance of natural variability and heterogeneity in ponderosa pine forests (Schoennagel et al. 2004), especially in the complex, mixed fire-regime forests of the Northwest (Arno 1980). Where possible, management approaches should be site-specific (Gildar et al. 2004). However, because of the difficulty in obtaining historical information at all locations, management may need to emphasize restoration of natural ecological processes, especially fire, rather than specific stand conditions. (Allen et al. 2002). Although some managed stands may require structural manipulation before fire can be reintroduced, restoration treatments should be guided by studies that separate fire exclusion from other anthropocentric impacts such as logging and grazing, and should take into account inherent spatial variability, even in forests with a long history of intensive management.

In addition to providing results reported here, research sites established in this study could be important for future research. Reference stands can provide before-disturbance data useful for studying later disturbance effects (van Mantgem et al. 2001, Laughlin et al, 2004). The establishment of natural reference stands should prove valuable as benchmarks for future research as fire, fire exclusion, and global change continue to alter natural forest communities.

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Table 1. Physiographic data and fire histories for all stands within seven sites

Site	# burns since 1880 [a]	Mean Aspect (deg)	Mean Elev. (m)	Mean Slope (deg)	Year 1st Burn	Year 2nd Burn	Year 3rd Burn	Year 4th Burn
23 Mile (TW)	2	113.1	827	35.9	1910	1934		
	3	134.7	869	33.3	1910	1934	1992	
MacKay Bar (MB)	1 *	236.0	1813	27.3	1919			
	3 †	250.7	1536	32.7	1919	1960	1987	
Whitewater Ranch (WW)	0 *	220.0	1285	30.0				
	1	206.7	1027	25.0	1919			
	3 †	93.3	949	35.0	1919	1933	1988	
Lake Como (LC)	0 *	304.7	1552	21.0				
	2 †	273.3	1577	35.0	1924	1988		
Bullion Ridge (BR)	1 *	61.3	1665	37.3	1914			
	3 †	49.3	1464	29.3	1914	1944	1992	
Moose Creek (MC)	0 *	270.0	957	33.3				
	1	116.7	1278	25.0	1910			
	4 †	258.0	915	42.3	1910	1934	1981	1987
Ditch Creek (DC)	0 *	166.0	805	17.3				
	1	124.0	832	28.3	1919			
	2 †	202.7	844	23.3	1919	1979		

[a] Marked stands were used for testing differences between "unburned" stands (*) and "burned" stands (†) across all sites.

Table 2. Within-group homogeneity from multi-response permutation procedures (MRPP) for understory (a) and overstory (b) grouping schemes with associated p-values from Monte Carlo test [a]

(a) Understory			b) Overstory		
Grouping Scheme	Within-group homogeneity (A)	Monte Carlo test p-value	Grouping Scheme	Within-group homogeneity (A)	Monte Carlo test p-value
4 fire groups	-.028	.895	4 fire groups	.017	.267
7 site groups	.227	.000	7 site groups	.000	.489
3 community groups	.120	.000	4 community groups	.166	.000

[a] MRPP used the Sorenson distance measure to evaluate within-group homogeneity (A) for three grouping schemes (fire, site, community). A Monte Carlo test generated p-values for tested groups compared to 1000 randomly generated groups.

Table 3. Indicator species for understory community groups and associated Monte Carlo test p-values [a]

Community Group	Scientific Name	Common Name	Monte-Carlo test p-value
Mesic	*Adenocaulon bicolor*	Pathfinder	.001
	Angelica spp	Angelica	.009
	Bromus spp	Bromus	.018
	Calochortus spp	Mariposa Lily	.051
	Ceanothus velutinus	Ceanothus (evergreen)	.024
	Moehringia lateriflora	Blunt-leaved Sandwort	.034
	Osmorhiza berteroi	Mountain Sweet-Cicely	.001
	Physocarpus malvaceus	Mallow Ninebark	.005
	Rubus parviflorus	Thimbleberry	.004
	Symphoricarpos albus	Common Snowberry	.003
	Vicia spp	Vetch	.046
Xeric	*Apocynum androsaemifolium*	Spreading Dogbane	.014
	Balsamrhiza sagittata	Arrow-leaved Balsamroot	.001
	Centauria maculosa	Spotted Knapweed	.032
	Ceanothus sanguineus	Red-stemmed Buckbrush	.038
	Festuca idahoensis	Idaho Fescue	.049
	Lupine spp	Lupine	.039
High-elevation	*Arctostaphylos uva-ursi*	Kinnikinnick	.040
	Calamagrostis rubescens	Pinegrass	.006
	Shepherdia canadensis	Canada Buffaloberry	.040
	Vaccinium globulare	Mountain Huckleberry	.009

[a] See methods for analysis details.

Table 4. Indicator species/size classes for overstory community groups and associated Monte Carlo test p-values [a]

Group	Group Description	Species	Size class	Monte-Carlo test p-value
Ponderosa pine - small (PIPO -sm)	Stand is dominated by ponderosa pine in practically all size classes. More pine in smaller size classes than in larger.	Ponderosa pine	10 cm	.004
		Ponderosa pine	20 cm	.008
		Ponderosa pine	30 cm	.004
		Ponderosa pine	40 cm	.015
Ponderosa pine - large (PIPO - lg)	Stand is dominated by ponderosa pine in practically all size classes. More pine in large size classes than in smaller.	Ponderosa pine	>60 cm	.029
Mixture of pine and fir (PSME)	Mixed dominance in large size classes, Douglas-fir dominant in smaller size classes.	Douglas-fir	10 cm	.025
Grand fir (ABGR)	Grand fir dominant in small and medium size classes. Ponderosa pine or grand fir dominant in large size classes.	Grand fir	< 5 cm	.004
		Grand fir	10 cm	.013
		Grand fir	20 cm	.013
		Grand fir	30 cm	.021
		Grand fir	40 cm	.001

[a] See methods for analysis details.

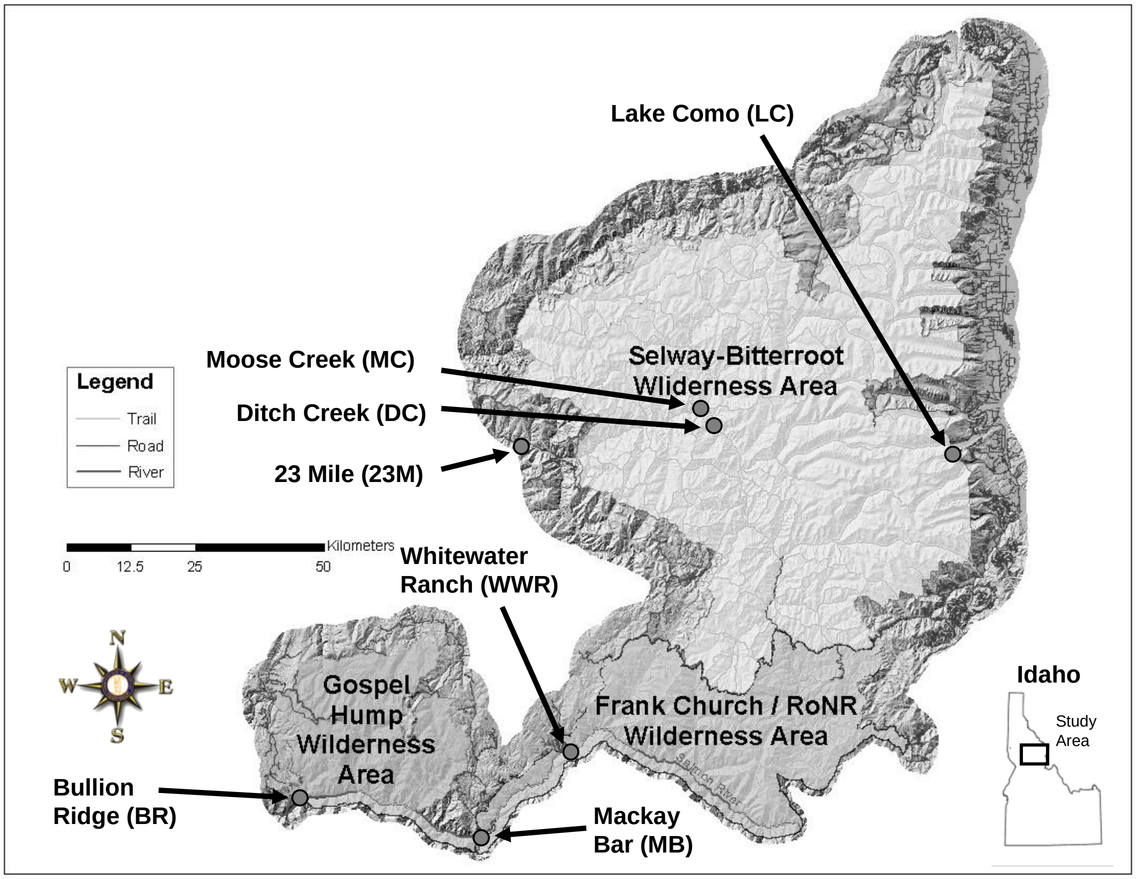

Figure 1. Study area and site locations (RoNR = River of No Return).

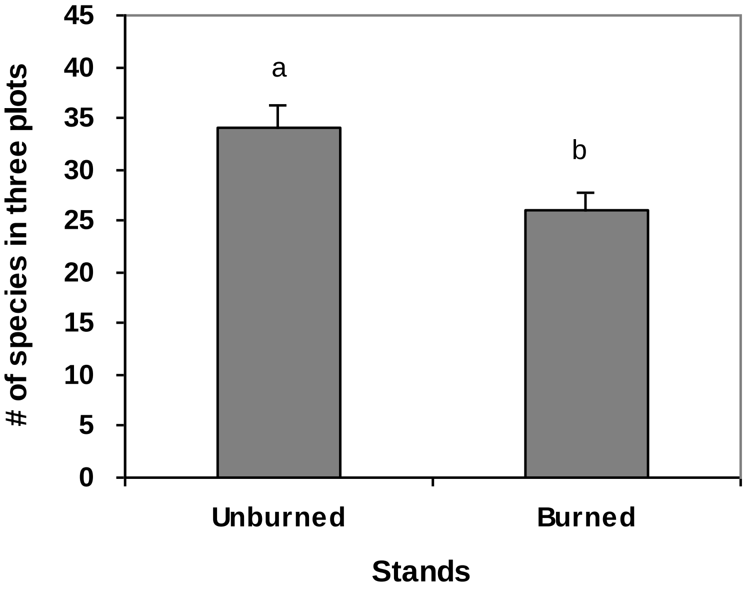

Figure 2. Mean species richness from lowest fire frequency stands ("unburned") versus highest fire frequency stands ("burned") (n=6). Error bars are standard errors. Bars with different letters denote significant differences between unburned and burned stands.

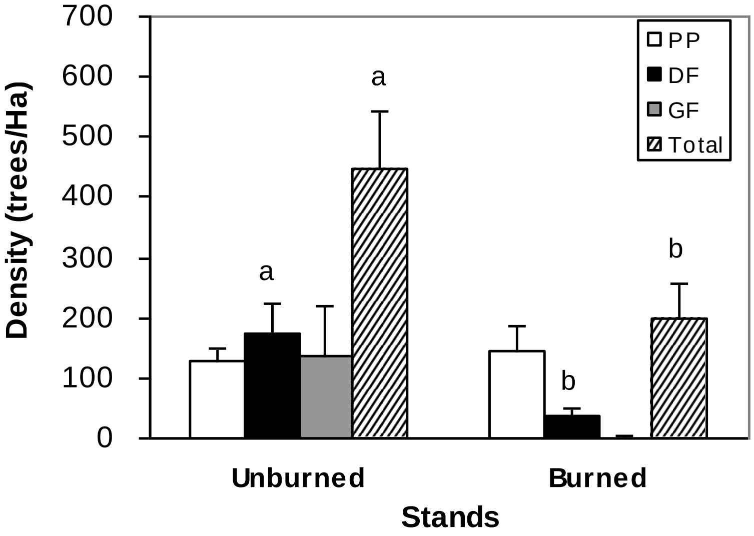

Figure 3. Mean tree densities for ponderosa pine (PP), Douglas-fir (DF), grand fir (GF) and total tree density (total) in the lowest fire frequency stands ("unburned") versus highest fire frequency stands ("burned") (n= 6). Error bars are standard errors. Bars with different letters denote significant differences between unburned and burned stands within a category.

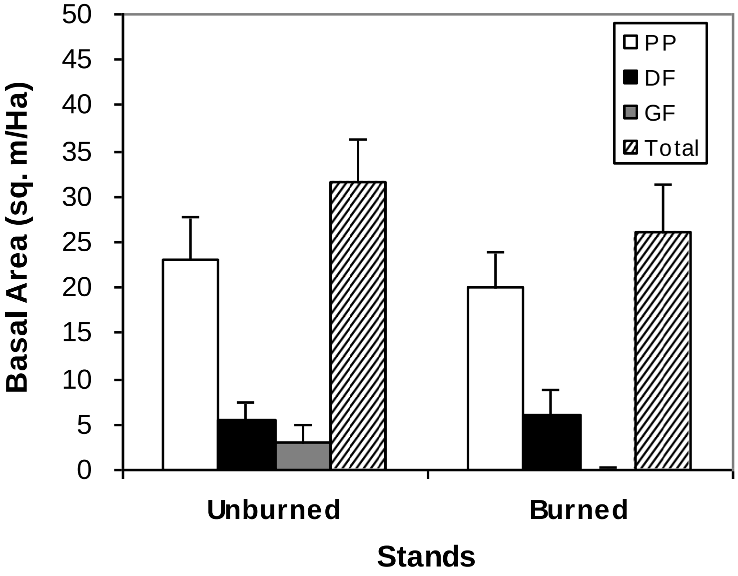

Figure 4. Mean basal areas for ponderosa pine (PP), Douglas-fir (DF), grand fir (GF) and total tree density (total) in the lowest fire frequency stands ("unburned") versus highest fire frequency stands ("burned") (n= 6). Error bars are standard errors. There were no significant differences between unburned and burned stands within a category.

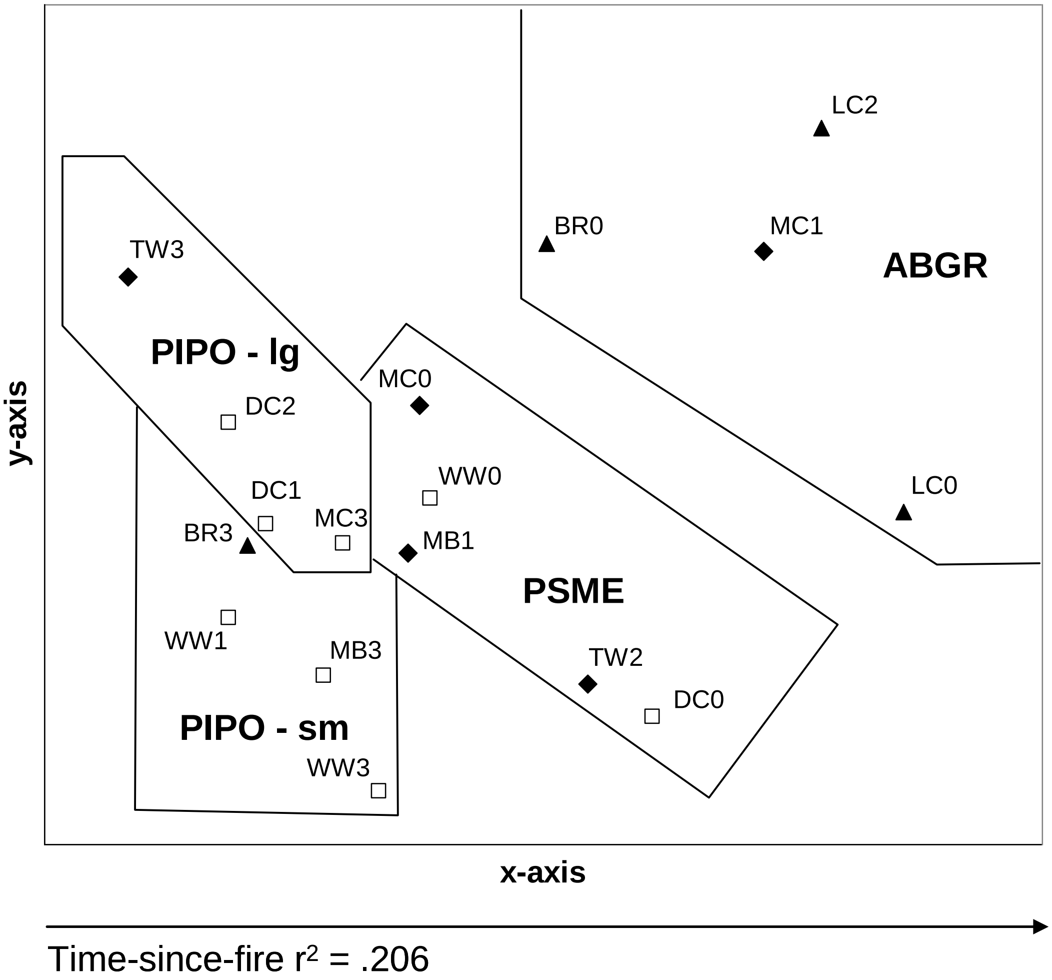

Figure 5. Non-metric dimensional scaling (NMS) ordination of stands based on overstory structure data (species in size-classes) with overstory groups overlaid in boxes (labeled) and understory groups overlaid with symbols (◆ = mesic □ = xeric ▲ = high elevation). Ordination explained 71.4% of variance in original data and was rotated so that time-since-fire correlated with x-axis. Sorenson distance measures were used. Understory and overstory groups are described in tables 3 and 4.

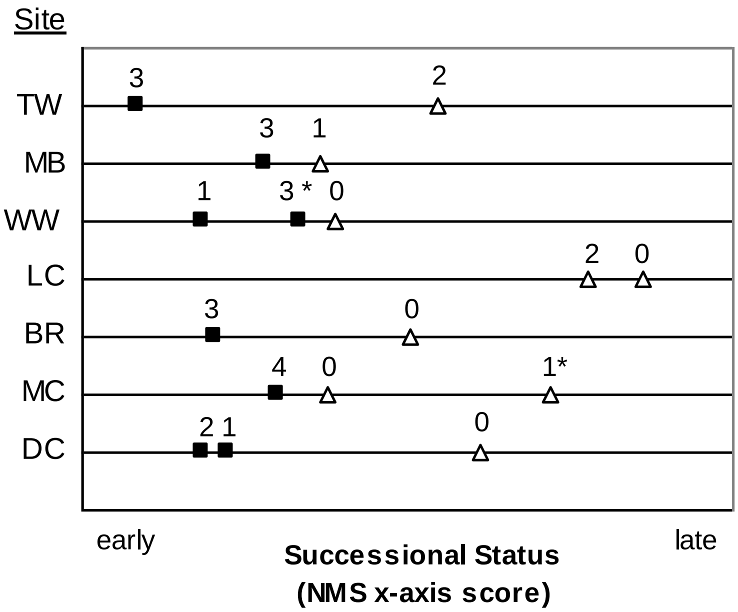

Figure 6. Successional status (early to late) of stands within sites inferred from NMS x-axis scores based on overstory species/size class data. Numbers above symbols refer to # of burns associated with that stand. ■ = stands classified into one of two early succession overstory groups (PIPO- sm, PIPO – lg). △ = stands classified into one of two late succession overstory groups (PSME, ABGR). See table 4 for further description of overstory groups. Stands with elevation and/or aspect greatly different from other stands at the same site are flagged with an asterix.

CHAPTER TWO

Effects of fire exclusion on physiological status of old-growth ponderosa pine in unlogged ponderosa pine/Douglas-fir forests

Abstract

Fire exclusion promotes successional replacement of seral dominant trees by late-successional, more shade-tolerant species. Increases in stand density and decreases in nutrient availability due to fire exclusion are thought to increase competition for limited resources among trees and to increase physiological stress of dominant, fire-adapted species. However, very little research has directly investigated effects of fire exclusion on the physiological status of old trees, especially in unmanaged forests. We tested whether the physiological status for dominant old-growth ponderosa pine trees in frequently burned, remote stands in the Selway-Bitterroot region of Idaho differs from trees in paired stands not burned during most of the 20th century. We hypothesized that trees in fire-excluded stands would exhibit signs of physiological stress due to increased competition for resources in higher density stands. Needle chemistry and morphological variables, fine root production, mycorrhizal infection rates, depth of soil water resources, and recent basal area growth rates were measured and compared for trees in "burned" stands (3-4 20th century wildfires) versus trees in "unburned" stands (stands not burned for at least 70 years) at four remote sites. Contrary to predictions, needle carbon isotopic ratio ($\delta^{13}C$) and fine root production, variables related to water stress, were slightly higher in burned stands driven by site specific responses, and there were no significant biological differences between trees in burned versus unburned stands in the remaining variables. These results suggest that nearly a century of fire exclusion has yet to produce differential physiological impacts on dominant, old-growth ponderosa pine trees in unburned stands compared to trees in frequently burned stands.

Introduction

Ponderosa pine forests are widespread in the western US, ranging from Mexico to Canada. In the drier, southern and low-elevation areas of its range, ponderosa pine is characterized as a climax species growing in mostly open forests that are maintained by frequent, low-severity fires (Oliver and Ryker, 1990). At more mesic, mid- to high elevation locations, and at more northern latitudes, many ponderosa pine forests historically experienced mixed fire regimes with both low-severity fires and higher severity stand-replacing fires (Schoennagel et al. 2004, Veblen 2003). In mixed-fire regime forests, ponderosa pine is considered an early-succession, or seral dominant, maintained by fires that eliminate shade-tolerant, late succession competitors (Oliver and Ryker, 1990). In the inland Northwest, the late-succession species are often Douglas-fir, or grand fir (Pfister et al.1977, Steele et al. 1981). Models for succession in this region predict that in the absence of fire, these competitors will eventually replace ponderosa pine and become the dominant trees in the stand (Pfister et al. 1977, Steele et al. 1981, Arno et al. 1985, Habeck, 1994, Keane et al. 1990, Arno 1995b). Consistent with these models, many studies have reported higher overall stand densities and increased abundance of shade-tolerant competitors in stands that have not burned at historical frequencies (Agee1993, Arno 1988, Keeling et al. 2006) although other factors such has increased tree recruitment after intense grazing (Bakker and Moore, 2007) or logging (Naficy et al. in review) may also contribute to these density increases. Although a consequence of natural successional processes, these changes are considered anthropogenic because the cessation of frequent fire is largely a result of over a century of fire-suppression policies.

Increases in stand densities have raised concerns that old-growth ponderosa pine may be threatened or weakened by increased competition from the incursion of competitor species such as Douglas-fir (Kolb et al. 2007). Of course, higher fuel loads associated with higher stand densities may pose a direct threat to trees if such conditions increase the likelihood of uncharacteristically severe stand-replacing wildfires (Arno and Allison-Bunell 2002). However, high fire risk in dense stands is also thought to be exacerbated by increasing numbers of weak, suppressed trees that are more likely to die, providing additional fuels (Arno & Fiedler, 2005, National Fire Plan 2001, quoted in

Veblen 2003). Recent reviews list competition-induced stress associated with fire-exclusion as an important threat to old-growth ponderosa pine (Kolb et al. 2007). In many restoration projects, improvement in the health and vigor of the dominant trees is a stated project goal alongside density reduction in reducing severe wildfire threat (USDA Forest Service http://www.fs.fed.us/r1/bitterroot/projects/mef1.shtml). These restoration projects seek to mimic the effects of fire and return stands to an early succession structure and function where pines are vigorous and continue to dominate.

The idea that competition from smaller and predominantly shade-tolerant tree species in understories poses a direct threat to the physiological vigor of dominant trees appears to be a common assumption of restoration forestry. Some research has indeed shown long-term growth declines associated with increasing stand density in unburned ponderosa pine stands in the southwest (Sutherland, 1983; Biondi 1996). These studies inferred the cause of growth declines from changes in stand density without stand manipulations or paired measurements in lower-density stands. Other studies experimentally reduce stand density and study the effect on residual trees. Most of these latter studies have demonstrated that thinning can produce immediate and often sustained physiological improvement in residual dominant trees (Sala et al. 2005, Latham and Tappeiner 2002, Stone et al 1999, Kolb et al 1997, Donner and Running 1986; Sala unpublished). Similar benefits would also be expected to accrue to trees in stands that have been thinned “naturally” over time by frequent wildfire, however this is much more difficult to test. Because there is a lack of studies that directly compare fire-excluded to frequently burned stands in a controlled fashion, it is not clear that natural wildfires have the same effects as stand manipulation treatments.

In fact, restoration treatments that include prescribed fire tend to produce more mixed results. This is probably due to the fact that mechanical thinning of stands generally produces immediate benefits for residual trees while fire can generate both positive and negative effects. Where fire treatments reduce stand density and understory vegetation, surviving trees may benefit due to reduced competition and improved access to resources, especially water. Fires also affect soil nutrient availability directly. Low severity fire can increase plant-available nitrogen in the soil in the short-term (Covington and Sackett 1992; Covington and Sackett 1986; Baird et al. 1999; Choromanska and

DeLuca 2001; Gundale et al. 2005). Conversely, more severe fire can lead to immediate nitrogen losses through direct volatilization and increased leaching or dispersion of nitrogen (Grier 1975; Landsberg et al. 1984). Fire may also have direct negative effects on trees. Scorched branches, needles, and buds may impede growth following fire. Heat from fire may harm cambial cells in the growing portion of the stem, and fine roots may be killed by ground fire heat (Agee 1993). These direct effects may offset positive benefits of reduced competition or increased soil nutrient availability.

It is unclear how these complicated positive and negative responses affect tree physiology in the long-term or whether long-term responses to a single fire will differ from responses to repeated fires. In the mid to long-term, reintroduction of fire has been shown to reduce N in soils (Monleon et al. 1997, Wright and Hart 1997, DeLuca and Zouhar 2000). However, DeLuca and Sala (2005) demonstrated that frequent fire increased available N over the long-term in unmanaged ponderosa pine/Douglas-fir forests in Montana and Idaho. Most studies have looked at one-time responses to direct manipulation of stand densities, either via mechanical thinning or prescribed burning. These before-and-after comparisons of manipulated stands may not realistically mirror conditions in natural forests where trees subjected to different fire-frequencies have had decades to adjust and adapt. There is evidence, for example, that ponderosa pine trees can compensate for low water availability by increasing sapwood area (Callaway et al. 1994) or tapping deeper water resources (Domec et al. 2004, Brooks et al. 2002). Similarly, trees may compensate for decreased soil N availability with increases in needle longevity and changes in root characteristics (Vogt et al. 1983, Gower et al. 1992, Reich et al. 1995, Schoettle 1994). Because of the possibility of compensation, it is not clear whether trees in fire-excluded stands will be more stressed than trees in frequently burned stands.

The uncertainties of how mature trees respond to frequent natural wildfire versus fire-exclusion are a reflection of the difficulties in finding natural reference stands with different fire histories suitable for comparative study. Because of these difficulties, most research has been conducted in forests that were logged some time in the past. Prior logging may produce high stand densities due to removal of older, fire-resistant trees which allow for the incursion of thick stands of younger trees (Laudenslayer and Darr

1990, Stephens 2000, Kaufmann et al. 2000). Recent research has documented stand density increases in previously logged, fire-excluded stands, over and above increases in unlogged stands experiencing fire-exclusion alone (Naficy et al. in prep). The release from competition in surviving trees following fire or fuel reduction in historically logged second-growth forests may be amplified since these treatments are reversing the effects of both prior logging and fire-exclusion. In order to separate effects of fire-exclusion from confounding effects of previous logging, there is a critical need for research in forests with no prior logging history.

Stress from increased competition may be detected in the biochemistry, morphology, and growth characteristics of leaves, roots, and stems. Although responses in these variables to natural wildfire are rarely studied, responses are thought to be predictable based on studies that use thin, and thin/burn treatments as a surrogate for fire. Needle chemistry (%N, C/N, $^{13}C/^{12}C$) provides an integration of the tree's nutrient and water status. Fire excluded trees experiencing competition-induced stress are expected to have lower %N (Stone et al. 1999, Feeney et al. 1998), higher C/N (Waring and Schlesinger, 1985), and higher carbon isotopic ratio ($\delta^{13}C$) (Adams and Kolb 2004, Wallin et al. 2004), the latter due to reduced discrimination against the heavy carbon isotope when stomata are closed during periods of water stress. Values of basic needle growth characteristics (average needle length, total needle biomass, bud width, bud length, and internode length) are expected to decrease for fire-excluded trees with increased competition-induced stress (Stone et al.1999, Feeney et al. 1998) although these factors will also be affected by the relative overall biomass allocation to leaves. Leaf specific area, (LSA, area/mass) reflects the tree's investment in needle longevity, which correlates with lower LSA (Reich et al. 1997). Fire-excluded trees experiencing insufficient resources are expected to invest in longer-lived needles, and have lower LSA. Investment in greater abundance of fine roots (Vogt et al. 1983, Gower et al. 1992) and mycorrhizal relationships (Smith et al. 2005) is also expected to increase in fire-excluded stands where soil water and nutrients are expected to be scarce. Fire-excluded trees experiencing greater competition for water are also expected to obtain water from deeper soil depths. Hydrogen isotopic signatures of water at different soil depths may be compared with the isotopic signatures in xylem water to determine the depth of water sources. Finally, stemwood (basal area) growth is expected to decrease in fire-excluded stands because of increased competition for water and nutrients.

Although it is often assumed that trees in fire-excluded stands are under physiological stress due to increased competition for limited resources (Arno & Fiedler, 2005), this hypothesis has rarely been tested using natural reference stands with differing fire histories. In this study we ask the question: Do old-growth ponderosa pine trees in fire-excluded stands show signs of competition-induced stress compared to trees in stands that have burned several times in the 20th century ? We sampled old-growth ponderosa pine trees in paired burned and unburned stands at four remote sites in Idaho. Because previous results from these sites showed higher stand densities and lower overall available N in fire excluded stands (see DeLuca and Sala. 2005, Keeling et al. 2006), we expected to find evidence of competition-induced physiological stress in fire-excluded stands.

Methods

Site Selection

In 2003, a total of seven remote study sites were located in unlogged, mid-elevation ponderosa pine/Douglas-fir forests within or on the periphery of wilderness areas in Idaho (see DeLuca and Sala 2005 and Keeling et al. 2006 [Chapter 1] for site selection details). From these sites, four were chosen for this study (Figure 1). At each site, a fire-excluded stand (“unburned”) was compared to a fire-maintained stand (“burned”). Unburned stands had not experienced fire for at least 70 years. Burned stands experienced 3-4 wildfires at intervals ranging from 6 - 58 years (mean = 34 years) throughout the 20th century. Table 1 shows environmental data and fire history information for all stands. Fire histories for all stands were based on U.S. Forest Service fire maps, field reconnaissance, and on-site fire scar analyses (see DeLuca and Sala 2005 and Keeling et al. 2006 [Chapter 1] for more detailed methods on fire histories). Note that the last fire was 12 years before the study was initiated therefore measurements are not short-term responses to fire. Although some physiographic differences between stands existed, on average there were no systematic physiographic differences between fire-excluded and fire-maintained stands from each site across the entire study (paired t-tests comparing slope, aspect, and elevation, $p>.05$). We cannot determine whether fires were actively suppressed even in these remote areas, therefore the term “fire-excluded” is not meant to imply human agency in determining the unburned status of these stands. The fire return intervals in our fire-maintained stands are within the historical (i.e. pre-1900) range, which can be more than 25 years for mixed ponderosa pine forests in the northwest region (Arno 1980; Arno and Allison-Bunnell 2002,; Heyerdahl et al. 2008b).

Data Collection

In June and July of 2004, an access route across each stand was chosen. Access routes were divided into 10 sections of equal distance. Within each section, a location along the route was randomly determined from which the nearest ponderosa pine was sampled. At each tree, elevation, aspect, slope, GPS coordinates, and tree diameter at breast height (DBH) were recorded. For needle chemistry and morphology, one exposed branch was collected from the mid canopy of every tree using a 12 gauge shot-gun aimed at the basal end of the terminal branch so as to sample all leaf cohorts. A 5.7 cm diameter steel cylinder was used to collect four soil samples, at a distance of 3 meters in four cardinal directions from the bole of each tree. At two sites (TW and BR), short (5cm) increment cores were extracted from each tree to measure the hydrogen isotopic ratio in xylem water. At these sites, four pairs of representative soil samples for measurement of hydrogen isotopic ratio, one at shallow depth (5-10 cm) and one at deep depth (65-70 cm) were taken per burned and unburned stand. All soil and branch samples were placed in plastic zip-lock bags and stored in a cooler with ice, or in dry-bags submersed in cold water for the duration of each field trip. Short increment cores were stored in water-tight plastic test-tubes. For basal area growth analysis, two complete increment cores to the pith were extracted from each tree and tree diameter at coring height (DCH) was recorded. Cores were taken at approximately 50 cm height from the ground. The two cores were taken from opposite sides of the tree, perpendicular to the direction of the slope. Four bark depth measurements were taken at coring height using a standard forester’s bark gauge. The soil and xylem water isotopic study was repeated in 2006. Also, in 2006 and 2007, increment cores for growth analyses were extracted from additional trees at BR and MB increasing sample sizes at these sites (sample sizes for all variables range from 6-19 trees per stand and are reported in figures).

Sample processing and analysis

Internodes separating annual needle cohorts were identified and internode lengths were measured with a ruler. Fascicles within each cohort were removed and counted. Average needle length for each cohort was measured to the nearest millimeter using a ruler, and all needles within each cohort were placed in envelopes, dried for 48 hours at 50° C in a drying oven, and weighed. Total needle biomass was calculated as the sum of the weight of all the needles on each branch. 10 fascicles from the one-year old cohort were randomly selected for estimation of specific leaf area. These 10 fascicles were weighed separately and leaf area for these needles was calculated by making a digital image of the needles. Needle area was calculated from the scanned images. Average specific leaf area was calculated as total area divided by total weight. Bud length and bud widths were measured with digital calipers (to .01mm). A subset of needles from each branch (1 branch per tree) was selected for needle chemistry analysis. Needles were ground to a fine powder to pass a 0.3 mm mesh, and samples were sent to the UC Davis Stable Isotope Facility for analysis (2 and 8 mg of sample for C and N analyses, respectively). Needle samples were analyzed for %N, C/N ratio, and carbon isotopic ratio $^{13}C/^{12}C$ (expressed as $\delta^{13}C$, the sample ratio minus the ratio of a known standard x 1000).

Soil samples were placed in trays of water to separate fine roots from soil. Roots were dried in an oven and weighed. Stand density for each stand had been previously measured and is reported in Keeling et al. 2006. The average fine root weight for each tree sampled was divided by the stand density in order to express the fine root content of the soil on a per-tree basis. A sub-sample of roots for each tree were examined under a microscope and root tips were categorized visually as infected or not infected by mycorrhizal fungi and infection rate was expressed as percent of root tips infected.

Due to time and cost constraints, analysis of hydrogen isotopic ratio in soil and xylem water was done for two sites only (MB and TW) in 2004 and 2006. Samples were sent to the UC Davis Stable Isotope Facility for measurement of hydrogen isotopic ratio.

Increment cores were processed, measured, and crossdated, and age estimates for each tree were obtained following procedures detailed in Keeling et al. 2008 in prep. The total basal area inside the bark was calculated as $pi*radius_1^2$ where $radius_1$ is the total radius inside the bark. Radius_1 was calculated as $\text{Radius}_1 = (\text{DCH} - 2\text{BD})/2$ where DCH is the diameter at coring height and BD is the average bark depth at coring height. The inside basal area was calculated as $\text{pi}*(\text{radius}_2)^2$ where radius_2 = the difference between radius_1 and the sum of ring widths for the years 1994-2003. The recent 10-year basal area increment (BAI) was calculated by subtracting the inner basal area from the total basal area. BAI for the two cores of each tree were averaged.

Statistical analyses

Statistical analyses were carried out in the software program SPSS 16.0. Variables were tested for normal distribution using a Kruzal-Wallis test and samples were tested for homogeneity of variance using Levene's test. Where necessary, variables were transformed using a log or square-root function. Comparison between burned and unburned stands of needle chemistry, needle morphology, and root/mycorrhizae variables were analyzed using 2-way ANOVA with site and stand (unburned and burned) as random factors, with stand nested within site. For variables that could not pass Levene's test after transformation, non-parametric Mann-Whitney U tests were used. Individual t-tests were used to test for significant differences between stands within sites. Depth of water sources at MB and TW in 2004 and 2006 were analyzed separately using 2-way ANOVA with sample location (shallow soil, deep soil, sapwood) as a fixed factor and stand (burn, unburned) as a random factor. Tests for which there were no overall significant differences between burned and unburned stands were evaluated using post hoc power tests. Minimum detectable changes (MDC) at a Type II error threshold of 1-beta = 0.8 were calculated for each test as described in Elzinga et al. 2001. Minimum detectable changes at this level of Type II error probability were converted into effect sizes using the formula: Effect size = MDC/standard deviation. Tests which were capable of detecting an effect size of .75 were considered to have sufficient power.

Results

Sample sizes varied slightly for each variable measured and ranged from 6 – 19 trees per stand (sample sizes are given in figure captions). There were no significant overall differences between burned and unburned stands in %N or C/N ratio (Figure 2a, 2b). Needle carbon isotopic ratio was slightly higher in burned stands overall (Figure

2c). This overall difference was driven primarily by the difference at one site (MB). There was no overall significant difference between burned and unburned stands in recent BAI, although BAI was significantly higher in the unburned stand at MB (Figure 2d)

Average needle length was greater in the unburned stand at one site (BR) but there was no significant difference across all sites (Figure 3a). Total needle biomass per branch was slightly but significantly higher in burned stands overall. There were no significant differences between burned and unburned stands in leaf specific area or internode length (Figure 3c, 3d). Bud widths were slightly greater in burned stands overall (Figure 3e). Bud lengths were greater in the burned stand at MB, but there was no significant difference across all sites (Figure 3f).

There were significantly more fine roots on a per-tree basis in burned stands overall (Figure 4a). This difference was driven mostly by a large, albeit non-significant, difference at one site (TW). There was no significant difference between burned and unburned stands in mycorrhizal infection (Figure 4b). However, the non-significant finding for mycorrhizae did not pass our criteria for sufficient power.

Results for hydrogen isotopic ratio in surface soils, deep soils and in xylem water of trees at burned and unburned stands at two sites (MB and TW) are shown for two years of data, 2004 and 2006 (Figure 4). There were no data for burned stands at TW in 2006. There were no significant differences in hydrogen isotopic signature between burned and unburned stands at either site for any of the sample categories (surface soils, deep soils, sapwood). In 2004, hydrogen isotopic signatures were significantly more negative in deep soils than in surface soils at both sites. In 2006, there was no difference between signatures of surface versus deep soil at MB. Signatures were again more negative in deep soil water at TW in 2006. At MB, hydrogen isotopic signatures in xylem water were also significantly more negative than surface soil isotopic signatures and even more negative than the values for the deep soil in both years although the difference between the deep soils and the xylem was statistically significant only in 2006. At TW isotopic signatures were intermediate between the signatures of surface and deep soil in both years.

Discussion

We hypothesized that trees in fire-excluded stands would show symptoms of physiological, competition-induced stress when compared to trees in frequently burned stands. In sharp contrast to much of the reported literature, and contrary to our hypothesis, we found surprisingly little evidence of adverse effects of fire-exclusion on mature ponderosa pine trees for the variables we measured

There were no significant overall differences in the needles of trees in unburned versus burned stands in %N, C/N ratio, needle length, leaf specific area, internode length, or bud length (Figures 2 and 3). Needle carbon isotopic ratio ($\delta^{13}C$) was slightly lower (more negative) in unburned stands. This result contradicts the hypothesis that needles in unburned stands would have a higher carbon isotopic ratio (because competition induced water stress increased the frequency of stomata closure) a common result in other studies (Adam and Kolb 2004, Wallin et al. 2004). Also contrary to expectations, trees in unburned stands had fewer rather than more fine roots overall (Figure 4a). These two variables ($\delta^{13}C$ and fine roots) could suggest improved physiological status in unburned stands, directly contrary to our hypothesis. However, the lack of consistent responses across all sites in these variables caution against such an interpretation. The results for $\delta^{13}C$ and fine roots appear to be driven mainly by one site in each case. In the case of $\delta^{13}C$, the difference at MB may be because of inherent environmental differences between the two stands. The burned stand at MB appeared to be a drier site, with rockier soil, and steeper slopes than the unburned stands. Two variables, total needle biomass per branch and bud width, were greater in burned stands, as predicted (Figure 3b, 3e). However, though statistically significant, these differences were not great in magnitude and are probably not biologically significant. There was no evidence that trees in unburned stands were tapping deeper water sources (Figure 5) as would be predicted during water stress. Finally, although basal area growth responses varied from site to site, there was no overall difference in recent growth between trees in burned versus unburned stands (Figure 2d). In general, these results do not support the hypothesis of increased physiological stress for old trees in unburned stands.

Finding suitable paired stands in remote unlogged forests posed a considerable challenge and conducting a study at this scale necessarily precluded extensive sampling within sites (see DeLuca and Sala, 2005, and Keeling et al. 2006 for further discussion). Ideally, more sites and more intensive sampling within sites would increase the confidence of findings of no difference between stands. However, for the variables that we measured, power tests indicated that our sampling was adequate to detect true differences that were reasonably small with moderate, but acceptably low probability of failure of detection (Type II error). More research with higher sample sizes is needed in Northwest ponderosa pine forests to confirm these results.

Our study relied on the assumption that trees in the "burned" and "unburned" stands experienced repeated vs. no fires, respectively for most of the 20th century. However, both fire atlas and fire scar data are susceptible to errors (Shapiro-Miller et al. 2007). Fire history from fire scars was conducted at two of our four sites – TW and MB (Heyerdahl et al. 2008b[1]). Results from this analysis showed some inconsistencies with the fire atlas perimeters at one of these sites, TW, where two earlier century fires (1910 and 1934) were not recorded in the fire atlas.. This discrepancy raises the possibility of fire history errors at the two sites where we do not have detailed fire scar data. However, fire atlas errors are more likely to occur for earlier century fires when the delineation and recording of fire perimeters was more imprecise than later in the century. If so, our general assumption that burned stands have experienced more recent fires than unburned stands still holds true.

The lack of differences may also be a reflection of the variables we measured. Other studies have also failed to find differences between treated and untreated stands in leaf chemistry and morphology (Zausen et al. 2005, Wallin et al. 2004, Skov et al. 2004), while more pronounced differences were found in gas-exchange variables such as photosynthesis rates and stomatal conductance (Sala et al. 2005). The remoteness of our sites precluded carrying the heavy instruments necessary to make these measurements. Therefore we are unable to fully compare our results to studies that measured gas exchange variables. Measuring a more comprehensive suite of response variables may reveal effects that were not detected in this study. However, basal area growth, a variable that integrates overall physiological response, was not different between burned and

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[1] Note that in Heyerdahl et al. 2008 sites are named differently: TW = TTM, and MB = COV.

unburned stands. Therefore, gas exchange differences between stands, if present, apparently were not significant enough to affect overall growth.

Our results suggest that roughly a century of fire exclusion has yet to produce significant physiological differences in dominant ponderosa pine growing in unburned stands compared to frequently burned stands. These results may be due to our focus on dominant trees in uneven-aged, old-growth forests. Despite higher densities and lower nitrogen availability (DeLuca and Sala 2005; Keeling et al. 2006), the dominant trees we sampled in fire-excluded stands may have better access to light and soil resources than smaller, sub-dominant competitors. In contrast, studies in second-growth, relatively even-aged stands, especially before-and-after mechanical thinning studies, generally record large effects due to stand density changes, because residual trees are released from the greater competitive effects between trees of the similar age and size (Latham and Tappeiner 2002, Stone et al 1999, Kolb et al 1997, Donner and Running 1986). Such treatments often reduce both density and overall basal area. At our sites, burned stands had lower densities in the small size classes, but did not have significantly lower overall basal area (Keeling et al. 2006). Therefore, competitive effects on the well-established dominant trees in our unburned stands may have been much smaller than would be the case in manipulated studies. Our results point to the possibility, consistent in thinning studies that differentiate between old and young trees, that older, pre-settlement trees are less sensitive to stand density changes (Skov et al. 2004, Skov et al. 2005). Because we focused on the large, dominant trees in the stand, we may have missed physiological differences between unburned and burned stands for trees in the smaller size classes. Uneven-aged stands are considered to be the historical norm for old-growth ponderosa pine (Arno & Fiedler 2005). Therefore our results may be more relevant for the management of natural, old-growth forests than results from stand manipulations in second-growth forests.

The divergence of our results and results from other studies may be a reflection of our sample design that controlled for the effects of prior logging on stand conditions. Stand density increases commonly attributed solely to fire-exclusion are likely to be even higher in stands that were previously logged (Naficy et al. in prep.). Therefore, studies that test for physiological differences between burned and unburned stands in previously logged forests are likely to find exaggerated differences between these stands. This bias also applies to studies that manipulate stand densities via thinning or prescribed fire. Stands receiving such treatments are more likely to respond if they are released from higher densities due to combined effects of prior logging plus fire exclusion. Our results suggest that the physiological effects of natural wildfire in unlogged, old-growth forests may be much more subtle than the effects of manipulations in studies designed to mimic natural processes and conditions.

The lack of difference between trees in more open, frequently burned stands versus denser, more nutrient poor unburned stands also raises the possibility of countervailing positive effects of fire-exclusion or negative effects of frequent fire. For example, it is possible that denser stands may retain more soil moisture by reducing evaporation. Fire may also directly harm important tissues in trees in burned stands, offsetting potential negative consequence of fire versus fire-exclusion. In a companion study where short-term growth responses to individual wildfires were assessed (see chapter 3), more recent fires tended to produce negative growth responses. These negative growth responses may be offsetting negative effects of fire-exclusion in our unburned stands, producing non-significant differences between stands. Our study was not designed to separate effects due to fire in the burned stands from effects due to higher densities in the unburned stands. More research is needed to separate these effects.

The longer, more realistic time scale of our study may also explain our results. We measured responses in trees exposed to prolonged conditions of fire exclusion or frequent fire, rather than short-term responses to management-style treatments. While other studies infer long-term negative effects of fire-exclusion from short-term positive effects of single manipulations that reduce densities, the realism of this approach may be questionable. Trees experiencing long-term fire exclusion may adjust to these conditions in ways that cannot be detected in simple before-and-after studies. Trees in our fire-excluded stands had not experienced fire for 70 to greater than 120 years. It is possible that mature trees may adjust to stand conditions through morphological or physiological changes that were not measured in our study.

This study points to the need for greater understanding of basic successional processes in ponderosa pine forests. Although models of succession successfully predict observed patterns of higher stand density and greater abundance of shade-tolerant competitors with lack of fire, the mechanism by which late succession species replace early succession species is not as clear, and warrants more research. It is commonly assumed that direct competitive effects on dominant, early-succession species play a role in successional change. We did not observe such effects for the variables we measured in this study. An alternative mechanism for the ultimate replacement of ponderosa pine may be increased competition in small size classes and lack of effective recruitment of ponderosa pine versus species such as Douglas-fir. The shift of focus to sub-dominant trees and recruitment may imply a restoration need of retaining more diversity in smaller size classes of ponderosa pine. More research is needed to fully understand the long-term effects of stand density reductions on future conditions in these forests.

The question of whether competition is the main mechanism by which successional replacement of ponderosa pine occurs has implications for management decisions in these forests. Our results suggest a need for greater clarity with respect to the use of the term "forest health" and management strategies that invoke this concept. While negative effects of fire exclusion on the physiology of trees tends to be assumed, our study suggests that this may not be the case for dominant trees in unlogged, uneven-aged forests, at least for timescales on the order of 100 years. In seral ponderosa pine forests considered to have mixed-severity fire regimes such as those studied here, high natural variation in stand conditions (see Keeling et al. 2006 [chapter 1]) means that there may not be a single baseline stand density that can serve as a reliable indicator of "natural" conditions. Our study suggests that perceived need for improvements in the "health" of individual old-growth trees may not provide a substitute rationale for stand density reduction, except in cases where trees are severely weakened by disease or insect damage.

In many areas, and especially near to urbanized areas, empirically established risk to property and forest resources from high intensity fire, rather than reference to "natural" conditions or presumed benefits to tree health and vigor should guide management strategies. In such locations, "forest health" often is used to refer simply to the probability of avoiding high severity fire. Where stand densities alone warrant thinning to protect from catastrophic fire, reference to physiological responses in remaining trees may be irrelevant. Such projects may incidentally increase the vigor of trees, especially in second-growth, even-aged stands. However, our results suggest that these treatments do not necessarily replicate responses to wildfire in mature trees in old-growth, uneven-aged forests.

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Table 1. Physiographic data and fire histories (based on U.S.F.S fire maps and on-site fire-scar analysis) for all stands within four sites

Site	Stand	# 20th century Burns	Mean Aspect (deg)	Mean Elev. (m)	Mean Slope (deg)	Year 1st Fire	Year 2nd Fire	Year 3rd Fire	Year 4th Fire
BR	Unburned	1	61.3	1665	37.3	1914			
	Burned	3	49.3	1464	29.3	1914	1944	1992	
MB	Unburned	1	236.0	1813	27.3	1919			
	Burned	3	250.7	1536	32.7	1919	1960	1987	
MC	Unburned	0	270.0	957	33.3				
	Burned	4	258.0	915	42.3	1910	1934	1981	1987
TW	Unburned	2	88.7	805	32.7	1910	1934		
	Burned	3	134.7	869	33.3	1910	1934	1992	

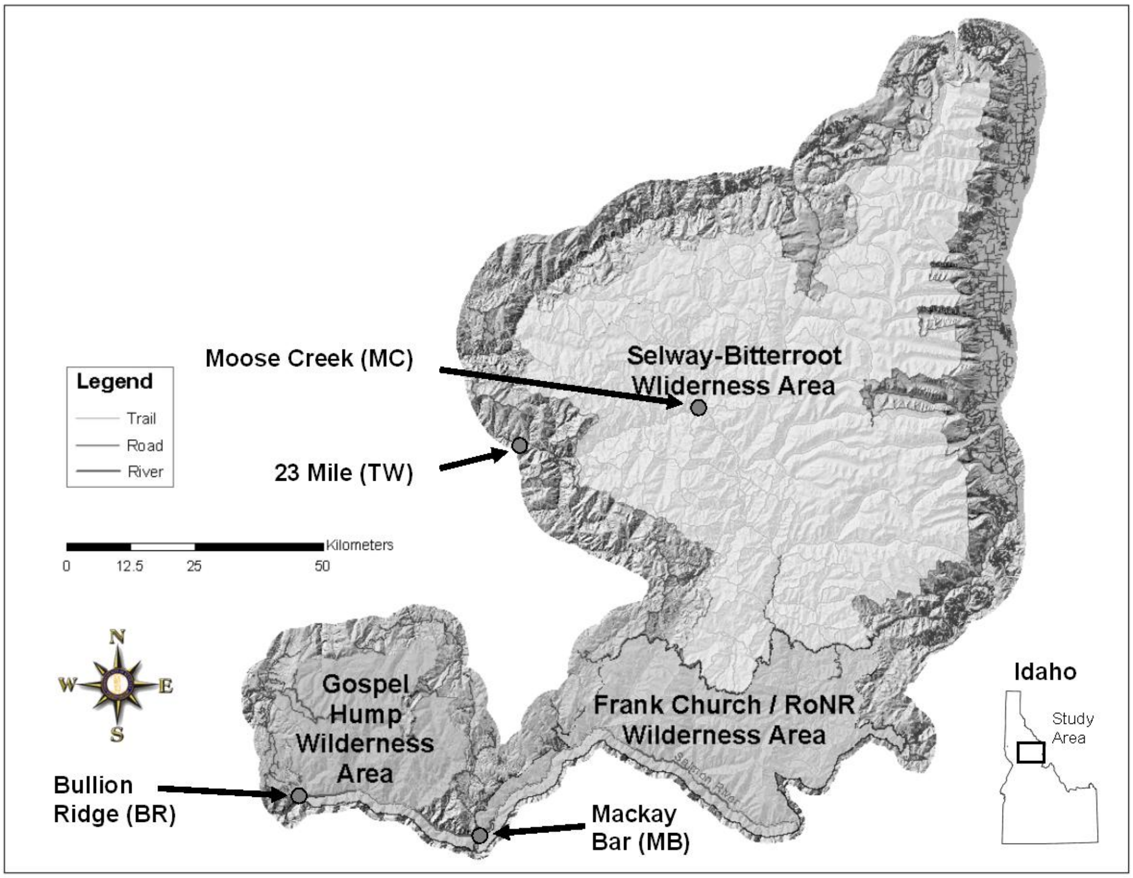

Figure 1. Study area and site locations (RoNR = River of No Return).

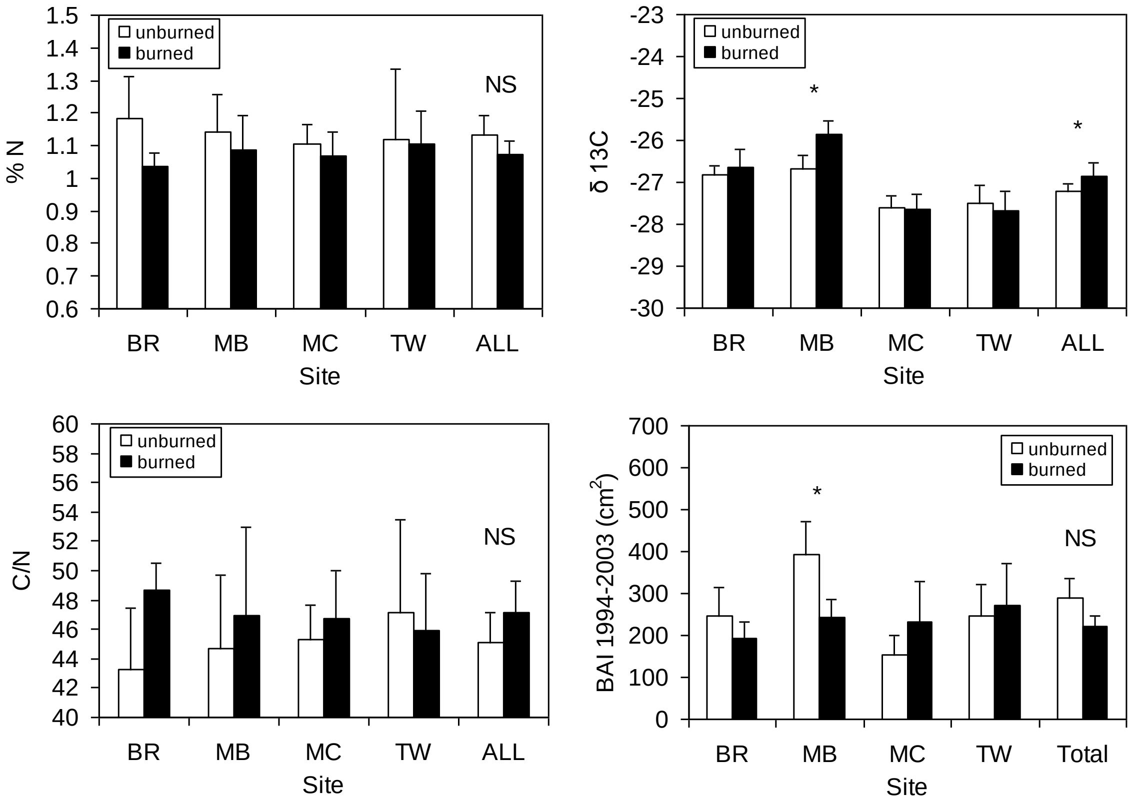

Figure 2. (a) % N, (b) C/N, (c) δ^{13}C, and (d) recent basal area increment (BAI) in ponderosa pine trees in unburned stands and burned stands at each of four sites and averaged across all sites. Error bars are confidence intervals. * = Significant overall differences between unburned and burned stands across all sites (2-way ANOVA with site and stand nested within site as random factors, $p \leq .05$) and significant differences within sites (t-test, $p \leq .05$). NS = Non-significant result which passed the post-hoc power test (minimum detectable change with effect size $\leq .75$ with beta ≤ 0.2). Sample sizes for %N, C/N, δ^{13}C (site: unburned, burned): BR: 10, 9, MB: 9, 10, MC 16, 9, TW: 9, 6. Sample sizes for BAI: BR: 8,17, MB: 9,19, MC: 10,9,
TW: 10,7.

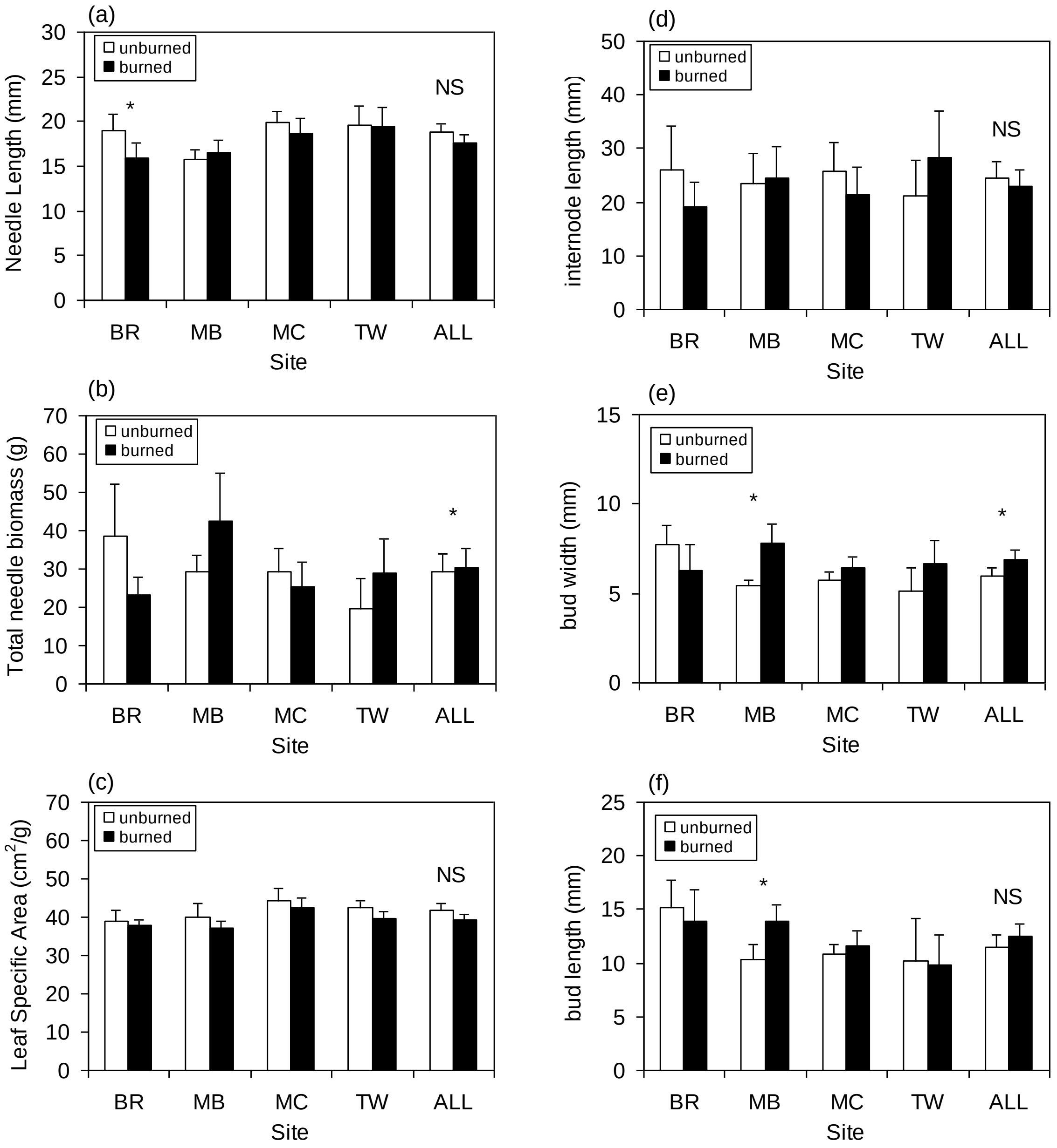

Figure 3. (a) Needle length, (b) total needle biomass, (c) leaf specific area, (d) internode length, (e) bud width, and (f) bud length in ponderosa pine trees in unburned stands and burned stands at each of four sites and averaged across all sites. Error bars are confidence intervals. * = Significant overall differences between unburned and burned stands across all sites (2-way ANOVA with site and stand nested within site as random factors, $p \leq .05$) and significant differences within sites (t-test, $p \leq .05$). NS = Non-significant result which passed the post-hoc power test (minimum detectable change with effect size ≤ .75 with beta ≤ 0.2). Sample sizes for all variables (site: unburned, burned): BR: 9, 7 (10,8 for dry wgt., internode length), MB: 9, 10, MC: 16, 9, TW: 9, 6.

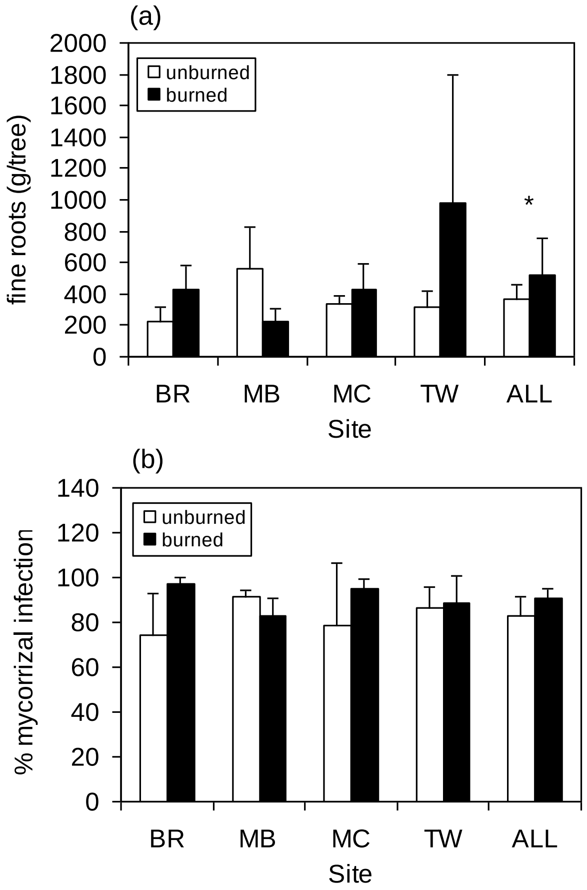

Figure 4 (a) Mass of fine roots per tree and (b) % mycorrhizal infection for roots of ponderosa pine trees in unburned stands and burned stands at each of four sites and averaged across all sites. Error bars are confidence intervals. * = Significant overall differences between unburned and burned stands across all sites (2-way ANOVA with site and stand nested within site as random factors, $p \leq .05$) and significant differences within sites (t-test, $p \leq .05$). NS = Non-significant result which passed the post-hoc power test (minimum detectable change with effect size ≤ .75 with beta ≤ 0.2). Sample sizes for all variables (site: unburned, burned): BR: 4, 4, MB: 4, 4, MC: 3, 4, TW: 4, 4.

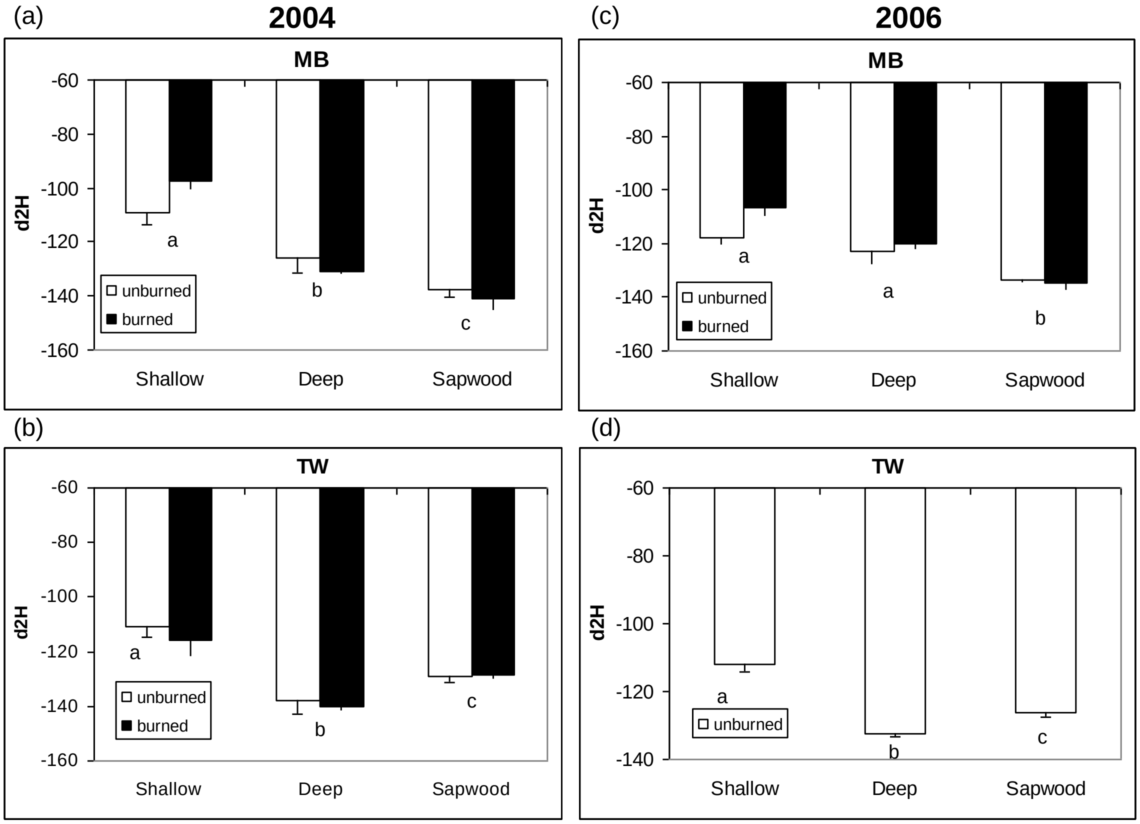

Figure 5. Deuterium (d^2H) values measured in three locations (shallow soil, deep soil, sapwood) for ponderosa pine trees in unburned stands and burned stands at (a) MB in 2004, (b) TW in 2004, (c) MB in 2006, and (d) TW in 2006. Error bars are confidence intervals. There were no significant differences between unburned and burned stands across all sites (2-way ANOVA with location (shallow, deep, sapwood) as a fixed factor and stand (unburned, burned) as a random factor. $p \leq .05$). Significant differences between samples are designated by different letters. Sample sizes (shallow, deep, sapwood): MB-2004, unburned: 5, 5, 6, burned: 4, 3, 5. TW-2004 unburned: 6, 5, 5, burned: 5, 5, 6. MB-2006, unburned: 4, 7, 5, burned: 5, 5, 5. TW-2006 unburned: 4, 3, 6.

CHAPTER THREE

Changing growth response to wildfire linked to climate in old-growth ponderosa pine trees

Abstract

Old-growth ponderosa pine forests are experiencing changes in fire-frequency, fire severity, and climate. These novel conditions are likely to alter tree responses to wildfire. However, growth responses to natural wildfires in unmanaged, old-growth forests (as opposed to prescribed fires or thinning treatments in managed, 2nd growth forests) have rarely been studied. There is also surprisingly little known about the long-term effects of multiple wildfires, whether responses to wildfire are changing over time, and how tree age affects response to fire. The common view is that recurrent wildfire benefits old ponderosa pine, but this view has rarely been tested in multi-aged, unmanaged stands over long periods.

We used basal area increments computed from tree-rings to compare basal area growth responses between trees in paired burned (3-4 20th century fires) and unburned stands (0-2 20th century fires) at four remote sites in the Selway-Bitterroot region of Idaho. Long-term (44-85 year) responses to multiple wildfires, and short-term (5 and 10 year) responses to individual wildfires were analyzed separately. The relationship of short-term fire responses to climate conditions, time-since-fire, and tree age were also studied. Contrary to expectations, only one site showed significantly higher long-term growth responses in burned compared to unburned stands. Short-term responses showed a trend of increasing negative effects of wildfire (reduced growth in the burned stand compared to the unburned stand) in recent years that had drier winters and warmer summers, but no effect of time-since-fire. There were no significant relationships between fire responses and tree age. Climate-driven negative growth responses to wildfire in old-growth forests could have important ramifications for forest productivity and carbon-balance under future climate scenarios.

Introduction

Pure and mixed stands of ponderosa pine forests range across western North America, from northern Mexico to southern Canada (Van Hooser and Keegan, 1988). Early settlers reported mostly open stands of large trees with little understory (Arno and Allison-Brunell 2002). Frequent, low-severity surface fires from lightning and Native American burning were probably important agents in maintaining such conditions (Arno 1988) although there is also evidence that higher elevation ponderosa pine forests burned less frequently and with mixed severity (Schoenagel et al. 2004). Ponderosa pine has thick bark and self-pruning branches that protect mature trees from fires and relatively frequent fires in these forests is thought to promote vigorous growth by limiting competition with smaller trees (Agee 1993). Historical wildfire has therefore been generally considered to have a positive effect on the growth and vigor of ponderosa pine, however this has seldom been tested, especially in remote, unmanaged stands. Therefore, although the long-term maintenance of ponderosa pine as the canopy dominant species appears to depend on periodic fires, the effect of fires on individual trees is less clear.

What is known about growth responses to fire comes from a wealth of research measuring growth responses after experimental manipulations (thin, burn, or combination), most often in 2nd growth forests. These studies have shown both positive and negative effects of fire on tree growth via several mechanisms. Reduction in stand density reduces competition and provides increased access to light, water (Donner and Running 1986, Stone et al 1999,) and soil nutrients (Covington and Sackett 1986; Covington and Sackett 1992; Baird et al 1999; Gundale et al. 2005). However, fire may harm trees directly by scorching branches and needles and killing cambial cells and fine roots. Severe fires may also lead to nitrogen losses (Grier, 1975; Landsberg et al. 1984, Monleon et al 1997; Wright and Hart 1997; DeLuca and Zouhar 2000) or destroy below-ground biotic communities responsible for nutrient cycling (Neary et al. 1999) producing further detrimental effects on surviving trees.

The combinations of effects from these various mechanisms make post-fire growth responses in surviving trees difficult to predict. Thinning to mimic fire usually produces positive responses (increased growth and/or reduced mortality) in the remaining trees (Kolb et al 1997, Feeney et al. 1998, Latham and Tappeiner 2002, Sala et al. 2005, Richie, 2008). Positive responses have also been found after burn treatments (Weaver 1967), or combined thin and burn treatments (Zausen et al. 2005; Fule et al. 2005). However, studies have also found negative responses after fire treatments (Landsberg et al. 1984; Busse et al. 1996; Maloney et al. 2008) or reduced benefits in thin-burn treatments relative to thinning alone (Ritchie et al. 2008). Although responses vary greatly from study to study, there appears to be a higher likelihood of negative responses when fire is included in the treatment as opposed to thinning alone.

The integrated long-term effect of multiple recurrent fires may be different from the sum of short-term responses to individual fires. For example, recurrent fires that individually harm surviving trees may benefit these same trees over the longer term by reducing competition. Long-term effects of frequent fire have seldom been studied, however. Sutherland (1983) found reduced long-term growth over time in fire-excluded stands, providing indirect evidence for positive effects of frequent fire, although there were no paired frequently-burned stands available for a controlled comparison. Contrary to the prevailing view that ponderosa pine benefit from frequent fire, some on-going prescribed fire treatments have found higher mortality and reduced growth in treated stands compared to pre-treatment (Thomas and Agee 1986; Swezy and Agee 1991). Models predict short-term negative and long-term neutral responses to single fires following fire-exclusion (Sutherland et al. 1991) and long-term positive responses to periodic fire (Covington et al. 2001) although field tests of these simulations are rare.

The short-term perspective of much of this research limits our understanding of how trees respond to recurrent fire under natural conditions over longer time frames. Even general conclusions about how individual wildfires affect tree growth may be difficult to draw from single manipulation studies because experimental treatments in managed forests may not mimic natural wildfire in unmanaged forests. Very few of the foregoing studies looked at growth responses to natural wildfire, in unmanaged, old-growth forests. The rare studies in unmanaged stands either used prescribed fire (Fule et al. 2005) or did not use paired burned and unburned stands (Sutherland 1983). For these reasons, current knowledge of tree growth responses to fire may be incomplete and suffer from a lack of realism. Importantly, we know of no study in unmanaged forests that measured separate repeated short-term responses to recurring natural wildfires or integrated long-term responses to multiple fires over time using paired burned and unburned stands.

These gaps in our current understanding of how trees respond to wildfire are compounded by the fact that tree responses to fire under natural conditions may not be stable over time. Over the course of the twentieth century, the characteristic high-frequency, low-intensity fire regime of many ponderosa pine forests has been changing. Many ponderosa pine forests did not burn at their historical frequencies during the twentieth century due to active fire suppression policies. This is true for mixed-regime forests with historically longer fire intervals as well. The relative lack of frequent fire in these forests is thought to have created uncharacteristically high stand densities and higher fuel loads. These conditions are thought to be a direct cause of increasing numbers of uncharacteristically high intensity wildfires in recent years (Arno and Allison-Brunell 2002, Miller et al. 2009a) and there is evidence that fires in high-density, fuel-loaded stands are more likely to burn with high intensity and harm residual trees (Raymond and Peterson, 2002; Strom and Fule 2007).

Confounding the effects of increasing fuels in many forests in recent years however, is evidence that fire activity may also be strongly linked to changing climatic conditions. Historically, years with large numbers of fires across our study region were warmer and drier than normal, while years when no fires burned regionally were cooler and wetter (Heyerdahl 2008a). In the 20th century, years with higher summer temperatures and earlier snowmelt had greater numbers of fires, and fires burned longer under these conditions (Westerling et al. 2006; Running 2006, Morgan et al. 2008). Warmer and drier climatic conditions are therefore a likely cause of increasing fire activity since 1980 (Westerling et al. 2006). There is uncertainty about whether fire intensities and severities are changing (Keane et al. 2008); however, it is probable that climatic conditions that produce larger, longer, and more numerous fires across landscapes also produce fires that are hotter and more destructive to trees and forests (Laverty and Williams, 2000; Keane et al. 2002; Ryan 2002).

How trees respond to natural wildfire is a basic question of disturbance ecology and ecophysiology. If these responses are changing, ecosystem processes such as productivity and carbon sequestration rates of forests may be affected. Old growth forests can store and continue to sequester carbon over many years (Carey et al. 2001; Luyssaert et al. 2008) however currently forests across the west are experiencing increases in background mortality rates, most likely due to drier climatic conditions (van Mantgem et al. 2009). There is some evidence that fire intensity may affect growth in surviving trees (Mutch and Swetnam 1995) but whether current climate trends are increasing fire intensities to the point of reducing tree growth after fire is a question that has received very little study. Integrated across a wide landscape, negative responses to fires under novel conditions could have ramifications both commercially and ecologically for forests. The relative importance of climate change versus increases in stand density and fuel loads in determining fire responses is a critical distinction for forest management in this context. In addition, response to fire may be affected by tree age (Kobziar et al. 2006). If young or small trees respond differently to fire under novel climate or stand conditions, predictions about future forest productivity may depend on stand age or development.

In this study we asked the following questions: 1) Are the long-term growth responses to multiple fires in burned stands positive or negative compared to unburned stands? 2) Have short-term (5- and 10-year) growth responses to individual fires changed over the course of the twentieth century and are these changes affected by climatic conditions or time-since fire? And, 3) are growth responses to fire affected by tree age? To our knowledge, ours is the first study to measure both long- and short-term tree growth responses to natural wildfire in unmanaged forests using paired burned and unburned stands. The unlogged status of our sites also ensures no confounding effects of prior logging on tree responses to wildfire (see Keeling et al. 2006 [chapter 1] for further discussion).

Methods

Site Selection

In 2003, a total of seven remote study sites were located in unlogged, low- to mid-elevation ponderosa pine/Douglas-fir forests within or on the periphery of wilderness areas in Idaho (see DeLuca and Sala 2005 and Keeling et al. 2006 [Chapter 1] for site selection details). From these sites, four were chosen for this study (Figure 1). At each site, a fire-excluded stand (“unburned”) was compared to a fire-maintained stand ("burned"). Unburned stands had not experienced fire for at least 70 years. Burned stands experienced 3-4 wildfires at intervals ranging from 6 – 58 years (mean = 34 years) throughout the 20th century. Table 1 shows environmental data and fire history information for all stands. Fire histories for all stands were based on U.S. Forest Service fire maps, field reconnaissance, and on-site fire scar analyses (see DeLuca and Sala 2005 and Keeling et al. 2006 [Chapter 1] for more detailed methods on fire histories). Although some physiographic differences between stands existed, on average there were no systematic physiographic differences between unburned and burned stands from each site across the entire study (paired t-tests comparing slope, aspect, and elevation, $p>.05$). We cannot determine whether fires were actively suppressed even in these remote areas, therefore the terms "unburned" or "fire-excluded" are not meant to imply human agency in determining the unburned status of these stands. The fire return intervals in our burned stands are within the historical (i.e. pre-1900) range, which can be more than 25 years for mixed ponderosa pine forests in the northwest region (Arno 1980; Arno and Allison-Bunnell 2002, Heyerdahl et al. 2008b).)

Data Collection

In June and July of 2004, an access route across each stand was chosen. Access routes were stratified into equal distances and points along the route were generated randomly within each stratified length. The nearest mature ponderosa pine tree to each point was selected for sampling. At least 10 mature trees were sampled in each stand. . At each tree, elevation, aspect, slope, GPS coordinates, and tree diameter at breast height (DBH) were recorded. Increment borers were used to extract two cores from each tree and tree diameter at coring height (DCH) was recorded. The two cores were taken from opposite sides of the tree, perpendicular to the direction of the slope. Cores were taken at approximately 50 cm height from the ground. Coring heights were recorded for each core. Four bark depth measurements were taken at coring height using a standard forester's bark gauge. Cross sections at ground level of three ponderosa pine seedlings were taken in each stand for use in estimating ages of trees at coring height. Heights of each seedling were recorded. In 2006 and 2007 additional trees of a wider variety of ages were sampled at BR and MB as part of a different study (sample sizes range from 8-21 trees per stand and are reported in figures).

Sample Preparation and Cross Dating

Cores were mounted on wooden core mounts and sanded until rings could easily be distinguished with a binocular microscope. Rings were counted and years were provisionally marked starting at the outermost ring and counting inward toward the innermost ring. The two cores from each tree were visually crossdated against each other and against a time-series of reconstructed Palmer Drought Severity Index for the region. Relatively narrow and wide rings, rings with notable latewood, suspected false or missing rings, and years of growth suppression or release, were recorded and used as an aid in cross-dating of all cores. Rings from all cores were then to the nearest .001mm using a Velmex measuring station. The program COFECHA was used to verify the dating accuracy and as an aid in determining missing and false rings which were then checked and corrected by eye on the cores (Holmes, 1983).

Age estimation

Once cores were cross dated, the year of the inner-most ring established a minimum estimate of tree age. However, because very few cores intersected the pith of the tree and because trees could not be cored at exactly ground height, it was necessary to add pith and height corrections to the date of the innermost ring in order to more accurately estimate age. For height corrections, seedling cross-sections were sanded and rings were counted. Height of each seedling was divided by age to compute growth rates (cm/yr) for each seedling and growth rates were compared using two-way ANOVA with site and burned status (burned vs. unburned) as factors. Growth rates did not differ by site or burn status, therefore all seedlings were pooled and a mean growth rate (cm/yr) was calculated. For each tree, coring height was divided by the mean growth rate to estimate the years to coring height. To estimate the number of rings to pith two methods were employed. Where the geometry of the inner 3 rings was easily measured, the distance to the pith was calculated from the height and length of the last incomplete ring and this distance was divided by the average of the 3 inner rings to estimate the number missing rings to the pith. On some cores, the use of transparent concentric circles was used to make the same estimate.

Calculation of basal area increments (BAI)

The radius of each tree was calculated by dividing measured DCH by two and subtracting the average bark depth. Annual radial growth increments were calculated using the proportional method described by Bakker (2005). Annual radial increments were then converted to annual basal area increments by assuming circular basal area with the pith at the center. Annual basal area increments (BAI) were averaged for the two cores from each tree.

Long-term growth responses to multiple fires

Mean annual basal area increments (BAI) were calculated for each stand and plotted by site in a time series. Pre-comparison periods and comparison periods were defined for each site as follows: The boundary between pre-comparison and comparison periods was the year of the earliest 20th century fire which affected the burned stand but not the unburned stand. ("Comparison period" here refers to the period during which fire exclusion was affecting the unburned stands and recurrent natural wildfire was affecting the burned stands.) For one site (MC) this boundary was the year of the first recorded 20th century fire in the burned stands. For two sites (MB, BR), this boundary was the second recorded fire in the burned stand, since both stands experienced the first fire recorded (see Table 1). Long-term growth responses were not computed for the fourth site, TW, because only a 1992 fire was unique to the burned stand and the comparison period was only 12 years. At MB and BR, the number of years in the comparison period was used to determine the length of the pre-comparison period. At MC, because the comparison period was much longer and trees were younger, the early boundary of the pre-comparison period for both stands was established at the first point going back in time where sample size was reduced because of the youngest tree falling out of the dataset. Because only similar aged trees were used within each site, age-related changes in growth from the pre-comparison period to the comparison periods are assumed to be similar for each of the paired stands within each site. Because pre-comparison and comparison periods are the same for each set of paired stands, climatic conditions between paired stands were also controlled.

For each tree, mean BAIs were calculated for comparison and pre-comparison periods. Each tree's average BAI in the comparison period was then divided by its average pre-treatment BAI to produce standardized growth values for each tree. These standardized growth values for each tree were averaged to produce mean standardized growth for each stand. By standardizing growth in each stand, environmental differences between stands that might confound growth differences between stands were controlled.

Growth responses at each site were expressed as (mean standardized BAI burned stand /mean standardized BAI unburned) - 1. Positive values for growth responses indicate higher standardized growth in burned stands compared to the unburned stands.

Short-term growth responses to individual fires

For short-term growth responses to fire, ANOVA was again used to test for overall differences in ages between trees in paired burned and unburned stands within sites (see Statistical Analysis, below). Five-year and ten-year periods, prior to and subsequent to the year of fires affecting the burned stand were used to calculate standardized growth differences (mean BAI after fire-year/mean BAI before fire-year) analogous to the long-term standardized growth calculations described above. Site responses were again expressed as burned/unburned -1.

Temporal trends and effects of climatic conditions and time-since-fire

The site growth responses (burned/unburned -1) to individual fires for each site and fire year were calculated as described above and plotted in a time series. Our goal in the climate analyses was to test whether climatic conditions that generally influence fire activity (size, duration, and number of regional fires) were correlated with tree growth responses after fire.. Dry and warm climatic conditions are the general characteristics of years with increased fire activity in this region (Heyerdahl et al. 2008a, Westerling et al. 2006). Monthly precipitation and temperature data were obtained for a nearby weather station (New Meadows station, ID). Growth responses for each site/fire year were tested for significant relationships with monthly and seasonal average precipitation and temperature data for the 12 months preceding the fire. Growth responses were also tested and plotted against time-since-fire, which was computed as the number of years since the previous fire.

Effect of tree age on growth response to fire

At two sites, (BR and MB), additional trees with a broader range of ages were sampled as part of a separate study (chapter four) This allowed an independent analysis of the effect of tree age on growth responses to fire. For this analysis, trees over 100 years old in the burned sites were used. At each site, two fires were included in the analysis and 5- and 10-year responses were computed as described above. The growth response values for each tree were then plotted against tree age to show the relationship between tree age and growth response.

Statistical Analysis

Statistical tests were carried out using the software SPSS 16.0. Special care was taken to ensure that differences in mean tree ages between burned and unburned stands were not a confounding factor. Short-term growth responses to individual fires were initially analyzed using 1-way ANCOVA with stand (unburned, burned) as the main factor and tree age as a covariate. However, there were no significant linear relationships between age and growth responses for fire events at MC and TW, and scatter-plots showed that weak non-linear relationships between age and growth responses for fire events at MB and BR were the result of higher responses to fire only in trees younger than 100 years old. Because an independent analysis of age-related growth at MB and BR showed that growth rates do not change significantly in a systematic way after age 100 at these sites (see chapter four), trees younger than 100 years old at the beginning of each fire year were removed from the data sets at MB and BR. This also had the effect of making mean ages more similar across all sites, since very young trees were not sampled at MC and TW. Two very old trees from the burned stand at MB were also removed from short- and long-term response analyses. Once these adjustments were made, ANOVAs showed no significant differences in mean ages between trees in unburned and burned stands within sites, with the exception of one fire event, 1910 at MC. However, the mean age difference between trees in the burned and unburned stands at MC in 1910 was not great (mean age unburned = 192, mean age unburned = 225).

All growth response and age data were tested for normality and homogeneity of variance using Kolmogorov Smirnov and Levene’s tests respectively and analyzed using one-way ANOVA with stand (unburned vs. burned) as the main factor. Five- and 10-

year growth response data that failed tests of normality or homogeneity were transformed using square-root or log transformations. If variance could not be stabilized by transformation, and a Kruzal-Wallis non-parametric test was employed in place of the ANOVA.

For long-term growth responses a similar approach was used to control for possible age-related effects. All trees were included for MC and TW where no young trees were sampled. For BR and MB, only trees that were older than 100 years old at the beginning of the pre-comparison period were used. Differences were tested as described above, using one-way ANOVA. Long-term growth responses were not computed for TW because the comparison period was too short for this site.

Results

Tree-ring series were successfully crossdated for all trees at all sites with the exception of two trees at MC. These trees were included in the long-term analyses but not the short-term analyses because dating errors would only significantly affect results of the short-term analyses. In addition, one tree at MC was too young to be included in the long-term analysis, and in the 1910 short-term analysis. Table 2 shows standardized growth results, sample sizes, mean ages, age ranges, and pre-treatment and comparison periods for long-term growth responses.

Long-term growth responses

Two sites (BR, MB) showed very small and statistically non-significant growth responses in burned stands relative to unburned stands (Figure 3a). At the third site (MC), there was a significant positive long-term growth response in the burned stand. Annual BAI's for all sites with fire-years and comparison and pre-comparison periods are plotted in Figure 2.

Short-term growth responses

Short-term growth responses varied depending on fire event (Figure 4a, Table 3). There were significant positive growth responses to fire at MC in 1910 and 1934. Ten-year responses were slightly stronger than 5-year responses. There were significant negative growth responses at MB in 1987, MC in 1987, and at BR in 1992. Again, 10 year responses were stronger than 5-year responses. Responses for the four other fires analyzed were not significant. Ten-year responses for the 1981 fire at MC are not shown because a subsequent fire occurred less than 10 years later. When responses were analyzed across all sites and fires, there was no overall significant response.

Temporal trends, climate and time-since-fire effects

There was a significant trend of more negative 10-year growth responses to fire in more recent years (Figure 5a). Five-year responses were similar although slightly weaker (results not shown). This trend was correlated with some of the climate variables we tested. Fires in years preceded by lower winter precipitation were more likely to produce negative 10-year growth responses to fire (Figure 5b). There was also a moderate, albeit statistically non-significant negative correlation between 10-year growth responses and June temperature (Figure 5c). There was no significant relationship between time-since-fire and growth response to fire (Figure 5d).

Effect of tree age on growth response to fire

There were no significant relationships between tree age and 10-year growth response to four fires at MB and BR (Figure 6). 5- year responses were similar and are not shown.

Discussion

To our knowledge this is the first study to measure both long- and short-term tree growth responses to natural wildfire in unmanaged forests using paired burned and unburned stands. Recent research has shown that climatic conditions may have strong effects on fire activity in dry forests of the American west (Heyerdahl 2008a; Westerling 2006). Changing climate and potentially higher fire severities may alter tree growth responses to wildfire. In this research, we measured both long- and short-term growth and stress responses to wildfires in old-growth ponderosa pine trees and studied the temporal trend of these responses and their relationship to climatic conditions, time since fire, and tree age.

The long-term growth results could be interpreted to suggest that a greater number of fires is more likely to produce long-term growth benefits for trees: The only site (MC) that showed a positive long-term response to fire was also the site with the greatest number of fires (4) in the burned stand. However, the two early fires at MC produced significant positive short-term growth responses in the burned stand while the later two fires produced negative short-term responses (Figure 4). Inspection of the entire time-series of growth at MC (Figure 2; panel MC) shows that the long-term positive growth response was largely a sustained period of higher growth in the burned stand after the first two fires. Therefore, the particular circumstances during the time of the two early fires at MC are probably responsible for the long-term positive response, rather than the sheer number of fires.

Figure 2 also shows that trees in the unburned stand at MC grew much faster than trees in the burned stand during the pre-comparison period. We have no information about stand conditions or fire history during the pre-comparison period at MC. Although trees were of roughly similar ages in the two paired stands at MC, it is possible that some difference between stands in stand conditions during the pre-comparison period is partly responsible for the positive growth response we measure after standardizing against the pre-comparison period. Figure 2 shows that annual mean BAI’s in the unburned stands were declining even during the years prior to the first fire in 1910 and this decline continued during the time period of the first two burns in the burned stand. The fact that trees in the burned stand increased in growth during this same time period suggests that the positive fire responses we have computed for these fires are real responses. However, the magnitude of the responses may be artificially inflated when standardized against the unexplained declining growth in the unburned stand.

Long-term growth responses need not be consistent with short-term responses to fire, because the mechanisms affecting growth are different in both cases. For long-term growth responses to fire, the main mechanism is maintenance of low density stands and reduced competition. For short-term growth responses, the main mechanisms are reduced growth due to direct damage from the fire, potentially offset by enhanced growth due to possible nutrient release from the fire. It is possible that trees may suffer direct short-term negative effects of fire and still reap the indirect benefits of lower competition over the long-run.

In our study, however, the short-term responses were generally consistent with long-term responses. For example, MC, the only site with a positive long-term response to fire, was also the only site with positive short-term responses. This relationship between long- and short-term responses suggests a large influence of the direct effects of fire on trees and a smaller, somewhat inconsistent influence of the indirect and longer-term effects via changes in competition. This pattern corresponds to results we report in an accompanying study where we show no significant physiological benefit to trees growing in the less dense, burned stands (see chapter 2). In general, the unburned stands in our study had lower available soil nitrogen (DeLuca and Sala 2005) and higher densities of small trees while overall basal area was similar among stands (See Keeling et al. 2006). The smaller trees in the denser, unburned stands probably pose little competitive threat to the mature trees we measured in this study and therefore the long-term responses to the recurrent fires that eliminated small trees in the burned stands were not significant. Our results highlight the importance of direct negative effects of fire that may in some cases overwhelm the long-term benefits of competitive release.

The exception to the pattern of similar trends in both short- and long-term responses was at the site BR, where both fires produced short-term negative responses, while the long-term growth response was slightly (albeit non-significantly) positive. Inspection of the size-class distributions of the burned and unburned stands at BR (data not shown) shows that the burned stand had fewer trees in both small and medium size classes. The fires at BR apparently reduced the density of medium sized trees (20-30 cm) that were competitive with the dominant trees. In this stand, a positive effect of density reduction in medium size classes in the burned stand may have partially offset the negative direct effects of wildfires. However, even in this case, density reduction failed to produce an overall significant positive long-term growth response in the burned stand.

To summarize, we did not consistently find significant positive or negative long-term growth responses to recurrent fire or fire exclusion. This finding suggests that lack of fire in ponderosa pine forests does not necessarily inhibit growth or increase the stress of mature trees in fire excluded stands relative to burned stands. Conversely, these results also suggest that recurrent natural wildfire does not reliably produce long-term growth benefits in mature ponderosa pine. These conclusions may have important implications for restoration and management of old-growth ponderosa pine forests. Mechanical thinning to mimic fire may produce growth responses in managed stands; however, by itself this outcome should not be used as a basis for restoration if such growth responses are not observed under natural fire conditions. Although the reestablishment of natural fire intervals in mixed conifer ponderosa pine forests is a generally desirable goal, presumed long-term growth benefits to trees may not add justification for management activities.

Short-term responses to individual fires show an interesting and potentially important trend: Recent fires appear to be more detrimental to tree growth than fires earlier in the 20th century (Figure 5a) at these sites. In fact, the only fires to produce significant positive growth responses were the two earliest fires we studied, 1910 and 1934 at MC. Fires in the mid-century at BR and MB produced non-significant and neutral growth responses, while recent fires at all four sites were more likely to produce significant negative responses. The relatively small number of fires analyzed in this work cautions against drawing broad conclusions about how widespread this trend may be. Also to be considered is the fact that this pattern is partly driven by two early fires at one site only (MC) where sample sizes were low and where a growth decline in the unburned stand during the period of the first two fires may be affecting results. However, the trend is apparent to a lesser degree at MB and BR, and the relatively strong negative responses to recent fires at all four sites is remarkable in itself given the historical notion of ponderosa pine as a positive responder to fire.

The increasing tendency for more recent fires to produce negative growth responses appears to be linked to climatic conditions. The late century negative responses were significantly correlated with lower winter precipitation (Figure 5b) and moderately, though non-significantly, correlated with higher summer temperatures (Figure 5c). This suggests that winter precipitation may be more important than summer temperatures as a driver of fire-intensities that produce reduced growth in surviving trees. In fact, the one outlier fire year (BR, 1944) that had low temperatures in June (lowest temperature value in Figure 5c) had a very dry winter suggesting that dry conditions may have been an overwhelming factor in the negative growth response after that fire. Fire responses were not as strongly associated with time-since-fire (Figure 5d) suggesting that fuel build up between fires during the 20th century may not be as strong a driver of negative growth responses to fire as changing climatic conditions at these sites. However, because we lack fire history data before 1880, we cannot compare growth responses to fires in earlier periods (before both the effects of fire suppression or climate change) to the growth responses we measure in this study. It is possible that long-term fuel build up beginning as early as the 18th century may be interacting with climate change to drive negative responses during the late 20th century.

Climate projections for the interior west predict increased drought (Westerling et al. 2006), declining winter snowpack (Mote et al. 2005), and increasing temperatures (IPCC 2007). Dry conditions during the winter and spring preceding the fire season have been shown to be correlated with increases in acres burned in the Idaho Rockies (Westerling et al. 2003) and in Yellowstone National Park (Balling et al. 1992). The implication of these studies is that warmer and drier conditions generate fires that burn larger areas, probably in part because of higher fire intensities or greater fuel availability. Our results show that fires under such conditions may be more likely to adversely affect growth in residual old ponderosa pine trees. Our results also show that these adverse climatic conditions and negative growth responses to fires appear to be becoming more prevalent in recent years.

To our knowledge, this study is the first to report a trend of increasing likelihood of adverse tree growth responses to modern fires with a possible link to climate change. This research is unique in that we studied natural wildfire in old-growth forests using a difficult sampling protocol, but one that offers greater realism over fire studies that measure responses to prescribed fire or thinning treatments. If corroborated across larger regions than studied here, an association between climate-driven increases in fire intensity and negative tree growth responses could have important implications for ecosystem processes. Recent research has found that mortality rates are increasing in forests across the west, most likely due to water deficits resulting from warmer, drier conditions (van Mantgem et al. 2009). Such widespread mortality increases will dampen rates of carbon uptake and storage in western forests. Our results point to the possibility that this reduction in carbon uptake and storage could be exacerbated if growth rates in surviving trees are slower because of the negative effects of high intensity fire.

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Table 1. Physiographic data and fire histories for unburned and burned stands within four sites (based on U.S.F.S fire maps and on-site fire-scar analysis).

Site	Stand	# 20^{th} century Burns	Mean Aspect (deg)	Mean Elev. (m)	Mean Slope (deg)	Year 1st Fire	Year 2nd Fire	Year 3rd Fire	Year 4th Fire
BR	unburned	1	61.3	1665	37.3	1914			
	burned	3	49.3	1464	29.3	1914	1944	1992	
MB	unburned	1	236.0	1813	27.3	1919			
	burned	3	250.7	1536	32.7	1919	1960	1987	
MC	unburned	0	270.0	957	33.3				
	burned	4	258.0	915	42.3	1910	1934	1981	1987
TW	unburned	2	88.7	805	32.7	1910	1934		
	burned	3	134.7	869	33.3	1910	1934	1992	

Table 2. Long-term growth responses to multiple fires. Standardized mean BAI and sensitivities are calculated as means for comparison period/means pre-comparison period (see Methods). Significant differences between unburned and burned stands within sites are **bold**.

Site	**Stand**	**# of trees**	**Mean age (range)**	**Pre-comparison period**	**Comparison period**	**Long-term standardizd mean BAI (after/before) Comparison period (C.I.)**
BR	unburned	8	330 (287-372)	1886-1944	1945-2003	.76 (.55)
	burned	17	341 (270-427)	1886-1944	1945-2003	.84 (.11)
MB	unburned	10	320 (158-355)	1918-1960	1961-2003	1.34 (.20)
	burned	21	344 (188-454)	1918-1960	1961-2003	1.21 (.06)
MC	unburned	10	210 (160-384)	1852-1910	1911-2003	**.75 (.24)**
	burned	9	223 (166-282)	1852-1910	1911-2003	**1.46 (.62)**

Table 3. Short-term growth responses to individual fires. Mean standardized basal area increments (BAI) for each fire are calculated as mean BAI after fire/mean BAI before fire. Responses using 5, and 10 year before and after periods are shown. Significant differences between unburned and burned stands for individual fire events are **bold**.

			Mean Standardizd BAI (after/before) 1st fire (C.I.) n			**Mean Standardizd BAI (after/before) 2nd fire (C.I.) n**		**Mean Standardizd BAI (after/before) 3rd fire (C.I.) n**		**Mean Standardizd BAI (after/before) 4th fire (C.I.) n**	
Site	**Stand**	**Mean age (range)**	**5 yr resp**	**10 yr resp**	**Mean age (range)**	**5 yr resp**	**10 yr resp**	**5 yr resp**	**10 yr resp**	**5 yr resp**	**10 yr resp**
BR	unburned	330 (287-372)	0.95 (.08) n=8	1.20 (.14) n=8	260 (142-372)	1.81 (.55) n=13	**1.65** **(.50)** **n=13**	NA	NA	NA	NA
	burned	341 (270-427)	0.86 (.08) n=17	1.05 (.09) n=17	255 (134-427)	1.27 (.13) n=31	**1.11** **(.13)** **n=31**	NA	NA	NA	NA
MB	unburned	320 (158-355)	1.00 (.11) n=10	1.03 (.10) n=10	250 (143-355)	**0.74** **(.08)** **n=17**	**.79** **(.11)** **n=17**	NA	NA	NA	NA
	burned	344 (188-454)	.96 (.08) n=21	1.07 (.12) n=21	312 (141-454)	**0.49** **(.08)** **n=25**	**.57** **(.07)** **n=25**	NA	NA	NA	NA
MC	unburned	192 (161-215)	**1.03** **(.06)** **n=9**	**0.99** **(.09)** **n=9**	192 (161-215)	0.88 (.09) n=9	**.87** **(.07)** **n=9**	0.83 (.06) n=9	NA	0.93 (.13) n=9	1.00 (.26) n=9
	burned	226 (167-282)	**1.19** **(.13)** **n=8**	**1.17** **(.12)** **n=9**	212 (105-282)	1.04 (.19) n=9	**1.14** **(.24)** **n=9**	0.88 (.07) n=9	NA	0.70 (.17) n=9	0.69 (.13 n=9
TW	unburned	181 (165-205)	1.10 (.14)	1.05 (.15)	NA	NA	NA	NA	NA	NA	NA
	burned	168 (156-189)	1.10 (.11)	.95 (.14)	NA	NA	NA	NA	NA	NA	NA

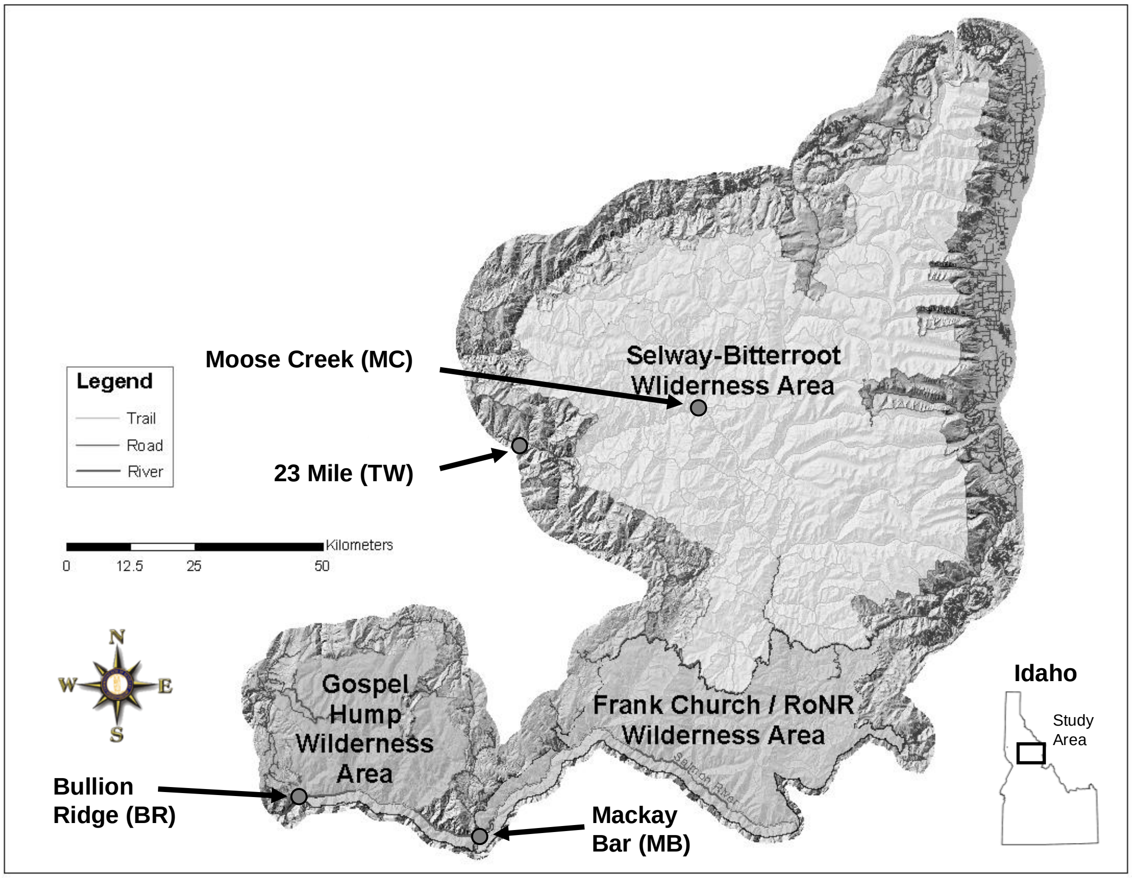


Figure 1. Study area and site locations. (RoNR = River of No Return).

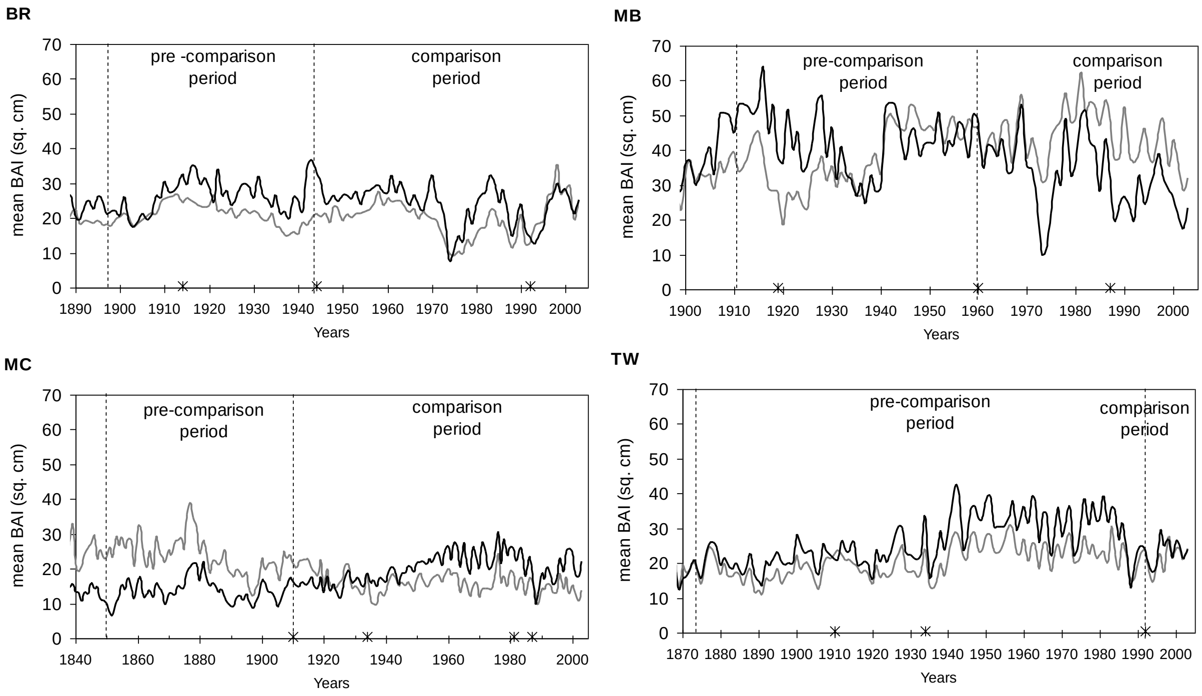


Figure 2. Ponderosa pine average annual mean basal area increments (BAI) at four sites. Unburned stands are grey lines and burned stands are black lines. Fire years are marked along the x-axis. Vertical dashed lines delineate pre-treatment and comparison periods used for mean standardized growth. Fires within pre-comparison periods occurred in both stands. Fires in comparison periods only occurred in burned stands.

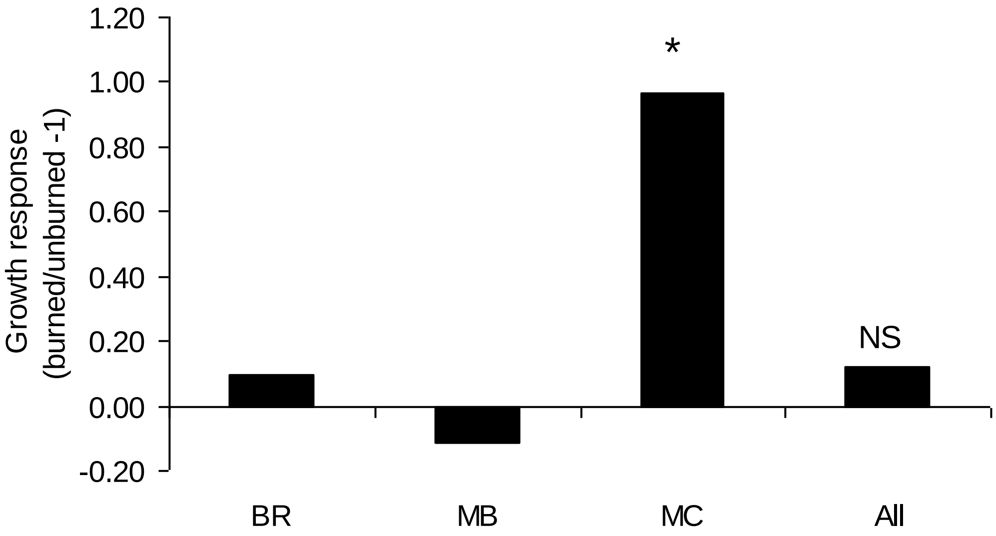


Figure 3. Ponderosa pine long-term growth responses to recurrent fires (mean standardized BAI burned stand/mean standardized BAI unburned stand – 1), for three sites and across all sites. Bars with an * are statistically significant responses (ANOVA, $p \leq .05$). Mean standardized BAI, confidence intervals, and sample sizes used to calculate long-term responses are in Table 2.

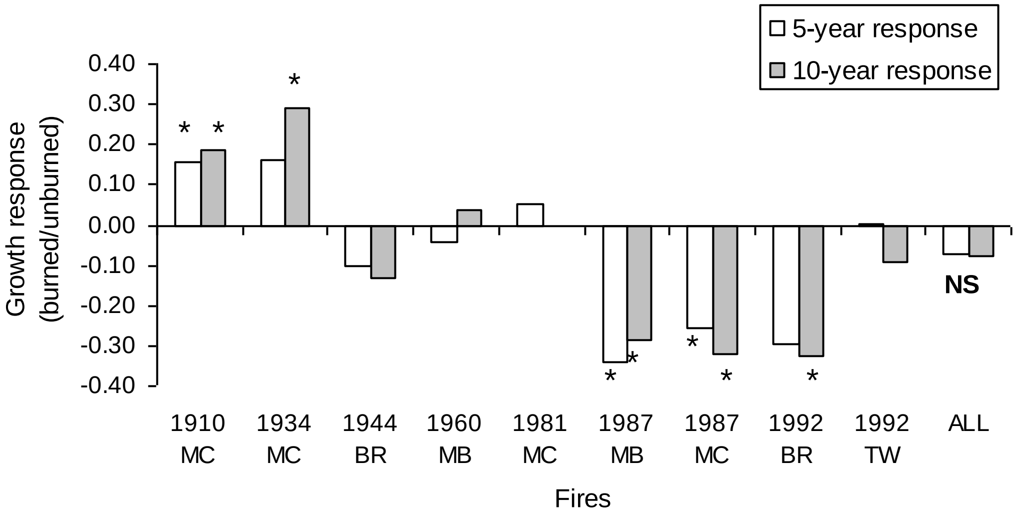


Figure 4. Ponderosa pine average short-term growth responses (mean standardized BAI burned stand/mean standardized BAI unburned stand – 1) to individual fires for nine fire events at four sites. Five-year responses are in white, ten-year responses are in black. Bars with an * are statistically significant responses (ANOVA, $p \leq .05$). Mean standardized BAI, confidence intervals, and sample sizes used to calculate short-term responses are in Table 3.

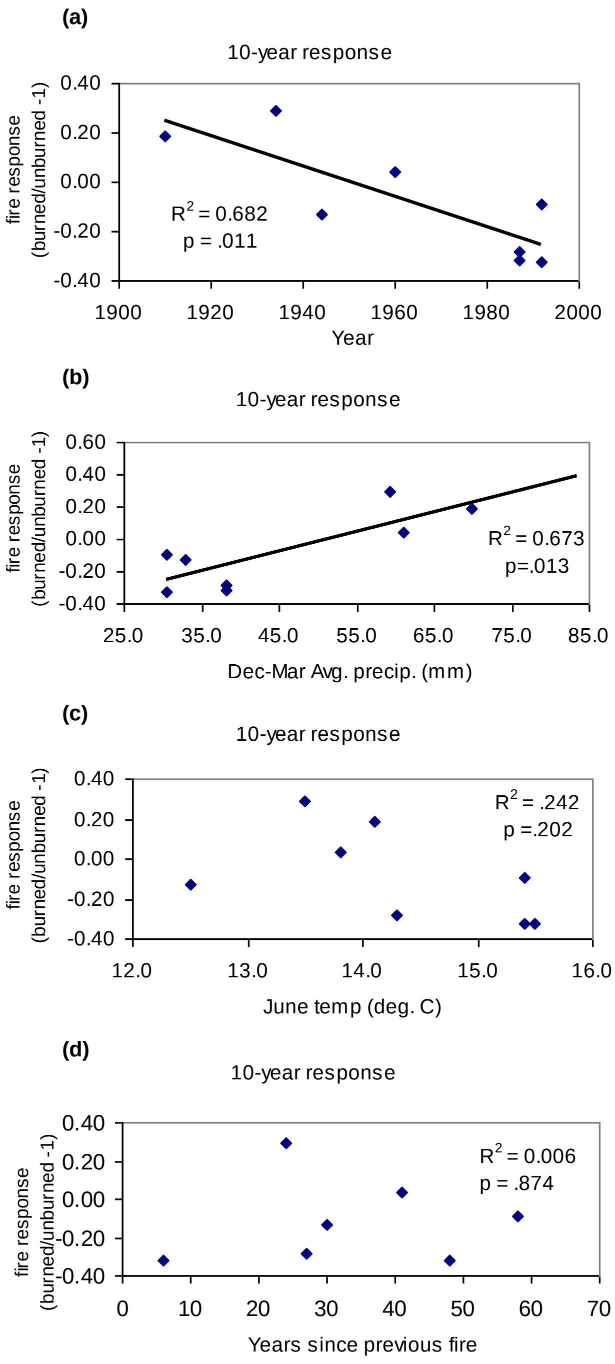
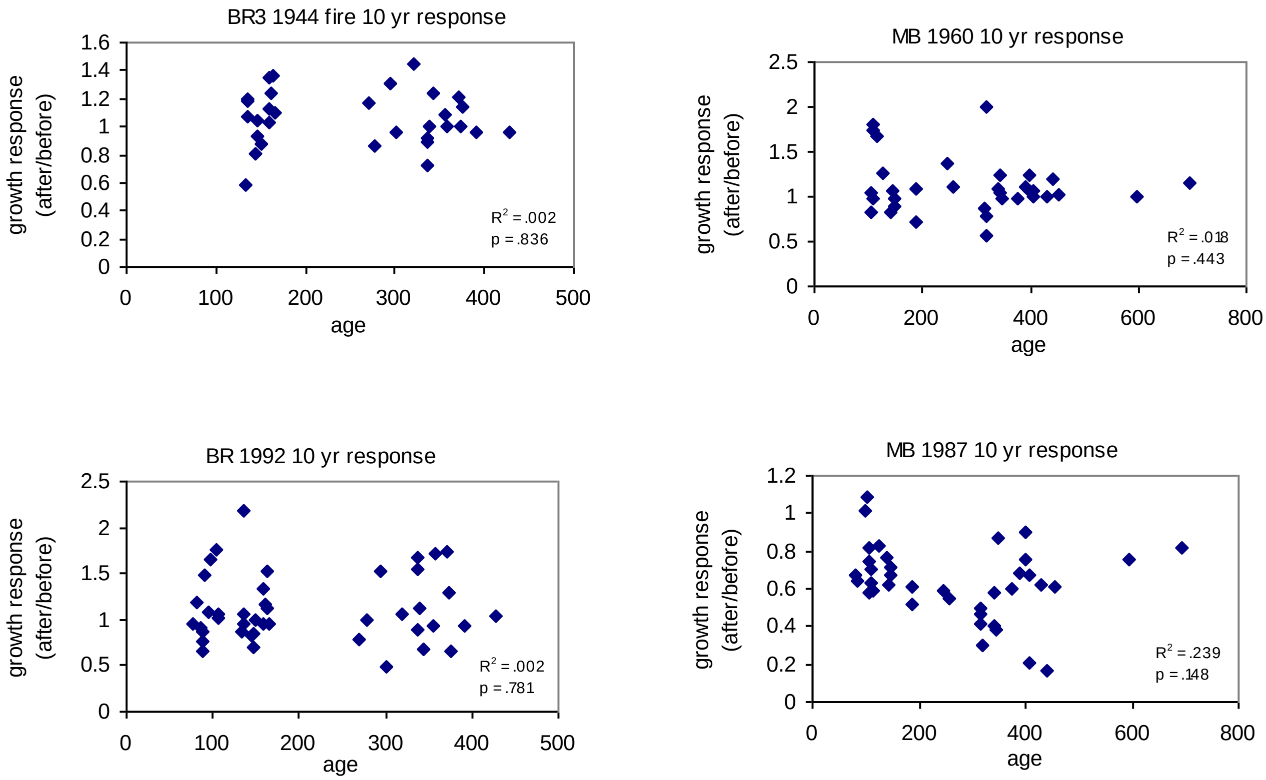


Figure 5. Ponderosa pine 10-year growth responses to individual fires for eight fire events at four sites plotted (a) as a time series, (b) against winter precipitation (average Nov.- Mar precipitation preceding fire year), (c) against June temperatures, and (d) against number of years since previous fire.


BR3 1944 fire 10 yr response

MB 1960 10 yr response

BR 1992 10 yr response

MB 1987 10 yr response

Figure 6. Ponderosa pine individual tree standardized growth responses (mean BAI after fire/ mean BAI before fire) in the burned stand for four fire events at two sites (BR and MB) plotted against tree age.

CHAPTER FOUR

Do slow trees grow old? Age, height, basal area growth and longevity in old-growth ponderosa pine trees

Abstract

A common informal observation in forests is that old trees appear to grow more slowly than young trees. Attempts to explain this decline point to the effects of tree age and/or size on growth rates. Neither the effect of age or size is conclusive, although research demonstrating increasing hydraulic constraints as trees grow tall supports the hypothesis of height-related limits to growth. However, research on the effects of age versus height on growth rates are especially lacking for very old trees. An alternative hypothesis based on life-history theory that is even more rarely investigated is the possibility that intrinsically slow-growing trees are more likely to reach old ages. This hypothesis challenges the widely accepted notion that “old trees grow slow” by suggesting instead that “slow trees grow old”. If true, this could have profound implications for how old forests are managed for sustained productivity or carbon sequestration and storage.

The main objectives of this study were to determine whether slow basal area growth in old ponderosa pine trees is related to tree age, tree height, or intrinsic differences in growth rates between old and young ponderosa pine trees. We sampled 139 trees of different ages in four remote old-growth stands in Idaho and converted annual tree-ring widths to basal area increments (BAI). There were no significant relationships between recent BAI, or growth efficiency (recent BAI/sapwood area) and tree age. In fact, many old trees had growth rates comparable to young trees. Contrary to expectations, there were weak positive relationship between growth characteristics and tree height suggesting non-significant effects of hydraulic constraints on basal area growth overall. After correcting for the fact that young and old trees have grown during eras of different climate, early-in-life growth rates were significantly higher for young trees than the same early-in-life growth rates of old trees. We conclude that old ponderosa pine trees have the potential to accumulate stemwood for centuries, often at rates comparable to younger trees. Furthermore, slow growth could be a causative process in determining longevity, rather than a necessary symptom of decline.

Introduction

Trees are the oldest, tallest, and most massive non-clonal organisms on earth. The lifetime growth potential of trees is of vital importance to human societies that depend on wood products and ecosystem services of old forests. However, the controls on growth and lifespan in trees are still open scientific questions. Old trees of many species eventually stop growing in height, and cursory inspection of tree-rings on stumps of felled trees usually reveals narrower rings toward the outside of the diameter of large, old trees. These informal observations lend credence to a general notion that old trees grow more slowly than young trees, a view consistent with the more rigorous observation that overall productivity declines when forest stands reach a certain age (Möller et al. 1954, Kira and Shidei 1967, Gower et al.1996, Ryan et al. 1997, Weiner and Thomas 2001). This forest "age-related growth decline" is a topic of great importance to foresters because declines in annual production at the stand level have traditionally governed when trees should be harvested for optimal yield (Curtis 1997, Assman 1970, McArdle et al. 1961). Recently, ecophysiologists have investigated causal mechanisms for age-related decline (Ryan et al. 1997, Ryan et al. 2006), but explanations at the individual tree level are frequently hampered by the fact that tree age and tree size increase together and could therefore be confounding factors in explaining growth decline. Accordingly, recent focus has been directed at disentangling effects of intrinsic age-related senescence (age *per se*) from the effects of increasing tree size (Peñuelas, 2005).

Various observations and experimental methods have been used to look for a causal connection between age-related senescence and decreasing growth rates in trees. Tissue cultivars of some agricultural woody plants and trees have been known to exist for hundreds of years, even while the individuals grown from such cuttings may only live for much shorter periods (Kozlowski et al. 1991, Nooden and Thompson, 1985). Recent research has also shown that meristematic tissue from older trees grafted into smaller root-stocks will behave like young tissue (Vanderklein et al. 2007, Mencuccini et al. 2005, Peñuelas 2005). Although contradictory results have also been obtained in grafting studies (see Day et al. 2001), the role of internally generated senescence at the level of meristematic cells (Medowar, 1957, Munne-Bosch, 2007) in determining aging processes in long-lived trees appears to be weak. This is consistent with studies of bristlecone pine, the oldest non-clonal organism in the world, which have failed to find any evidence of senescence (Lanner and Connor, 2001). However, relationships between growth rates and age *per se* remain largely uninvestigated for most tree species.

In contrast to weak support for senescence as a cause of slower growth, there appears to be mounting evidence that growth in trees may be affected by tree size, not age *per se*. Early work proposed that respiration and maintenance costs increase with tree size and place an absolute limit on a tree's ability to maintain positive carbon balance (Kira and Shidei 1967, Waring 1987). More recently, researchers have focused on the observation that water transport from the roots to the leaves may be constrained as trees grow tall (Friend 1993, Yoder et al. 1994, Ryan and Yoder 1997, Hubbard et al. 1999, Mencuccini and Magnani 2000, Delzon et al. 2004). The "hydraulic limitation hypothesis" stated that such hydraulic constraints should ultimately limit a tree's ability to grow beyond a certain height due to stomatal closure in taller trees thereby limiting carbon uptake and growth (Ryan and Yoder 1997). There is no support for the hydraulic limitation hypothesis as initially stated (Ryan et al. 2006). Instead, height-related growth constraints appear to be due to lower turgor pressure that reduces growth in bud and leaf cells (Waring and Schlesinger 1985, Woodruff et al. 2004, Ryan et al. 2006) or limitation in phloem transport (Sala and Hoch, 2009). Regardless of the precise physiological mechanism, hydraulic constraints due to increased height appear to be a plausible factor in growth decline that could lead to possible deficits in resources available for defenses against insects or pathogens, thereby increasing mortality risk.

There is little information about how hydraulic constraints affect diameter growth in very old trees, however. It is well established that trees in many old-growth stands can live long after their heights have culminated (King, 1990) and can continue diameter growth during these later years (Assman, 1970). Most studies that have measured the physiological effects of tree height have been conducted in plantations or otherwise young forests and ignored growth effects later in life. Although the concept of hydraulic constraints suggests that taller trees will grow slower, this has not been well tested for trees in the potentially prolonged life-phase when height growth is greatly slowed or ceased altogether.

Age and height limitation hypotheses invoke principles of tree physiology to explain the common observation that old, large trees appear to grow more slowly than younger trees in the same stand. An alternative hypothesis that may also account for this observation is provided by life history theory. The general evolutionary strategy of trees is characterized by large size, long-lifespan, and reproductive output spread over many years (Petit and Hampe 2006). The long lifespan of trees requires investments in supportive and protective structures such as thick bark and chemical defenses, with the necessary trade-off of reduced growth rates (Loehle 1988). On the other hand, slow growth rates may also increase mortality for juvenile trees facing strong competition for resources in dense stands (Loehle 1988). Therefore, trees may face an inevitable trade-off between the short-term competitive advantages of fast growth versus a long-term advantage of increased lifespan associated with slow growth. This fundamental trade-off between growth rate and longevity provides the basis for an alternative hypothesis for slow-growing old trees: Intrinsically slow-growing trees are more likely to reach old age, while fast-growing trees are more likely to die young. This hypothesis challenges the widely accepted notion that "old trees grow slow" by suggesting instead that "slow trees grow old". This hypothesis has not been adequately examined as very few tree-growth studies have considered growth changes in trees over their entire life-cycle (Petit and Hampe, 2006).

In the life-history theory outlined above, slow growth is a necessary consequence of allocation to structures such as thick bark or chemical defenses. In this case, the connection between slow-growth and longevity is indirect. However, slow growth may also promote longevity directly by generating tree stature or wood quality conducive to higher survival rates. Tall trees are prone to wind-throw or wind-snap (King, 1990) and may be at particular risk if height growth outpaces the necessary diameter growth to provide mechanical stability (McMahon, 1973, King 1990, Niklas 2006). The notion that tallness may present a mortality risk to trees is supported by the observation that the oldest known trees, such as the bristlecone pines in California, often grow on relatively harsh sites and are often below the maximum potential size for their species (Schulman 1954). Stunted trees growing on rocky cliffs likewise reach great ages while remaining much smaller than individuals of the same species growing in more common conditions

(Larson et al. 1999, Larson 2001). Slow growth may also provide protective characteristics to stemwood by producing higher density xylem with a greater proportion of thick-walled late-wood cells. Higher density wood in many species of trees has been shown to be more resistant to rot, decay, or pathogen attack (Loehle 1988). Stronger wood may provide a further protection (with smaller stature) against wind-caused mortality and other mechanical risks (Reiners and Reiners 1965, Niklas, 1992, Putz et al. 1983, Meyer et al. 2008, Gibbons et al. 2008, Read and Stokes, 2006). In addition to their stunted stature, the cliff trees studied by Larson also had higher wood density and rot resistant characteristics (Larson 2001).

The notion that slow growth is associated with longevity in trees has received very little direct research, although the idea is not new. Schulman (1954) proposed a general connection between growth rates and longevity when he reported the great ages of bristlecone pines and speculated on possible mechanisms for the slow-growth old-age relationship such as site harshness and higher insect defenses. Since that time, the tendency for slower-growing tree species to be of greater ages than fast-growing species has been reported generally (Bazzaz 1979; Loehle 1988) and at specific research sites (Orwig and Abrams, 1994; Abrams and Black 2000; Abrams and Orwig 1996; Abrams et al. 2000). There is much less conclusive evidence that differences in growth rates may affect lifespan within trees of the same species growing in the same stands. The dramatically slower growth rates and greater ages of eastern white cedar growing on cliffs compared to adjacent bottomlands (Larson 2001) shows that intraspecific differences in growth rate and longevity are clearly possible. However, the two populations were growing under extremely different environmental conditions. The most compelling evidence for within-species relationships between growth rates and longevity comes from a recent meta-analysis of tree-ring data for four conifer species in the American West (Black et al. 2008). They found that the longest-lived trees also had the slowest growth rates and that these old slow-growing individuals appeared to be mixed with fast-growing trees in the same stands. However, Black et al. acknowledged several important limitations in their study due to the constraints of meta-analysis, including potential inaccuracies and biases in the calculation of ages and early growth rates because databases did not include estimations of numbers of missing early rings and lacked height corrections (estimates of the age of the tree at coring height). More importantly, they did not directly address the problem that early growth in old trees occurred under greatly different climatic conditions than early growth in young trees. These limitations clearly point to the need for a more rigorous study of the possible relationship between growth rate and longevity within tree species.

The possibility that slow growth in old trees may be due to intrinsic growth differences between old and young trees, rather than effects of age or tree height, challenges the long-held view that old trees have little potential for sustained growth into the future. If slow trees grow old, old trees may be capable of accumulating stem wood at stable, albeit slow rates for centuries without significant age-related decline. If true, this could have a profound influence on how we manage old forests. However, there has been very little direct investigation of the relationships between age, height, growth, and longevity in old-growth forests.

The main objectives of this study were to determine whether slow growth in old ponderosa pine trees is related to tree age, tree height, or intrinsic differences in growth rates between old and young trees. We sampled old-growth ponderosa pine trees growing in four remote stands within, or on the periphery of wilderness areas in Idaho. The great ages of the trees we sampled provide an exceptional opportunity to study the effects of age versus size on tree growth in old-growth forests for which knowledge is currently lacking. We computed recent basal area growth and growth efficiency (growth per sapwood area) in old trees that were likely to be very near or past the point of maximum height growth such that height and age were decoupled. This study also provides the first field-based test of the relationship between slow-growth and longevity in ponderosa pine trees by comparing early growth rates between young and old trees while accounting for time-period (i.e. climate effects).

The specific objectives were designed to determine: 1) if basal area growth and growth efficiency are functions of tree age *per se* (Do older trees grow slower?), 2) if basal area growth and growth efficiency are functions of tree height (Do taller trees grow slower?), and 3) whether early-in-life growth rates are lower in old trees than in younger trees? (Do slow trees grow old?).

Methods

Site Selection

The four stands selected for this study were originally sampled in 2003 and 2004 for a study of the effects of frequent fire on tree growth (Keeling et al. in prep – CH-3). The four stands selected for this study were located on ridges above the Salmon River, two stands (MB1 and MB 3) near Mackay Bar, ID and the other two stands (BR1, BR3) about 40 km downriver. The nearest weather station (New Meadows, ID) reports annual average precipitation of 580.7 mm (22.9 inches), average July temperatures of 17.1 °C (62.8°F) and average December temperatures of -6.0 °C (21.2°F) for the period 1903 - 2001. The fire study showed no long-term effects of frequent fire on tree growth in the paired burned and unburned stands within two sites (MB and BR, see Figure 1). This result allowed us to reason that occurrence of fire probably has not had a great affect on growth rates at the stands at these two sites. We returned to all four stands in 2006 and 2007 to increase our sample size and sample a greater range tree sizes and ages within each stand.

Data Collection

Relatively open-grown ponderosa pine trees in a range of size-classes were sampled from a specified area of similar topography or along an access route through each stand. In general, all large, canopy-dominant ponderosa pine trees of varying diameters and a roughly equal distribution of smaller size-classes were sampled within the specified sample area. Trees with visible fire-scars, rot or insect damage, and trees growing directly adjacent to neighbor trees were avoided. For smaller size classes, trees experiencing obvious suppression from neighboring trees were again avoided. This criterion means that recent suppression effects on growth were minimized or at least equalized for all trees sampled.

At each tree, elevation, aspect, slope, GPS coordinates, and tree diameter at breast height (DBH) were recorded. A forester’s basal area prism was used to visually assess competitive relationships of each tree by estimating surrounding basal area. Increment borers were used to extract two cores from each tree and tree diameter at coring height (DCH) was recorded. The two cores were taken from opposite sides of the tree, perpendicular to the direction of the slope. Cores were taken at approximately 50 cm height from the ground. Coring heights were recorded for each core. Four bark depth measurements were taken at coring height using a standard forester's bark gauge. Tree heights were measured using a laser range-finder (Impulse 200) from two vantage points located approximately 90 degrees apart.

Sample Preparation and Crossdating

Cores were mounted on wooden core mounts and sanded until rings could easily be distinguished. Rings were counted and provisionally marked starting at the outermost ring and counting inward toward the innermost ring. The two cores from each tree were visually cross-dated against each other and against a time-series of reconstructed Palmer Drought Severity Index (http://www.ncdc.noaa.gov/paleo/drought/drght_pdsi.html) for the region. Relatively narrow and wide rings, rings with notable latewood, suspected false or missing rings, and years of growth suppression or release, were recorded and used to as an aid in cross-dating of all cores. Rings from all cores were then measured to an accuracy of .001 mm using a Velmex measuring station. The program COFECHA was used to verify the dating accuracy and as an aid in determining missing and false rings which were then checked and corrected on the cores (Holmes 1983).

Age estimation

Once cores were cross dated, the year of the inner-most ring established a minimum estimate of tree age. However, because very few cores intersected the pith of the tree and because trees could not be cored at exactly ground height, it was necessary to add pith and height corrections to ring counts in order to more accurately estimate age. For height corrections, three seedlings from each stand were harvested and cross-sections were sanded and rings were counted. Height of each seedling was divided by age to compute growth rates (cm/yr) for each seedling. Seedling growth rates were not significantly different (ANOVA $p \leq 0.05$) across the four stands, therefore all seedlings were pooled and a mean growth rate (cm/yr) was calculated. For each tree, coring height was divided by the mean growth rate to estimate the years to coring height. To estimate the number of rings to pith two methods were employed. Where the geometry of the inner 3 rings was easily measured, the distance to the pith was calculated from the height and length of the last incomplete ring and this distance was divided by the average of the

3 inner rings to estimate the number missing rings to the pith. On some cores, the use of transparent concentric circles was used to make the same estimate.

Calculation of basal area increments (BAI)

The radius of each tree was calculated by dividing measured DCH by two and subtracting the average bark depth. Annual radial growth increments were calculated using the proportional method described by Bakker (2005). Annual radial increments were then converted to annual basal area increments by assuming circular basal area with the pith at the center. Annual basal area increments were averaged for the two cores from each tree.

Height-age and height-DBH relationships

Analyses were based on the assumption that for very old trees, height and age would be decoupled. To test this, individual heights and ages for all trees were plotted in a scatter plot and curves were fit to the height-age relationship for each stand using a best-fit analysis in SPSS 16.0. The plot and analysis showed that height was linearly related to age for young trees but then leveled off with age at all sites. Linear correlation analysis was performed on trees >245 years of age at all sites to determine significant height-age relationships for old trees only. Tree heights were also plotted against DBH for all trees and linear regression lines were fit to each site individually.

Effects of age vs. height on recent growth and growth efficiency.

Recent BAI was computed as the sum of ten annual BAIs from the years 1994-2003. Growth efficiency is customarily defined as basal area growth increment (recent BAI) per leaf area. Because leaf area is difficult to estimate for individual trees, we followed other researchers (McDowell et al. 2006, Martínez-Vilalta et al. 2007, Fajardo et al. 2007) and used sapwood area as a surrogate for leaf area, relying on a generally accepted assumption that leaf area and sapwood area are strongly correlated. We verified this relationship in a separate pilot project by relating leaf area to crown profile area calculated from photographs for a harvested tree, and relating crown profile area to sapwood area at one of our stands (MB3) (Keeling et al. in process). However, because sapwood area is correlated with both height and age, residuals from a scatter plot of recent BAI vs. sapwood area were used instead of the ratio of recent BAI to sapwood area. Recent BAI and growth efficiency residuals for all stands were each plotted against both tree age and tree height first for old trees (>245 years) and then for all trees, and linear regression analyses were conducted in SPSS to determine significant relationships. Correlation coefficients and p-values (<.05 considered significant) were obtained for relationships within each stand, and for all trees combined.

Calculation of the regional growth (RCS) curve and chronology.

To validly compare early growth between old and young trees, it was necessary adjust annual BAI values using annual indices that represent relative long-term, low-frequency variation in external conditions affecting basal area growth, most likely a climate-related signal. To create such a chronology of tree-ring indices, dendrochronologists typically remove internal trends in ring-width, notably the age- or size-related decrease in ring widths along a cross-sectional radius of the tree, by fitting a curve, usually a negative exponential or linear function, to each tree's ring-width series. The fitted curve is seen as expected age or size-related growth and dividing each annual ring width (actual growth) by the expected growth and averaging these residuals for all trees and all years generates the chronology of indices that represents annually resolved external growth forcing.

In our study, we compared the standard curve-fitting approach for generating expected growth and producing a tree-ring index chronology (outlined above), with an alternative approach known as Regional Curve Standardization (RCS) (Briffa et al. 1996). Rather than fitting a curve to each tree-ring series, the RCS method was used to calculate a single regional age-related growth curve by averaging the BAI values at each biological (cambial) age for all the trees in the dataset. These average cambial age growth values were then fitted to an appropriate function using a spline, and that same function was adjusted to each tree's basic growth rate and used to detrend each BAI series. The RCS method requires a dataset with good distribution of different age-classes (Briffa et al. 1996). Our sample included 139 trees with ages ranging from 54 to 695 yrs old (mean=209). We employed the RCS method because it tends to preserve more low-frequency variation in the resulting chronology, whereas conventional curve-fitting methods often remove low-frequency variation (Cook et al. 1995, Briffa et al. 1996). Because we were interested in using the chronology to adjust early growth in order to validly compare trees growing, in some cases several centuries apart, the preservation of low-frequency change in the indices was crucial to our methods.

The program ASTAN-41d (Cook and Holmes 1986) was used to generate the two chronologies of indices, one using the standard curve-fitting approach applied to raw ring widths, and one using the RCS approach applied to BAIs. The two chronologies were plotted and compared with time series BAI plots of individual trees to see which chronology appeared to capture the low-frequency variation in growth seen in the individual growth curves.

Calculation of time-period adjusted annual growth

Calculation of time-period adjusted growth was necessary to make valid comparisons between trees growing in different time periods. Annual chronology index values greater than 1.0 relate to years that were better than average years for growth. Index values less than 1.0 were unfavorable years. To adjust each tree's annual growth based on growing conditions reflected in the selected chronology, each tree's annual BAI value was divided by the annual chronology index value. The effect of climate-driven growth is thereby removed. The result is a time series of annual time-period adjusted BAI values for each tree.

Age-band analysis of time-period adjusted growth

For each tree, time-period adjusted BAI values were averaged within 50 year cambial age-bands. For example, growth between the years 10-60, 20-70, 30-80, etc. were compiled and averaged. Age-band averages were not calculated in 50-year segments for which rings were not present in the cores. For example, a tree missing 35 inner rings would have 40-90 as its first age-band. Likewise a tree that was 153 years old would have 100-150 as its last age-band.

Comparing early growth between different age-classes of trees

Trees were placed into one of three age-classes based on their estimated ages in 2007. The three classes were 126-250, 251-350, and 351-700 years old. For each age-class of trees, the average growth of each age band was plotted in a time series. Because points along this time series contain overlapping data (e.g. years 50-100 are followed by years 60-110) the time-series is akin to a moving average. The plot revealed differences between the three age-classes during periods of early growth (age bands 60-110 through 90-140). A single two-way ANOVA with age-class and site as factors was used to test for differences in average BAI during extended period of growth from age 60-140.

Results

The relationship between tree height and age shows that height growth slows with age in all stands (Figure 2, left panel). Logarithmic curves were the best fit functions for the height-age relationship in each stand. Linear regression analysis on age-class subsets revealed the strongest linear relationships between height and age were for trees under 200 years of age at all sites. Linear regression for trees older than 245 years old showed no significant relationships between height and age, indicating that these two variables were decoupled for old trees in all stands. Figure 2 reveals differences in height growth among stands. Trees were shorter for the same ages at MB3 and taller at MB1. Heights of trees were intermediate in the two other stands. Trees at MB3 were also shorter for their diameter than trees in other stands (Figure 2, right panel).

Overall, neither recent BAI nor growth efficiency were significantly ($p < .05$) related to tree age for trees >245 years old (Figure 3) although there were significant negative relationships between growth and age at one site, MB1. In contrast, overall there were weak positive relationships between recent BAI and height ($r^2 = .172$, $p = .002$) and between growth efficiency and height ($r^2 = .079$, $p = .040$) for old trees > 245 years (Figure 4). Within stands, however these weak relationships between growth and height were not significant. When both young and old trees were plotted there was a very weak negative relationship between recent BAI and tree age ($r^2 = .033$, $p = .033$) driven by one stand (MB3) and a very weak positive relationship between recent BAI and tree height ($r^2 = .041$, $p = .018$) also driven by a single site (BR3) (Figure 5).

When the two chronologies of indices (standard vs. RCS) were compared, it was clear that the RCS-generated time series captured substantially more low-frequency variation in growing conditions (Figure 6). In particular, the RCS chronology captured positive conditions for basal area growth experienced in the late 19th century and early 20th century. This period of favorable growth was evident in the BAI growth curves of many individual trees of a variety of ages (not shown). The RCS chronology also showed that the period from 1650-1850, commonly referred to as the Little Ice Age, was relatively unfavorable for diameter growth. The standard chronology did not effectively capture the differences between these periods. Because the purpose of the chronology was to adjust early basal area growth in young and old trees that grew under different climatic conditions, the RCS chronology was considered the more accurate and conservative approach to remove bias in early growth that might be a result of time period. For this reason, the RCS generated chronology was used to adjust annual BAI for all trees to account for time-period (i.e. climate) effects on annual growth.

The RCS growth curve that was used to detrend each tree shows the overall mean annual BAI (grey line) and the variation in BAI for all trees at each cambial age (Figure 7). The mean line shows an increase in growth up to approximately age 100 and then a very slow decline out to age 350 after which sample size decreases. The dark portion of the plot shows the considerable variation in actual individual tree growth that generated this average curve. For purposes of detrending individual tree BAI series, the mean line was truncated at 350 years and a spline was fit to the portion of the curve below 350 years to generate a smooth curve. These procedures were carried out in the program ARSTAN-41d.

Figure 8 shows annual BAIs that have been divided by the annual indices in the RCS chronology and averaged in overlapping 50 year segments for three age classes of trees. After removing the effect of time period, young trees (126-250 years old) grew significantly faster when they were young (between ages 60-140) than old trees (350 – 700 years old) grew during the same period of their lives (2-way ANOVA with age-class and stand as factors, p = .023). Trees of medium ages (251-350 years) were intermediate in early growth rates. Medium age trees (251-350 years old) also maintained higher growth rates than old trees (351-700 years old) up to approximately age 200 although the difference was not significant (Figure 9). Standard deviation and ranges in early growth was highest in the medium age-class (Figure 9). There was no significant interaction between the effects of site and age-class on early growth differences between age-classes. (p=.676).

Discussion

The goals of this study were to determine whether slow growth in old ponderosa pine trees was related to tree age, tree height, or intrinsic differences in growth rates between old and young trees. A distinguishing feature of the data gathered was that age and height were not strongly correlated for trees older than 245 years (Figure 2, left panel). This allowed us study the effect of these variables separately on current growth and growth efficiency in old trees. We expected that older and taller trees would have smaller growth increments than younger, shorter trees. Consistent with theories of increasing hydraulic constraints on growth in tall trees, we expected this negative effect on growth to be stronger with height than age.

Our results suggest that the term “age-related decline” may be potentially misleading if it is applied at the individual tree level rather than the stand level. Recent basal area growth rates and growth efficiencies were not strongly related to tree age (Figure 3, Figure 5 left panel). This result was supported by the shape of the mean RCS growth curve (Figure 7) which shows a surprisingly slight and very gradual decline in mean BAI between ages 100 – 350. The literal shape of this mean line should not be interpreted as accurately representing the lifetime growth pattern of individual trees, as the actual individual BAI growth curves varied substantially around that mean. However, this result provides additional evidence that basal area growth is not strongly affected by age. Our results suggest that “age-related decline” may occur at the individual tree level very early in the life of trees, but may not be relevant on the multi-century scale studied here.

There was a very weak positive correlation between both growth rates and growth efficiencies with tree height (Figure 4, Figure 5 right panel). Superficially, this result suggests little or no effect of hydraulic constraints on tree growth. However, the height-age curves (Figure 2) indicate that maximum height varies from stand to stand and possibly at smaller scales. We interpret the weak positive correlation between height and growth as evidence that environmental conditions for trees that grow tall are more favorable in general and this produces slightly higher basal area growth rates in these trees. This result is not inconsistent with the presence of height-induced hydraulic constraints on growth, since the height at which growth slows down due to such constraints may vary from tree to tree and trees in productive sites may experience these constraints only at very tall heights. However, strong basal area growth rates in trees in the stand with the tallest trees (MB1, see Figure 2) shows that hydraulic constraints may not yet have large effects on growth in trees that are surprisingly tall (40-50 m) and quite old (200-400 yrs). These trees may be currently growing in both diameter and height. At the site with the shortest trees (MB3, see Figure 2), it is more likely that a majority of the old trees are at or very near their maximum heights. However, even under such conditions, old trees still appear to be able to maintain basal area growth rates comparable to trees at more productive sites. These results are consistent with the idea that height affects growth not via reduction in carbon sources, which would decrease carbon available for all growth processes, but rather through reduced turgor pressure at the tops of trees (a carbon sink reduction), which would affect height growth but not necessarily basal area growth. The general conclusion is that while hydraulic constraints at a certain height may act to slow or stop height growth, the height at which this occurs may be surprisingly high at productive sites, and the effect of being at maximum height (and presumably experiencing maximum hydraulic constraints) even at an unfavorable site, appears not to have strong effects on basal area growth.

If age and height only weakly affect basal area growth in old trees, there remains the hypothesis that slow growth rates are intrinsic to trees that live to great ages. The RCS chronology used to adjust early growth rates in trees showed the period 1650-1850 as relatively unfavorable for growth while the period after 1850 was substantially more favorable. Although climate reconstruction was not one of the objectives of this study, this chronology supports for the proposition that Little Ice Age temperature minima, well described for Europe, may have affected North America as well. Similarly, testing of dendrochronological methods was not a chief objective of this study, however, the application of the RCS detrending method to BAI series appeared to produce a more plausible time series of climate-related indices with greater low-frequency variation than the standard method of curve-fitting to raw ring-widths. The limitations of the standard detrending methods have been the focus of recent scrutiny (Melvin and Briffa, 2008) and our use of BAI and the RCS detrending method may be of interest in the context of these methodological issues (Biondi & Qeadan, 2008).

These interesting features of our chronology aside, for our purposes, dividing BAI growth by these indices provided confidence that our comparisons of early growth rates in old and young trees were not biased by time-period. Even after adjusting for the advantageous climate conditions experienced by young trees, we found higher early growth rates in young trees than old trees (Figures 8 and 9). These results provide the first empirical evidence from a field study to support the hypothesis that slow growing trees may be more likely to live to great ages compared to fast-growing trees of the same species growing in the same stands. In other words, our findings support the idea that "slow trees grow old". Our results provide corroboration for the findings of the meta-analysis of Black et al. (2008) with the important added controls provided by field sampling of all trees, pith and height corrections for more accurate ages and early growth rates, and adjustment of early growth to differing climate conditions experienced by old and young trees.

Our study did not directly investigate mechanisms for the relationship between slow-growth and longevity. However, a number of suggestive differences between trees in one stand (MB3) and the other three stands allow us to theorize about possible mechanisms for this relationship. Trees at MB3 were, on average, older than trees in the other stands. Nine of the ten oldest trees in our entire dataset were at MB3, and the two absolute oldest trees (596 and 695 years old) were more than 150 years older than the oldest tree from the other three sites. Trees at MB3 were also shorter for their ages (Figure 2, left panel), suggesting this stand was less productive. From a companion study on tree physiological characteristics (Keeling et al. in prep – CH 2), we found that needle carbon isotopic ratios were higher in trees at MB3 than other stands, indicating drier conditions. Finally, trees at MB3 had more girth for their given heights than trees at other sites (Figure 2, right panel) suggesting that dry conditions may affect tree allometric relationships (Callaway 1994). These three observations indicate that the drier environment at MB3 may produce trees with overall lower heights and lower height/girth ratios, factors which may provide stability and protection from heavy winds. In contrast, trees at more productive sites can grow taller (and may need to do so compete for light in a highly competitive stand) but fast growth, tall stature, and height/girth ratios closer to the buckling point (McMahon 1974) may expose trees to a greater risk of blow-down in high winds.

Higher wood density in slow-growing trees may be another factor producing longevity. Slow diameter growth produces wood with a greater quantity of high-density latewood cells, and thicker cell walls. Although we have not measured wood densities in our core samples, it is also possible that the old, slow-growing trees in our study have superior wood quality that may protect them against rot, pathogens or insects. Curiously, tree-ring studies have established a connection between climate during the period in the Little Ice Age known as the Maunder Minimum, and the high quality wood used for Stadivarius violins made in Europe from trees that grew at that time (Burkle and Grissino-Mayer, 2003). The older trees in our study also grew during this time period, and the chronology for our stands indicates that similar climate conditions to those experienced by trees in Europe may have affected our trees.

Some uncertainties and important questions were brought to light by our results. For example, our study did not investigate the extent to which the relationship between growth rates and longevity may have a genetic component. The foregoing discussion suggests that environmental conditions such as low productivity sites or unfavorable climate conditions, rather than genetics, are more likely to be the main factors in producing slow-growing, long-lived trees. However, inspection of BAI growth curves for individual trees showed a large variation in lifetime growth patterns even for similar aged trees growing in the same stands. For example, one 441 year old tree at MB3 grew fast during the period 1600 – 1750 and then slow up to the present era, a pattern directly opposite our general finding that on average, old trees grew slowly when they were young. In addition, we saw slightly higher variance and greater ranges in early growth rates in the medium age class (ages 201-350) which shows that some fast growing trees may reach relatively old ages in some cases (Figure 9). Such anomalous growth patterns point to a possible interplay between genetics and environmental factors that can produce great variation and complexity in the relationship between lifetime growth patterns and longevity. The causal relationship between slow growth and longevity is therefore likely to be general and probabilistic, not specific or narrowly deterministic. The hypothesis that slow trees grow old is difficult to test directly because fast-growing trees that may have died young in the past are not available for study today, and determining the future conditions of fast versus slow growing trees growing today would require century-long observations. Despite these limitations and uncertainties, our results provide strong indirect evidence for relationship between slow-growth and longevity in ponderosa pine trees.

A premise of this study was that old trees grow slower than young trees. The central findings of this study are that basal area growth in old ponderosa pine trees is not strongly affected by age *per se* or tree height, but alternatively, slow growth appears to be an intrinsic feature of trees that reach old age. Contrary to our premise, however, many of the old trees we measured were not growing significantly slower in basal area than many of the younger trees in the same stands (Figure 5, left panel). Furthermore, the very slight higher average growth rates among younger trees, especially at one site (MB3), do not necessarily imply age-related growth decline, and are consistent with the alternative idea that both fast- and slow-growing young trees exist in these populations but slow-growing trees have a higher probability of reaching old age. From the relationships between recent growth and age shown in Figure 5, and the RCS growth curve that plots the average biological growth curve when all individual growth curves are averaged (Figure 7), the conclusion we draw is that age-related decline in basal area growth is negligible in these trees and that many old trees can add basal area at rates comparable to younger trees in the same stands. In the higher productivity stands, old trees may also be continuing to grow in height as well as basal area.

From these results we conclude that old ponderosa pine trees have the potential to accumulate stemwood for centuries, often at rates comparable to younger trees. Furthermore, slow growth could be a causative process in determining longevity, rather than a necessary symptom of decline and increased mortality risk. These findings are extremely important for consideration of old trees and old-growth stands as carbon sinks and reservoirs of carbon. The growth potential of old trees and the link between growth rates and longevity adds an important tree-level perspective to recent research at the stand or ecosystem scale that highlights the carbon sink potential of old forests (Carey et al. 2001, Phillips et al. 2008, Luyssaert et al. 2008) and calls into question the previous idea that old forests are insignificant as carbon sinks (Jarvis 1989, Melillo et al. 1996). Our results challenge the common assumption that young trees will take up carbon faster than old trees, and also raises the important question of whether fast-growing trees might be more prone to premature mortality, making them less reliable for long-term carbon storage. In contrast, old trees may have the ability to take up carbon at rates comparable to young trees, and slow-growing trees may possess the growth characteristics, stature, or wood quality to survive for longer time periods. This means that old trees are both a valuable sink for carbon, as well as an important and stable pool of stored carbon.

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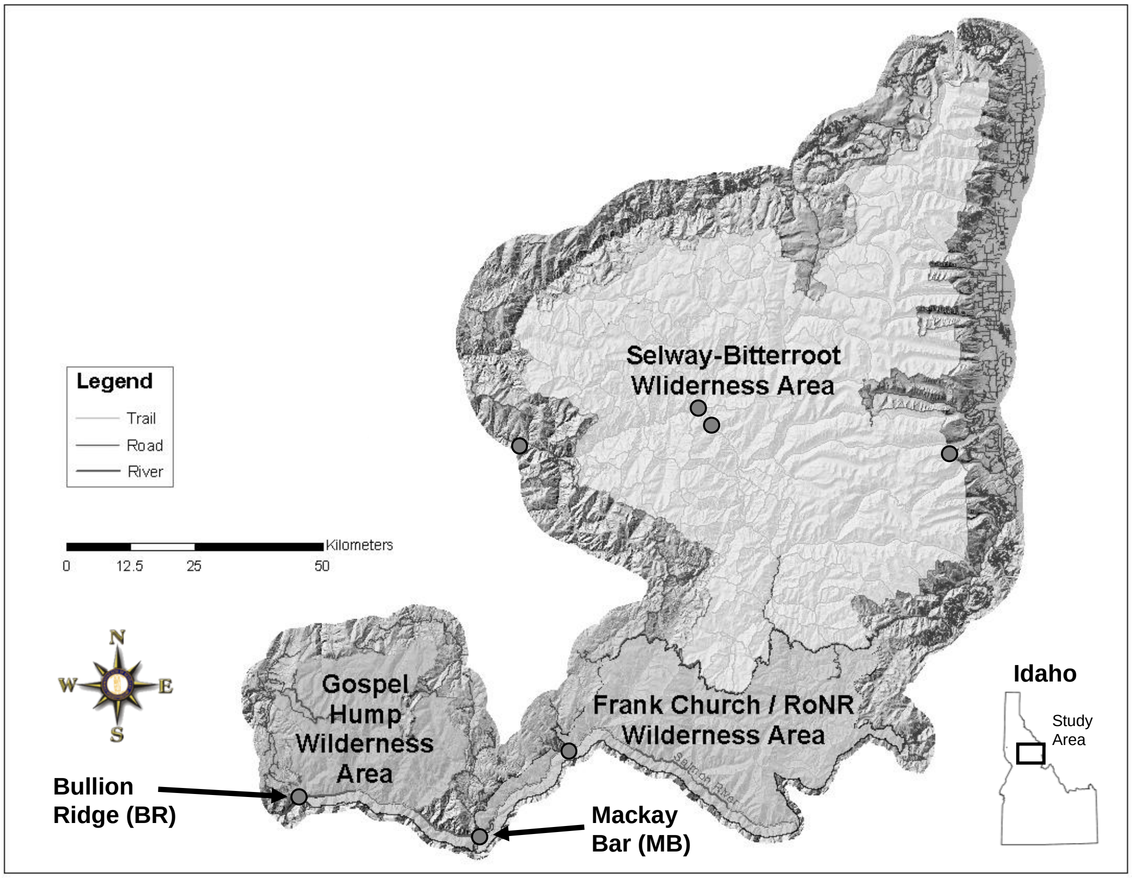


Figure 1. Study area and site locations (RoNR = River of No Return).

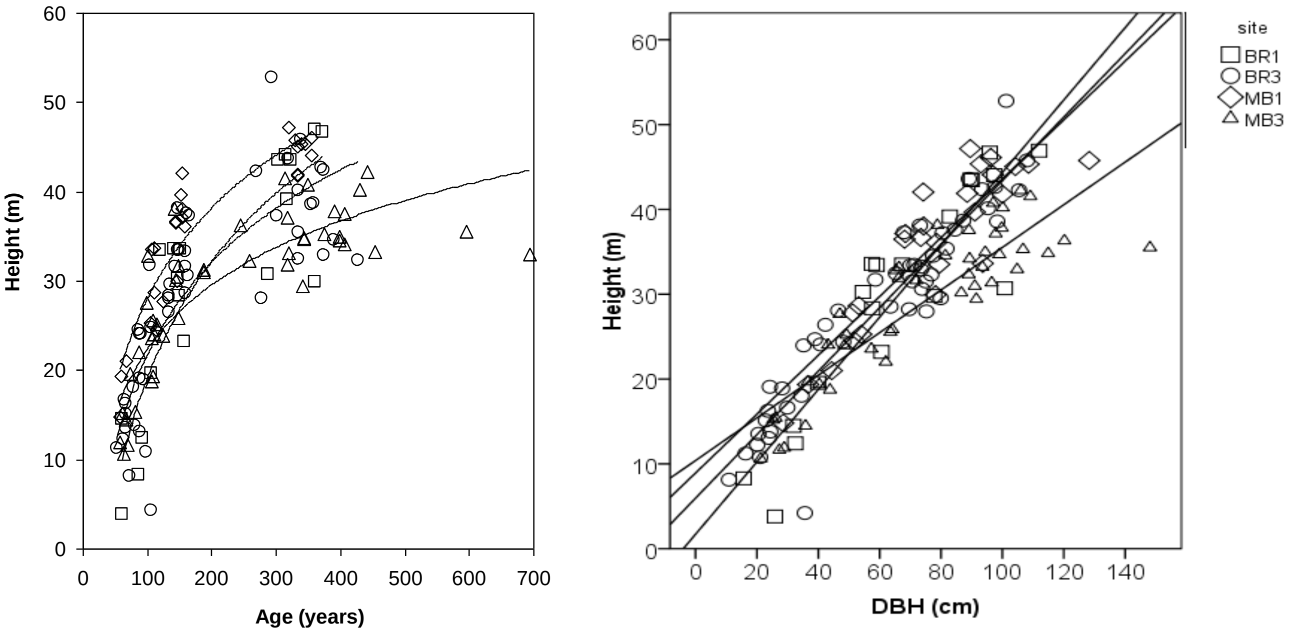


Figure 2. Tree heights plotted against age (left panel) and DBH (right panel) in four stands. Logarithmic functions for height vs. age: BR1: $r^2 = .771$, $p = .000$, BR3: $r^2 = .686$, $p = .000$, MB1: $r^2 = .853$, $p = .000$, MB3: $r^2 = .728$, $p = .000$. Linear functions for height vs. DBH: BR1: $r^2 = .832$, $p = .000$, BR3: $r^2 = .884$, $p = .000$, MB1: $r^2 = .897$, $p = .000$, MB3: $r^2 = .777$, $p = .000$

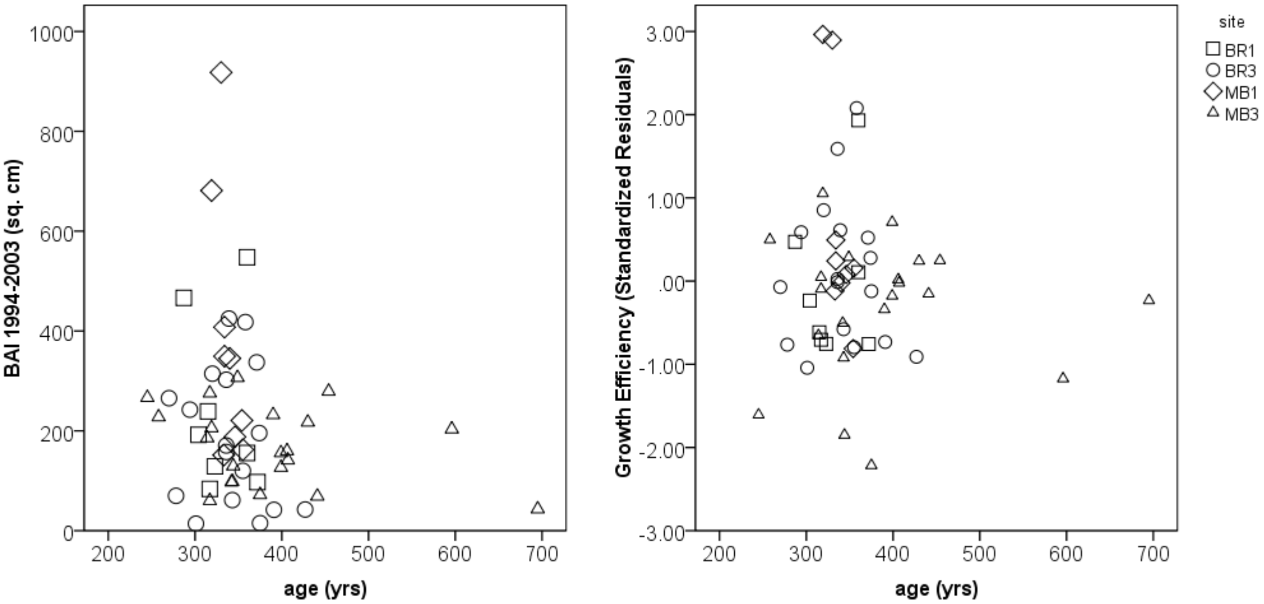


Figure 3. Recent basal area increment (BAI) for years 1994-2003 (left panel) and growth efficiency (residuals from recent BAI vs. sapwood area) (right panel) plotted against age for trees >245 years old in four stands. Linear regression for recent BAI vs. age: overall: $r^2 = .048$, p =.148 BR1: $r^2 = .018$, p = .753, BR3: $r^2 = .029$, p = .516, MB1: $r^2 = .472$, p = .042, MB3: $r^2 = .092$, p = .182. Linear regression for growth efficiency vs. age: overall: $r^2 = .011$, p = .451, BR1: $r^2 = .038$, p = .642, BR3: $r^2 = .003$, p = .835, MB1: $r^2 = .558$, p = .021, MB3: $r^2 = .000$, p = .972.

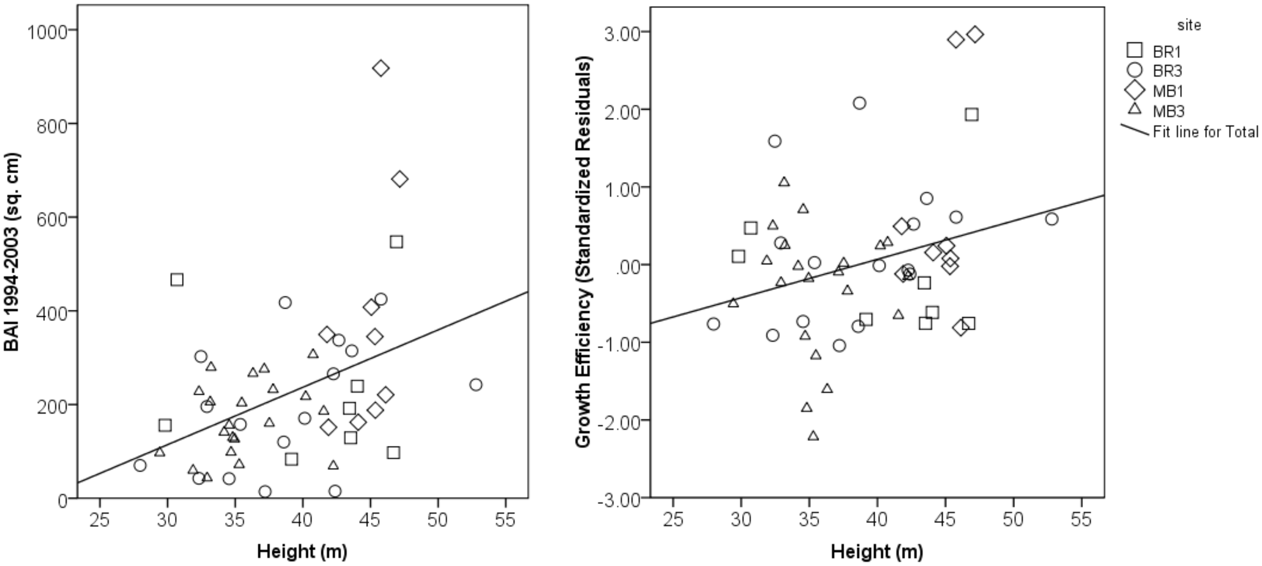


Figure 4. Recent basal area increment (BAI) for years 1994-2003 (left panel) and growth efficiency (residuals from recent BAI vs. sapwood area) (right panel) plotted against height for trees >245 years old in four stands. Linear regression for recent BAI vs. height: overall: $r^2 = .172$, p = .002, BR1: $r^2 = .004$, p = .888, BR3: $r^2 = .192$, p = .089, MB1: $r^2 = .224$, p = .198, MB3: $r^2 = .086$, p = .198. Linear regression for growth efficiency vs. height: overall: $r^2 = .079$, p = .040, BR1: $r^2 = .003$, p = .906, BR3: $r^2 = .091$, p = .256, MB1: $r^2 = .166$, p = .207, MB3: $r^2 = .001$, p = .872.

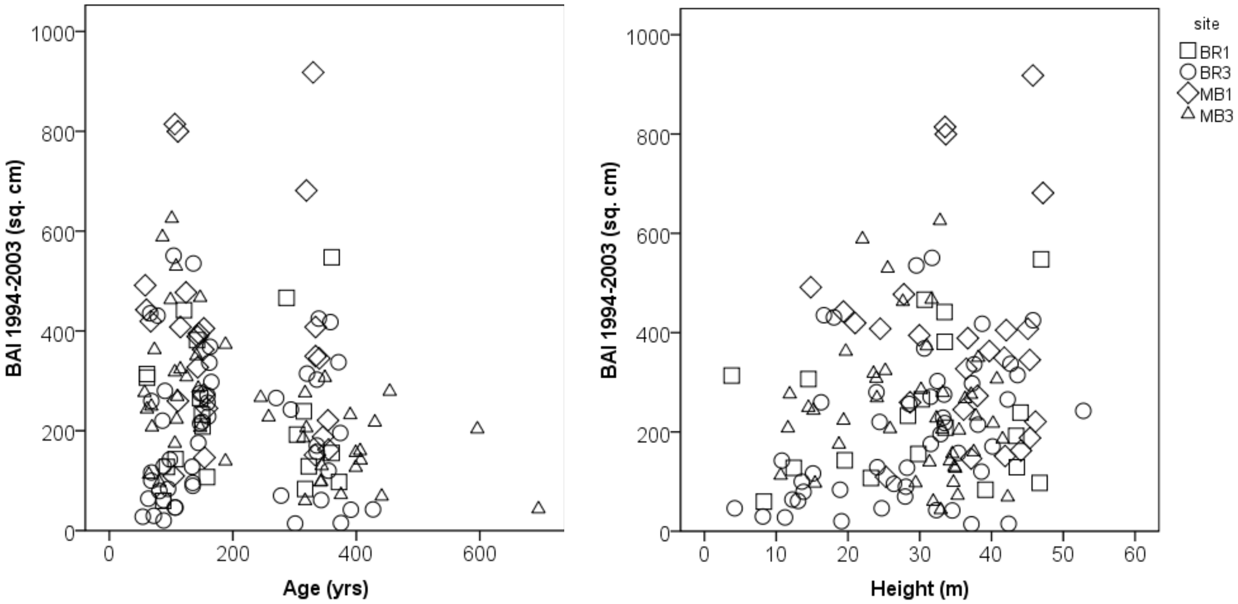
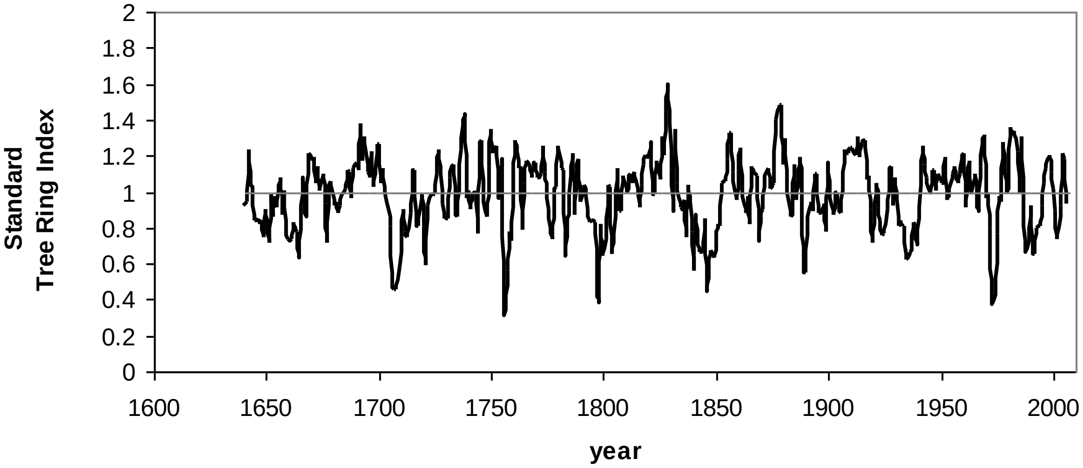


Figure 5. Recent basal area increment (BAI) for years 1994-2003 plotted against age (left panel) and against height (right panel) for all trees in four stands. Linear regression for recent BAI vs. age: overall: $r^2 = .033$, $p = .033$, BR1: $r^2 = .000$, $p = .979$, BR3: $r^2 = .000$, $p = .949$, MB1: $r^2 = .016$, $p = .535$, MB3: $r^2 = .261$, $p = .000$. Linear regression for recent BAI vs. height: overall: $r^2 = .014$, $p = .018$, BR1: $r^2 = .026$, $p = .512$, BR3: $r^2 = .128$, $p = .012$, MB1: $r^2 = .002$, $p = .845$, MB3: $r^2 = .016$, $p = .417$.



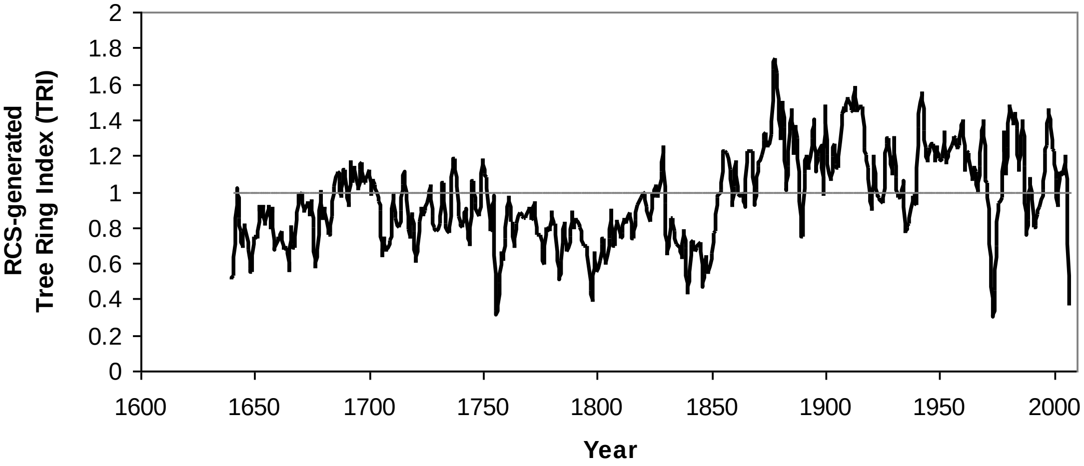


Figure 6. Chronologies of indices of favorable and unfavorable growing conditions generated using the standard curve-fitting detrending method applied to raw ring widths (top panel) and using the Regional Curve Standardization (RCS) detrending method applied to basal area increments (bottom panel). Index values >1.0 indicate relatively favorable growth conditions, index values <1.0 indicate relatively unfavorable growth conditions.

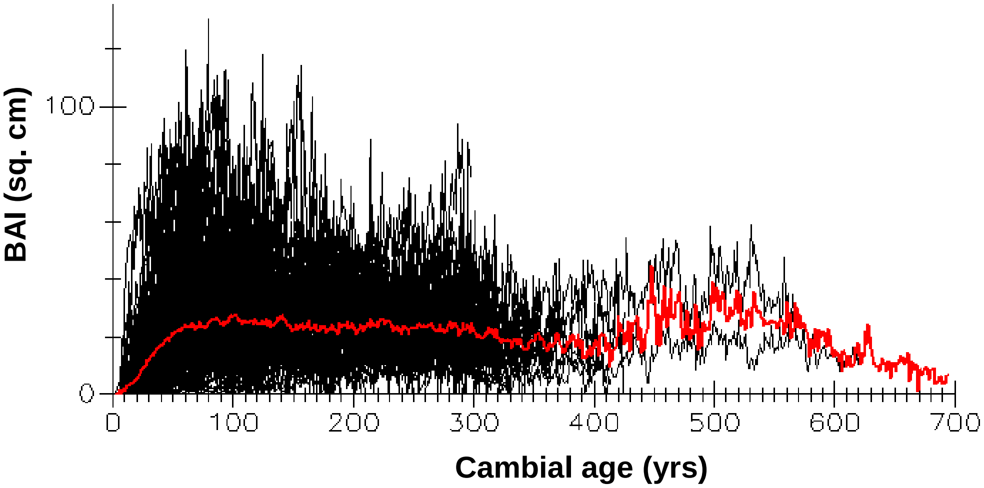


Figure 7. Annual BAIs by cambial age for all trees (black) and overall mean (red) generated by Regional Curve Standardization (RCS) method using computer program ARSTAN. RCS curve used to detrend individual tree growth curves was based on a spline fit to the mean line truncated at age 350.

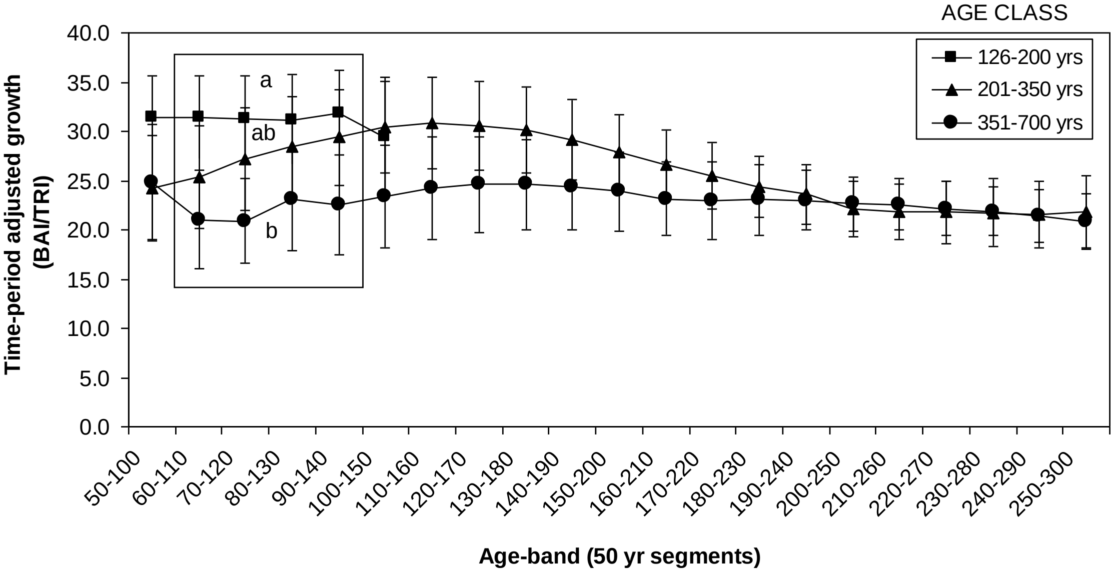


Figure 8. Mean time-period adjusted basal area growth (BAI/RCS chronology indices) in overlapping 50 year age-bands for three age-classes of ponderosa pine trees from all stands combined. Error bars are 95% confidence intervals for each mean. Differences in mean time period adjusted growth between ages 60-140 were tested using a 2-ANOVA with age-class and stand as factors. Significant differences between age-classes (p <.05) are depicted with different letters.

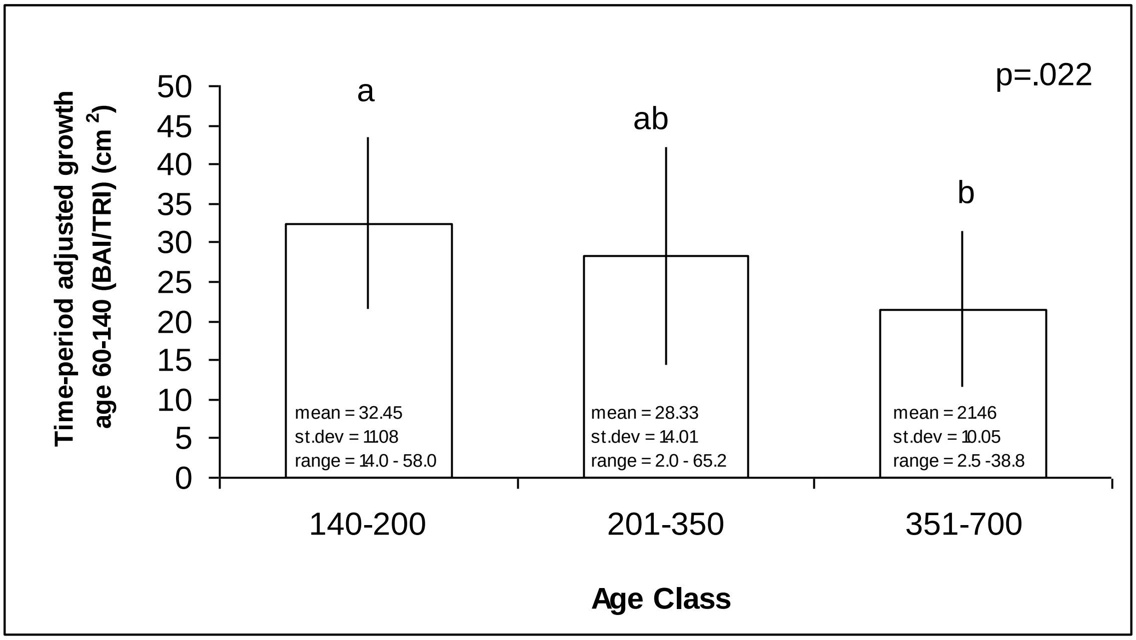


Figure 9. Mean time-period adjusted basal area growth during ages 60-140 (the boxed region in Figure 8) for three age-classes of ponderosa pine trees from all stands combined. Error bars are standard deviations. Differences in mean time period adjusted growth between ages 60-140 were tested using a 2-ANOVA with age-class and stand as factors. Significant differences in the means between age-classes (p <.05) are depicted with different letters.