Fire Exclusion Effects on Riparian Forest Dynamics in Southwestern Oregon

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Abstract

Euro-American settlement and organized fire suppression have been associated with structural and compositional changes in many upland forests of the western United States, but little is known about the impacts on riparian forests, portions of the landscape protected for habitat and water quality. In this study, we used dendro-ecological methods to characterize the pre-settlement disturbance and tree recruitment processes of riparian forests in the Rogue River basin of southwestern Oregon and to identify changes to the forest structure and composition post-settlement. Our results suggest riparian forests in our study area developed with frequent disturbance by fire and that Euro-American land management shifted these forests onto a new successional trajectory. Our findings indicate the current hands-off management regime for riparian forests under the Northwest Forest Plan will continue along this altered trajectory and have ecologically undesirable consequences. We suggest that the restoration of pre-settlement forest dynamics in fire-prone forests of southwestern Oregon will be most effective where it includes density reductions in overstory trees and prescribed fire in both upland and riparian forests.

Keywords: Fire ecology; Douglas-fir; Riparian; Stand structure; Fire suppression

1. INTRODUCTION

Euro-American settlement and organized fire suppression have effectively excluded fire from many portions of the western United States, and this exclusion has been associated with structural and compositional changes in forests that historically burned under low- or mixed-severity fire regimes (Agee, 1993). While the impacts on upland forests have been well documented (Agee, 1993; Agee 1998; Sensenig 2002), little is known about the impacts on riparian forests, portions of the landscape protected for habitat and water quality. Under the 1994 Northwest Forest Plan (NWFP), a riparian reserve system was created to protect riparian ecosystems from the impacts of timber harvest and other anthropogenic disturbance (FEMAT, 1993; USDA and USDI, 1994; Hann *et al.*, 1997; Sedell *et al.*, 1997; USDI *et al.*, 1999). The hands-off management approach for riparian forests under the NWFP has led some to question how separate management practices for riparian reserves might affect natural disturbance processes (Everett *et al.*, 2003). Previous studies of fire disturbance in Pacific Northwest riparian forests have focused on fire history reconstruction (Skinner, 1997; Everett *et al.*, 2003; Olson and Agee, 2005), drivers of riparian fire severity (Halofsky and Hibbs, 2008), and post-fire vegetation response (Halofsky and Hibbs, 2009). The effects of fire exclusion on riparian forest structure and composition remain largely unknown.

Fires occurred frequently in southwestern Oregon, a part of the Klamath-Siskiyou bioregion (Taylor and Skinner, 1998), making it an excellent area in which to study the role of fire in riparian forest systems and the changes in structure and composition that may have occurred with fire exclusion. The Mediterranean climate of southwestern Oregon is characterized by cool and moist conditions for much of the year, with a summer drought and fire season typically lasting over three months. Frequent fires have shaped upland forests throughout southwestern Oregon and fire exclusion effects have been documented in these uplands

(Sensenig, 2002; Taylor and Skinner, 2003). Fires have likely been important in shaping and maintaining riparian forests as well.

In this study, we used temporal and spatial recruitment patterns, fire scar evidence, and the autecological characteristics of co-occurring species to make inferences about what type of fire regime historically shaped riparian areas within low- and mid-elevation forests of southwestern Oregon. The fire regime of upland mixed conifer forests of southwestern Oregon and the greater Klamath-Siskiyou bioregion has been described as mixed-severity, in which topographic complexity is a major driver of the spatial patterns of fire and its effects on vegetation (Taylor and Skinner, 2003). We expected the fire regime and stand structures in riparian areas of our study region to be similar to that of the adjacent uplands; however, we considered the riparian microclimate could have moderated fire effects (Halofsky and Hibbs, 2008) and resulted in denser forests than were present upslope with a greater representation of shade-tolerant and fire-sensitive species. The objectives of this study were to (1) characterize the pre-Euro-American settlement fire regime and stand characteristics for riparian forests in the region and to determine the changes in (2) overall tree density, (3) species composition, (4) age structure, and (5) temporal recruitment patterns that have occurred since Euro-American settlement. We hypothesized that riparian forests in southwestern Oregon developed with frequent disturbance by low- and mixed-severity fire and that Euro-American settlement and fire suppression shifted these forests into a new successional trajectory with (1) uncharacteristically high tree densities, (2) increased recruitment of fire-sensitive species and (3) temporal patterns of tree recruitment unlike those of the past.

2. METHODS

2.1. Site Selection

We investigated structural and compositional changes in riparian forests of two fire-prone regions of southwestern Oregon: the upper Applegate Valley and the Butte Falls Resource Area of the USDI Bureau of Land Management (BLM). Both regions are part of the greater Rogue River basin and are managed by the BLM and USDA Forest Service (USFS). We used BLM and USFS data sources to identify all unmanaged, first and second order headwater stream reaches (hereinafter referred to as 'sites') in our study area. We then inspected potential sites to select those with no evidence of tree harvest or hydraulic mining. We chose among the acceptable sites a group that represented the range of stream sizes and forest vegetation types in our study area. The selected sites ranged from 500 to 1000 m in elevation and are representative of the low- to mid-elevation forests held by the BLM and USFS in southwestern Oregon. Riparian forests sampled in both study regions were dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and bigleaf maple (*Acer macrophyllum* Pursh), with adjacent upland forests in two vegetation zones: the more mesic Mixed Conifer (*Pinus-Pseudotsuga-Calocedrus-Abies*) and the more xeric Interior Valley (*Pinus-Quercus-Pseudotsuga*) (Franklin and Dyrness, 1973). Each of these vegetation zones represents a geographic area with a similar climate, similar species composition, and similar historic disturbance regime. Vegetation zones were the basis for our sampling design and are the primary units for analysis. Fifteen sites were sampled during the summer of 2007 in the upper Applegate Valley region, with eight sites in the Mixed Conifer vegetation zone, and seven in the Interior Valley zone (Fig. 1). In the summer of 2008, thirteen sites were sampled in the Butte Falls Resource Area of the Bureau of Land Management, with seven sites in the Mixed Conifer zone and six in the Interior Valley zone.

2.2. Site Descriptions

The Mixed Conifer vegetation zone is typical of mid-elevation forests in the southern Oregon Cascade Range and eastern Siskiyou Mountains and is the northern extent of the Sierran montane or mixed-conifer forests (Franklin and Dyrness, 1973). The Mixed Conifer zone is bounded by the Interior Valley and *Abies concolor* types at its lower and upper limits, respectively. Annual precipitation varies from about 900 to 1,300 mm, little of which occurs in the summer months. The major overstory tree species in Mixed Conifer riparian forests include: Douglas-fir, white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), incense cedar (*Calocedrus decurrens* (Torr.) Florin), white alder (*Alnus rhombifolia* Nutt.) and to a lesser extent, ponderosa pine (*Pinus ponderosa* subsp. *benthamiana* Hartw.), and sugar pine (*Pinus lambertiana* Dougl.). Mid-story and understory tree species include bigleaf maple, canyon live oak (*Quercus chrysolepis* Liebm.), Pacific madrone (*Arbutus menziesii* Pursh.), vine maple (*Acer circinatum* Pursh.), and Pacific yew (*Taxus brevifolia* Nutt.). Understory conditions in Mixed Conifer sites typically include a variety of shrub species, deep accumulations of organic matter on the forest floor, and abundant coarse woody debris. Stream-flows in this vegetation zone are typically perennial.

The Interior Valley vegetation zone encompasses the low-elevation valley bottoms and lowlands of the Rogue River valley and its tributaries, such as the Applegate Valley in the eastern Siskiyou Mountains. This vegetation zone is the warmest and driest west of the Cascade Mountains (Franklin and Dyrness, 1973). As a result of its location in the rain shadow of the Coast and Siskiyou Mountain ranges to the west, this region receives approximately 500 to 800 mm of precipitation per year (Franklin and Dyrness, 1973). Vegetation in the Interior Valley zone consists of a mosaic of grasslands, oak savannas and woodlands, coniferous forests, and sclerophyllous shrub communities (chaparral). Within riparian forests, the major tree species include: Douglas-fir, incense cedar, ponderosa pine, Oregon white oak (*Quercus garryana* Dougl. ex Hook.), California black oak (*Quercus kelloggii* Newb.), Pacific madrone, and bigleaf maple. Understory conditions in Interior Valley sites typically include grasses, many shrub species, and relatively low accumulations of organic matter or coarse woody debris. Stream-flow in this vegetation zone is typically intermittent or ephemeral.

2.3. Sampling Strategy

Our sampling was stratified to represent the two vegetation zones in our study area, which were the ultimate unit of interest in our analysis. Within each vegetation zone, we sampled the tree populations at different sites (stream reaches). At each site, we used a nested plot design with sampling intensity based on the type and size of trees. 3 to 5 higher-intensity small plots (10x20 m each) were nested within a single lower-intensity large plot, 300-500 m long and 10 m wide, at each site. Large plots were installed on one side, parallel to the stream and extended 10 m into the forest, where we recorded the species and DBH of each large tree (conifers >50 cm dbh and hardwoods >25 cm dbh), its location in the long plot (x,y), and collected one increment core (to pith) approximately 40 cm from the ground on the uphill side. We also recorded the species and the DBH of standing dead trees and downed logs that met the size criteria.

Conifer species < 50 cm DBH and hardwood species < 25 cm DBH occurred at much higher densities than the larger trees, so we did not need to sample as great an area to achieve a representative sample. The smaller nested plots were spaced at 100 m intervals within the large plot. For all trees within each nested plot, we measured the DBH and took an increment core approximately 40 cm above the ground. When saplings (> 1.37 m tall) were too small to take an increment core, we cut a basal disc. We also recorded the species and the DBH for all standing dead trees and downed logs.

We searched for physical evidence of past fires (fire scars) to improve our understanding of past disturbance in our study area. In this search, we were limited to the opportunistic cutting of cross-sections from the base of recently downed trees or recently cut stumps in and near our study sites (within two tree-heights of the stream).

2.4. <u>Tree Ring Data</u>

All increment cores and fire-scarred cross sections were prepared by sanding with progressively finer grits up to 400 or 600-grit. Ages for increment cores were determined by hand-counting annual growth rings under a binocular microscope with up to 40x magnification. When increment cores did not intercept the pith (biological center of the tree), the number of years from the innermost ring to the pith was estimated using pith locators (transparencies with concentric circles for different ring curvatures). We measured ring-widths for a sub-sample (18%) of all cores using a computer-compatible incremental measuring machine and the software program. COFECHA to aid in the cross-dating of tree ring series, to check for missing annual rings, and to create a ring width index that was used in cross-dating the fire-scarred cross sections (Holmes, 1983; Grissino-Mayer, 2002).

As a result of heartwood decomposition, we were unable to obtain increment cores for some trees (mostly large diameter) and therefore unable to determine their age. To approximate ages for the most prevalent and commonly affected species, Douglas-fir, white fir, and incense cedar, we used our sample of trees with known ages to develop species-specific linear regression models to estimate age as a function of DBH. Trees without increment cores comprised 18% of the combined Douglas-fir and white fir on Mixed Conifer sites and 18% of the combined Douglas-fir and incense cedar on Interior Valley sites. R^2 values ranged from 0.47 to 0.66. The inclusion of trees with estimated ages affected the interpretation of our data, so we excluded them from our analysis.

2.5. Temporal recruitment and climate relationships

To examine temporal recruitment patterns in riparian forest stands, we graphed relative frequency age distributions of overstory conifer species for each site (conifer species that are capable of reaching the upper canopy). We judged stand conditions within each vegetation zone to be similar enough to average the data from all but 3 of our sites (two with scattered, old stumps and one with few live Douglas-fir) to graph the average age distribution for trees in each vegetation zone. We excluded these three outlier sites from all analyses except for our spatial analysis of tree recruitment.

We examined the relationships between conifer recruitment and climate using three common indices for the Pacific Northwest climate: Palmer Drought Severity Index (PDSI), Pacific Decadal Oscillation (PDO), and El Nino-Southern Oscillation (ENSO) (Cook *et al.*, 2004; MacDonald and Case, 2005; Braganza *et al.*, 2009). None of these relationships were sufficiently explanatory to be included in our analysis.

2.6. Douglas-fir diameter growth

To make inferences about relative differences in stand density over time, we examined the relationship between the date of origin and the average basal area increment (BAI/tree age) of all Douglas-fir (the dominant species) with complete increment cores in each vegetation zone

(82% of each vegetation zone). As we did not measure most tree ring samples, we calculated the average BAI for each tree by dividing its basal area ($\pi \times ½ \text{DBH}^2$) by its age. Because the average BAI was a relatively coarse measure of stand conditions at the time of germination, we also measured and averaged the first twenty cambial years of a subset of Douglas-fir increment cores that either intercepted the pith or came within 10 years of it. When the pith was not intercepted, we estimated the growth rate for the innermost annual rings using a geometric model. With this model, we calculated the distance to pith, the number of rings missing, and a ring-width correction (Duncan, 1989). We applied a Lowess scatter plot smoothing (locally weighted regression) to the data using S-PLUS (smoothing factor: r =0.15) to demonstrate the temporal trends in early growth rates. For this analysis, we included 74 samples (tree ring series) for Mixed Conifer sites and 123 for Interior Valley sites.

2.7. Douglas-fir spatial recruitment patterns

To better understand historic stand development and disturbance processes at our sites, we analyzed the spatial distribution of tree ages for Douglas-fir ≥ 50cm DBH, for which we have x and y coordinates (Ettema and Wardle, 2002). We chose Douglas-fir for this analysis because it was the most abundant tree in both vegetation zones and its recruitment is an indicator of past disturbance. We used the spatial statistics module in the S-PLUS statistical software package to calculate autocorrelation (spatial dependence) with the robust semivariance statistic $\gamma(h)$ for a range of distance intervals h:

$$\gamma(h) = \frac{\frac{1}{2}\left[\frac{1}{N(h)}\sum\left|z(s_i) - z(s_i + h)\right|^{1/2}\right]^4}{\left(.457 + \frac{.494}{N(h)}\right)}$$

where N(h) is the number of pairs of observations separated by distance h, $z(s_i)$ is the value of the variable of interest at location s_i, and $z(s_i+h)$ is its value at a location at distance h from s_i (MathSoft, 2000).

We used Douglas-fir data from the large plots (one large plot per site) to calculate semivariance for each of the two vegetation types. We included 193 trees from Mixed Conifer sites and 210 from Interior Valley sites. All trees lacking a complete increment core were excluded from this analysis, making semivariance calculations conservative. Individual sites did not contain enough trees to calculate semivariance for all of the distance intervals of interest, so we pooled all of the trees within each of the two vegetation zones. To prevent age comparisons between sites. , the x-coordinates for trees at each site were separated by 1000 m and the maximum distance for comparison was set to 250 m. Empirical variograms were constructed with the data from each vegetation zone, which describe how tree age is correlated with physical distance. When constructing empirical variograms, the user can control the degree of smoothing by adjusting the size of the distance bins (‘lags’), the number of points per bin, and the distance of reliability (maximum distance for comparison) (MathSoft, 2000). After exploratory analyses, we set the lags to 8 m, the lag tolerance to 4 m, and the maximum distance to 176 m and 250 m for Mixed Conifer and Interior Valley sites, respectively. Testing for geometric anisotropy was not applicable due to the dimensions of our large plots, 10x500 m.

3. RESULTS

3.1. Conifer age distributions

3.1.1. *Mixed Conifer Zone*

Looking back across four centuries of tree establishment dates, two distinct patterns of tree recruitment in our study area were apparent, 1) a pulsed pattern of peaks and valleys of recruitment, and 2) starting around 1900, continuous recruitment with a corresponding shift from Douglas-fir to white fir. Prior to 1850, the age distribution of live Douglas-fir and white fir across all sites in the Mixed Conifer zone, followed a pulsed pattern of recruitment (Fig. 2). Recruitment peaks occurred around 1800 and again around 1850. Another cohort dated to the mid to late 1700's (1740-1770), though few trees from that period were alive at the time of sampling. The oldest tree of our sample dated to 1547. After the recruitment pulse of 1850, our data show abundant conifer recruitment, comprising the majority (84%) of live trees sampled. Many Mixed Conifer sites showed a dramatic increase in recruitment of the more shade-tolerant and fire-sensitive white fir after 1900. White fir comprised 51% of live trees recruited after 1900, but only 18% of live trees recruited before 1900. We did not determine the age of conifer seedlings (< 1.37 m tall), but their cover averaged less than one percent for all species sampled.

3.1.2. *Interior Valley Zone*

The majority (79%) of live Douglas-fir and incense cedar in the Interior Valley zone recruited after 1850, while the oldest tree dated to 1586. The density of large-diameter conifer snags and logs was relatively low (~21/ha) compared with the Mixed Conifer zone (~39/ha) (Table 2). At 11 of the 13 Interior Valley sites, two periods of recruitment were apparent, with broad peaks dating to 1870 and 1950 (Fig. 2). Two of the 13 Interior Valley sites showed only a single pulse of recruitment, which occurred in the late 19^{th} century. After the recruitment pulse of the mid-20^{th} century, tree recruitment declined rapidly. Conifer seedling cover averaged less than one percent for all species sampled.

3.2. Douglas-fir growth rates

3.2.1. *Mixed Conifer Zone*

Initial growth rates (first 20 years) and average basal area growth rates (BAI/tree age) of Douglas-fir varied widely throughout our 450 year record (Figs. 2, 3). Slow-growing trees were present in all recruitment cohorts and many have persisted for over 200 years. However, few trees established since 1920 showed high growth rates. Lowess scatter plot smoothing of initial Douglas-fir growth rates showed a trend of faster initial growth for trees that recruited early in recruitment pulses (Fig. 2).

3.2.2. *Interior Valley Zone*

As seen in Mixed Conifer sites, initial growth and average basal area growth rates of Douglas-fir in Interior Valley sites were also highly variable since 1800 (Figs. 2,3). Since the recruitment of the mid-20^{th} century cohort, there have been no fast-growing trees. Lowess smoothing of initial Douglas-fir growth rates in the Interior Valley zone corresponded with the pulsed pattern of tree recruitment (Fig. 2). Trees germinating in the first half of a recruitment pulse experienced higher growth rates than those in the second half of the pulse. Initial growth rates achieved in the 1850 and 1950 pulses on Interior Valley sites were equally high, with a dramatic reduction in growth rates following the 1950 pulse.

3.3. Pre-settlement spatial recruitment patterns

3.3.1 *Mixed Conifer Zone*

Spatial analyses of Douglas-fir recruitment patterns demonstrated different patterns in pre-settlement stand development between vegetation zones (Fig. 4). At Mixed Conifer sites, Douglas-fir recruited over long periods of time in a mosaic of similar-aged patches. Tree age was highly autocorrelated at near distances, which decreased rapidly to distances of approximately 30 m. Beyond 30 m, tree ages were spatially independent of one another. Semivariance ($\gamma(h)$) on Mixed Conifer sites followed a negative exponential function with a range of 27.99, a sill of 3510.54, and a nugget of 0 (Fig. 4). At distances less than 30 m, where tree age was spatially autocorrelated, the median difference in age between pairs of trees ranged from 9.5 yrs at distances less than 5 m, to 37 yrs at distances between 20 and 25 m (Fig. 5).

3.3.2. *Interior Valley Zone*

Most Douglas-fir trees on Interior Valley sites recruited over a short period of time relative to Mixed Conifer sites, resulting in even-aged stands with scattered, older individuals. Tree ages at Interior Valley sites demonstrated a much lower degree of spatially structured autocorrelation than at Mixed Conifer sites. While $\gamma(h)$ values in Mixed Conifer sites ranged from 0 to over 4000, in Interior Valley sites the range was 200 to ~800 (excluding outliers), indicating a smaller range of variability in tree age at all distances (Fig. 4). Semivariance ($\gamma(h)$)

follows a Gaussian function with a range of 31.12, a sill of 493.16, and a nugget of 186.71. The median difference in age between pairs of trees ranged from 9 years at distances less than 5 m to 13 years at distances between 20 and 25 m (Fig. 5).

3.4. Fire scar record

We successfully cross-dated 26 fire scars from 13 recently downed logs or stumps, located at eight different riparian sites (five Mixed Conifer, three Interior Valley) across our sampling regions (Fig. 2). Of the 13 samples, 10 were from Douglas-fir, 2 from incense cedar and 1 from ponderosa pine. Only 3 of the 13 cross-sections displayed outward physical evidence of fire scarring, leading us to believe that there were many more fire-scarred trees at our sample sites than our sampling was able to capture. The 26 cross-dated fire scars span from 1748 to 1918, with the highest number (10) occurring in the early settlement period (1850-1900).

3.5. Shade-intolerant hardwoods

The most abundant shade-intolerant hardwood species was Pacific madrone, present at 85% of Interior Valley sites at an average density of 50 live and 15 dead stems per hectare and at 33% of Mixed Conifer sites at an average density of 40 live and 23 dead stems per hectare (Tables 1, 2). California black oak was present at 62% of Interior Valley sites at an average density of 59 live and 17 dead stems per hectare. Oregon white oak was the least common shade-intolerant hardwood species in riparian forests, present at only 23% of Interior Valley sites, where it existed primarily as snags overtopped by the young cohort of Douglas-fir (~20 live/ha and ~134 dead/ha).

4. DISCUSSION

4.1. *Mixed Conifer Zone*

Pre-settlement forest structure and composition along first and second order streams in the Mixed Conifer zone resembled upland forests in the region (Agee, 1991; Wills and Stuart, 1994; Sensenig, 2002). A mixed-severity fire regime maintained complex, multi-aged stands with large, old (200+ years) fire-resistant trees (predominantly Douglas-fir), a variety of hardwoods, and patches of even-aged trees within stands that were thinned by reoccurring fires and competition. Unburned patches within the mixed-severity matrix provided refugia for fire-sensitive species such as Pacific yew and white fir.

Fire exclusion in the 20th century triggered a shift in the stand dynamics of riparian forests in the Mixed Conifer vegetation zone from a model characterized by frequent fire disturbance and shade-intolerant tree recruitment in large canopy gaps to one characterized by the replacement of overstory trees by shade-tolerant species through individual tree-fall gaps. Fire-sensitive and shade-tolerant white fir is represented in far greater numbers than it was prior to 1900 and few Douglas-fir trees that recruited after 1900 are on the trajectory to canopy dominance.

Tree recruitment during the pre-settlement period in the Mixed Conifer zone was episodic, with broad pulses occurring approximately every 50 to 60 years. Douglas-fir's moderate shade-intolerance (Minore, 1979) and its mineral soil requirement for establishment (Stewart, 1986) limited its recruitment in existing stands to large canopy gaps that were periodically opened within the mixed-severity fire mosaic (Agee, 1993; Wills and Stuart, 1994; Zenner, 2005). Douglas-fir can recruit without fire, but this phenomenon typically occurs in drier forest types and grasslands where it receives sufficient sunlight and mineral soil is exposed

(Thilenius, 1968; Tveten and Fonda, 1999; Heyerdahl *et al.*, 2006). Our record of fire scars, though not exhaustive, also indicates fires were relatively common throughout the region in the pre-settlement period (Fig. 2). While Douglas-fir recruitment in the Mixed Conifer zone was limited to large canopy gaps, they were apparently created with sufficient frequency throughout a stand for Douglas-fir to maintain canopy dominance (Table 1).

Our analysis of spatial autocorrelation in pre-settlement tree ages provides evidence of these patches of post-fire Douglas-fir recruitment (Figs. 4, 5). Douglas-fir trees located close to each other are more likely to be similar in age that those farther apart, up to a distance of 30 m. This type of pattern is indicative of small-scale heterogeneity in age, creating a landscape of many small, discontinuous patches of tree recruitment commonly found in mixed-severity fire regimes (Arno *et al.*, 2000; Ettema and Wardle, 2002; Taylor and Skinner, 2003). This pattern of patchy cohort recruitment is not observed where single-tree gaps are the primary means of recruitment into the overstory (Mast and Veblen, 1999). Our data suggest tree recruitment within patches may have been a prolonged process lasting at least 10 years (Fig. 5). This is consistent with previous work in upland Douglas-fir forests in the Klamath-Siskiyou region, which has shown post-fire tree regeneration commonly spans a 10 to 20 year period (Wills and Stuart, 1994; Shatford *et al.*, 2007).

We also found evidence of unburned patches within the mixed-severity fire mosaic, which provided refugia for fire-sensitive species in Mixed Conifer riparian forests. Interactions between successive fires in mixed-severity regimes are particularly important in shaping the species composition, fuel characteristics, and future fire-severity in a given patch (Thompson *et al.*, 2007; Collins *et al.*, 2008). Unburned patches in the fire mosaic would have accumulated heavier fuel loads over time and therefore may have subsequently burned at a higher severity than the surrounding forest – potentially producing a canopy gap for Douglas-fir recruitment. Patches that burned in low-severity would have been more likely to burn at low-severity during subsequent fires, which would have favored Douglas-fir over more fire-sensitive species (Thompson *et al.*, 2007). However, patches that escaped fire for multiple fire cycles permitted fire-sensitive species to persist for prolonged periods of time, reaching ages over 200 years. Although large-diameter white fir and Pacific yew trees were relatively uncommon (~7/ha, ~15/ha respectively), their presence suggests that fire severities in portions of pre-settlement riparian forests were quite low and unburned patches played a key role in maintaining species richness and structural complexity.

Until the late 19th or early 20th century, it appears most tree recruitment into the overstory of Mixed Conifer riparian forests occurred in large canopy gaps (<30 m in diameter) created by fire. Growth rates of Douglas-fir recruited during the 20th century, however, suggest they were not growing in canopy gaps, but in the shaded understory. Nearly all Douglas-fir trees that recruited during the 20th century were growing much slower than the older, dominant trees (Figs. 2, 3). In the shade, 20th century Douglas-fir trees would not have received enough sunlight to support the rapid growth rates achieved by the dominant trees from older cohorts. Previous work in old-growth, upland forests of southwestern Oregon found that the majority of dominant trees were the largest trees in their cohort at age 50 and they tended to remain dominant for at least 250 years (Sensenig, 2002). The dominant trees in riparian forests would likely have been the individuals that recruited into canopy gaps after fire where they were able to develop full crowns and grow rapidly out of the 'lethal flaming zone' (Mast *et al.*, 1999). Few Douglas-fir trees that recruited after 1900 are on the trajectory to replace the large-diameter trees that currently dominate the canopies of Mixed Conifer riparian forests because slow-growing, suppressed trees have reduced potential to become large, dominant trees later in life.

4.2. *Interior Valley Zone*

Our data suggest riparian forests along first and second order streams in the Interior Valley zone were shaped by a low-severity fire regime during the pre-settlement period, where frequent fires killed most tree seedlings and maintained open savannas or woodlands with shade-intolerant hardwoods and scattered, open-grown conifers. The age structure of live Douglas-fir observed for Interior Valley sites suggests the survival of trees to a fire-resistant size was infrequent, resulting in low conifer densities relative to Mixed Conifer sites (4 percent of live conifers on Interior Valley sites recruited prior to 1850 versus 14 percent on Mixed Conifer sites). Low pre-settlement tree densities may also explain the high growth rates in Douglas-fir that recruited during this period relative to those that recruited during the 20th century (Figs. 2, 3) as well as the presence of large-diameter, shade-intolerant hardwoods. Although widespread stand-replacing fires prior to the mid-19th century could explain the relatively small number of older trees at Interior Valley sites, early Euro-American settler accounts in the Rogue River and Willamette Valleys noted the widespread use of fire by Native Americans in maintaining open oak savanna and woodland communities with conifers existing as scattered, open-grown individuals (Thilenius, 1968; LaLande, 1995). In addition, large-diameter conifer snags and logs were present at low densities in this vegetation zone (~21/ha) relative to Mixed Conifer sites (~39/ha) which suggests pre-settlement tree densities were low and that large, stand-replacing fires were less common (Table 2).

In the post-settlement period, fire exclusion was associated with high survival rates in conifers (predominantly Douglas-fir) that recruited during the late 19th and early 20th centuries, resulting in the establishment of a closed-canopy conifer forest with fewer shade-intolerant hardwoods. Around 1850, our data show the beginning of a broad conifer recruitment pulse larger than any in our record of the pre-settlement period (Fig. 2). Twenty percent of live conifers on Interior Valley sites recruited from 1850-1900, five times the number from the previous 280 years combined. A second pulse occurred in the 20th century, lasting from approximately 1920 until the early 1980s with the most abundant recruitment occurring mid-century. Most Douglas-fir that recruited during the 20th century grew much slower than their older counterparts. Our data indicate fast growth rates did occur in a relatively small portion of trees recruited in the mid-20th century, but the vast majority of trees have suppressed growth rates resulting from stand densities that are likely much higher than those of the pre-settlement era. Many shade-intolerant hardwoods are also being over-topped by Douglas-fir, particularly at our driest sites where most white oaks are already dead.

Active fire suppression efforts likely contributed to the high survival rates of Douglas-fir in the 20th century; however, the apparent shift in tree recruitment dynamics in the Interior Valley zone occurred much earlier, dating to the arrival of Euro-American settlers. The combined effects of Euro-American land management and reduced indigenous burning may have excluded fire from riparian forests, or at least reduced fire frequencies sufficiently to allow more conifers to reach a fire-resistant size.

5. CONCLUSIONS

Our findings support our hypothesis that riparian forests in southwestern Oregon experienced frequent fires and that fire exclusion has altered the structure, composition, and successional trajectory of these forests. We were surprised, however, to find many of the structural and compositional changes evident today, date back 20 to 70 years prior to effective fire suppression (approximately 1920) (Sensenig 2002). Historically, fires in riparian areas would likely have had similar effects on forest vegetation as those seen in upland forests, where low- and mixed-severity fire regimes maintained spatially patchy, multi-aged stands of fire-resistant conifer and hardwood species.

In riparian forests of the Mixed Conifer zone, patches of high-severity fire within the mixed-severity matrix apparently created canopy gaps in which new cohorts of Douglas-fir could establish within existing stands and perpetuate Douglas-fir overstory dominance. Fire exclusion has been associated with an increase in tree density and an increase in the recruitment of white fir, a fire-sensitive, shade-tolerant species. Without large canopy gaps, Douglas-fir recruitment has been restricted to the shaded understory where it grows very slowly and is unlikely to replace the large canopy dominant Douglas-fir trees that recruited before 1900. The Douglas-fir dominated canopy may eventually be replaced by white fir, which does not produce high quality, large diameter, more decay-resistant standing snags and coarse woody debris that are desired for both terrestrial and aquatic species habitat.

Interior Valley riparian forests were most likely shaped by a low-severity fire regime, similar to that of Southwestern ponderosa pine (Mast *et al*. 1999), where frequent fires killed most tree seedlings and maintained open savannas or woodlands with shade-intolerant hardwoods and scattered, open-grown conifers. Fire exclusion has been associated with high survival rates in Douglas-fir recruited during the late 19th and early 20th centuries, resulting in the establishment of a closed-canopy conifer forest. Douglas-fir recruitment since the mid-20th

century has been declining and those that have recruited have been growing very slowly in the shaded understory.

While shade-intolerant hardwoods continue to thrive in some upland portions of the Interior Valley zone, they are being over-topped by Douglas-fir in riparian forests of both the Mixed Conifer and Interior Valley zones. Hardwoods as well as shade-intolerant, deciduous shrubs are an important source of food and habitat for aquatic and terrestrial wildlife. Deciduous hardwood litter differs from coniferous litter in a variety of ways, including nutritional content, quantity, and seasonality, and therefore contributes to the aquatic food web in ways that coniferous litter does not (Volk, 2004; Wipfli and Musslewhite, 2004). Shade-intolerant hardwoods, such as Oregon white oak, California black oak, and Pacific madrone are also important food sources for the dusky-footed wood rat (*Neotoma fuscipes*) (Franklin *et al.*, 2000). In turn, the wood rat is a primary food source of the northern spotted owl (*Strix occidentalis caurina*) (Franklin *et al.*, 2000), a species of management concern listed as 'threatened' under the Endangered Species Act.

Our findings indicate the policy for riparian management areas (RMA) in the Pacific Northwest, though well intentioned, may be detrimental to the long-term health of riparian forests in regions shaped by fire such as southwestern Oregon. Protecting RMAs from all anthropogenic disturbances will also limit the implementation of restoration or fuels treatments in upland forests by dissecting manageable units into isolated pieces too small to effectively treat. Under the Northwest Forest Plan, RMAs extend one-to-two tree heights from the stream edge, including intermittent headwater streams. Implemented across the entire landscape, these RMAs occupy a surprisingly large portion of the land surface – particularly in topographically complex regions such as the Klamath-Siskiyou, where up to 50 % of a mile-square section may be within a RMA.

Given the historic continuity of fire disturbance between riparian forests and the adjacent uplands (Everett *et al.*, 2003; Olson and Agee, 2005), it may be beneficial to permit partial harvest treatments and prescribed fire in some riparian areas to allow the restoration of desirable characteristics of the pre-settlement forest structure and composition. Treatments may include the creation of large canopy gaps, un-treated ‘islands,’ clumps and irregularly spaced trees. Because most riparian forests have not burned for 70-100 years, many trees that would have been killed by low- or moderate-severity fires are now too large to be killed by low-severity prescribed fires. Mimicking the stand structure produced by the low- and mixed-severity fire regimes that were present in the pre-settlement period would promote the recruitment of shade-intolerant, fire-resistant tree species, increase overall tree vigor, increase structural diversity, and create a more discontinuous forest canopy, restricting the spread of high-severity crown fires.

If thinning and prescribed fire treatments are to be applied within and adjacent to riparian forests in southwestern Oregon, future management guidelines will need to balance those objectives with the in-stream habitat requirements of anadromous fish. In particular, the need for a steady supply of large woody debris and a well-shaded environment may appear incompatible with the restoration of savanna or woodland conditions in the Interior Valley zone; however, reductions in tree density upslope for restoration or fuels reduction purposes may increase water infiltration into the soil, reduce transpiration loss, and result in greater stream flow and cooler in-stream temperatures. Further research may be required with respect to the short- and long-term effects that riparian restoration treatments might have on in-stream habitat conditions.

Recognizing the role of natural disturbances and the dynamic nature of vegetation communities in this fire-prone region will be necessary for outlining the future of landscape-level forest management.

ROLE OF THE FUNDING SOURCE

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Table 1. Summary of live tree attributes for Mixed Conifer and Interior Valley sites.

Species	Vegetation Zone	N	Average density (stems/ha)	Large tree density (stems/ha)	% of total stems	% of sites present	DBH range (cm)	DBH mean (cm)
Abies concolor	Mixed Conifer	204.0	183.2	7.3	11.2	66.7	1.3-105.0	21.9
	Interior Valley	3.0	12.0	2.0	0.2	23.1	8.1-59.5	25.4
Acer macrophyllum	Mixed Conifer	274.0	106.0	25.8	15.0	93.3	1.6-146.3	27.7
	Interior Valley	283.0	156.2	30.7	21.2	92.3	0.1-123.5	29.1
Alnus rhombifolia	Mixed Conifer	168.0	129.3	25.4	9.2	66.7	1.8-76.5	24.5
	Interior Valley	18.0	58.7	8.7	1.3	23.1	7.7-65.4	37.8
Arbutus menziesii	Mixed Conifer	28.0	40.3	12.0	1.5	33.3	0.5-67.6	33.8
	Interior Valley	180.0	96.6	26.9	13.5	84.6	2.9-66.8	32.8
Castanopsis chrysophylla	Mixed Conifer	8.0	37.0	2.0	0.4	13.3	0.8-40.0	8.6
	Interior Valley	0.0						
Calocedrus decurrens	Mixed Conifer	129.0	105.8	12.2	7.1	73.3	0.5-134.1	32.2
	Interior Valley	77.0	84.3	12.7	5.8	69.2	1.6-141.5	34.3
Cornus nuttallii	Mixed Conifer	34.0	38.5	0.0	1.9	60.0	0.8-13.9	6.0
	Interior Valley	3.0	10.0	0.0	0.2	23.1	0.2-10.2	5.0
Fraxinus latifolia	Mixed Conifer	31.0	83.0	14.0	1.7	26.7	1.0-43.0	13.9
	Interior Valley	31.0	51.8	5.3	2.3	38.5	0.5-70.5	16.9
Pinus lambertiana	Mixed Conifer	2.0	12.0	2.0	0.1	13.3	25.4-54.5	40.0
	Interior Valley	3.0	2.7	2.7	0.2	23.1	64.3-111.5	83.4
Pinus ponderosa	Mixed Conifer	3.0	22.0	2.0	0.2	13.3	3.0-122.5	47.8
	Interior Valley	20.0	30.2	5.8	1.5	53.8	3.2-94.5	58.8
Pseudotsuga menziesii	Mixed Conifer	676.0	265.2	57.8	37.0	100.0	0.3-193.0	55.3
	Interior Valley	639.0	335.7	48.6	47.8	100.0	1.0-150.4	42.3
Quercus chrysolepis	Mixed Conifer	42.0	66.3	2.0	2.3	53.3	0.7-34.1	9.0
	Interior Valley	37.0	82.9	6.7	2.8	30.8	1.7-61.5	19.6
Quercus garryana	Mixed Conifer	0.0						
	Interior Valley	6.0	20.5	3.0	0.5	23.1	1.6-47.5	21.5
Quercus kelloggii	Mixed Conifer	3.0	37.5	0.0	0.2	6.7	1.9-16.8	7.3
	Interior Valley	31.0	58.7	2.7	2.3	61.5	0.7-50.8	14.5
Taxus brevifolia	Mixed Conifer	226.0	127.6	15.7	12.4	86.7	0.9-63.0	18.5
	Interior Valley	5.0	17.3	6.0	0.4	15.4	9.7-40.4	22.8

Notes: N= number of individuals sampled, DBH= diameter at breast height (1.37 m).
Large tree density' refers to the average density of conifers > 50cm DBH (except Taxus brevifolia), hardwoods > 25cm DBH, and Taxus brevifolia > 25cm DBH.

Table 2. Summary of dead tree (standing snags and downed logs) attributes for Mixed Conifer and Interior Valley sites.

Species	Vegetation Zone	N	Average density (stems/ha)	Large tree density (stems/ha)	% of total stems	% of sites present	DBH range (cm)	DBH mean (cm)
Abies concolor	Mixed Conifer	31.0	45.7	4.0	9.4	46.7	2.0-81.9	19.8
	Interior Valley	0.0						
Acer macrophyllum	Mixed Conifer	11.0	18.5	2.0	3.3	46.7	3.2-42.5	18.1
	Interior Valley	16.0	16.6	4.1	5.6	53.8	8.3-71.4	33.0
Alnus rhombifolia	Mixed Conifer	6.0	53.0	3.0	1.8	20.0	5.2-37.5	18.6
	Interior Valley	3.0	3.0	3.0	1.0	15.4	39.7-48.8	44.3
Arbutus menziesii	Mixed Conifer	7.0	23.3	3.3	2.1	26.7	2.2-40.0	26.3
	Interior Valley	33.0	58.7	4.5	11.5	76.9	3.4-54.5	25.7
Calocedrus decurrens	Mixed Conifer	15.0	27.4	3.0	4.5	46.7	2.4-135.0	65.7
	Interior Valley	8.0	17.0	2.0	2.8	38.5	4.0-90.0	28.3
Cornus nuttallii	Mixed Conifer	1.0	10.0	0.0	0.3	6.7	11.0	11.0
	Interior Valley	0.0						
Fraxinus latifolia	Mixed Conifer	0.0						
	Interior Valley	1.0	10.0	0.0	0.3	7.7	19.5	19.5
Pinus lambertiana	Mixed Conifer	2.0	4.0	4.0	0.6	6.7	99.8-170.0	134.9
	Interior Valley	0.0						
Pinus ponderosa	Mixed Conifer	2.0	2.0	2.0	0.6	6.7	55.0-60.0	57.5
	Interior Valley	10.0	24.7	2.2	3.5	46.2	2.7-98.7	54.4
Pseudotsuga menziesii	Mixed Conifer	212.0	63.2	26.2	64.0	93.3	1.5-159.5	71.7
	Interior Valley	177.0	112.9	17.3	61.5	100.0	1.3-165.5	37.9
Quercus chrysolepis	Mixed Conifer	5.0	32.0	2.0	1.5	13.3	8.4-30.4	18.1
	Interior Valley	1.0	12.5	0.0	0.3	7.7	4.3	4.3
Quercus garryana	Mixed Conifer	0.0						
	Interior Valley	31.0	134.0	5.7	10.8	23.1	7.5-66.5	19.9
Quercus kelloggii	Mixed Conifer	0.0						
	Interior Valley	8.0	17.3	2.3	2.8	30.8	3.5-50.3	22.6
Taxus brevifolia	Mixed Conifer	37.0	78.8	29.3	11.2	53.3	4.5-51.9	17.6
	Interior Valley	0.0						

Notes: N= number of individuals sampled, DBH= diameter at breast height (1.37 m).

Large tree density' refers to the average density of conifers > 50cm DBH (except Taxus brevifolia), hardwoods > 25cm DBH, and Taxus brevifolia > 25cm DBH.

Figure Legends

Figure 1. Locations of riparian study sites in the Mixed Conifer and Interior Valley vegetation zones, Rogue River basin, Oregon. Topography of the study area is displayed in the left panel, with higher elevations appearing lighter.

Figure 2. [*a*] Average age distribution (left axis) of Douglas-fir and white fir on 11 Mixed Conifer riparian sites in the Rogue River basin, Oregon, with the smoothed initial growth rates (right axis, average of first 20 yrs.) for a subsample of Douglas-fir. [*b*] Fire scars recorded at five Mixed Conifer riparian sites. [*c*] Average age distribution (left axis) of Douglas-fir and incense cedar on 12 Interior Valley riparian sites in the Rogue River basin, Oregon, with the smoothed initial growth rates (right axis, average of first 20 yrs.) for a subsample of Douglas-fir. [*d*] Fire scars recorded at three Interior Valley riparian sites.

Figure 3. Average basal area increment (BAI) of live Douglas-fir as a function of the year of origin for Mixed Conifer (left) and Interior Valley (right) vegetation zones. A Lowess smoothing line (smoothing parameter: f=0.1) is included as a visual guide.

Figure 4. Empirical semivariogram (points) and fitted model (line) for [*top*] 193 Mixed Conifer and [*bottom*] 210 Interior Valley Douglas-fir trees ≥ 50cm DBH, showing tree age semivariance estimates as a function of increasing distance (in meters) between neighboring trees. The sill provides an estimate of total population variance. The nugget (intercept) represents the variance due to sampling error, and/or spatial dependence at scales not explicitly sampled. The range (asymptote) signifies the extent of heterogeneity, or patch size, beyond which data are stochastically independent (Ettema and Wardle 2002).

Figure 5. Box plots of age difference as a function of increasing distance between neighboring Douglas-fir trees ≥ 50cm DBH for Mixed Conifer [*top*] and Interior Valley [*bottom*] vegetation zones. The upper and lower boundaries of the box represent the 75^{th} and 25^{th} percentiles, the line inside the box represents the median, and the whiskers above and below the box represent the 90^{th} and 10^{th} percentiles, respectively. Outliers are represented as dots.

Figure 1.

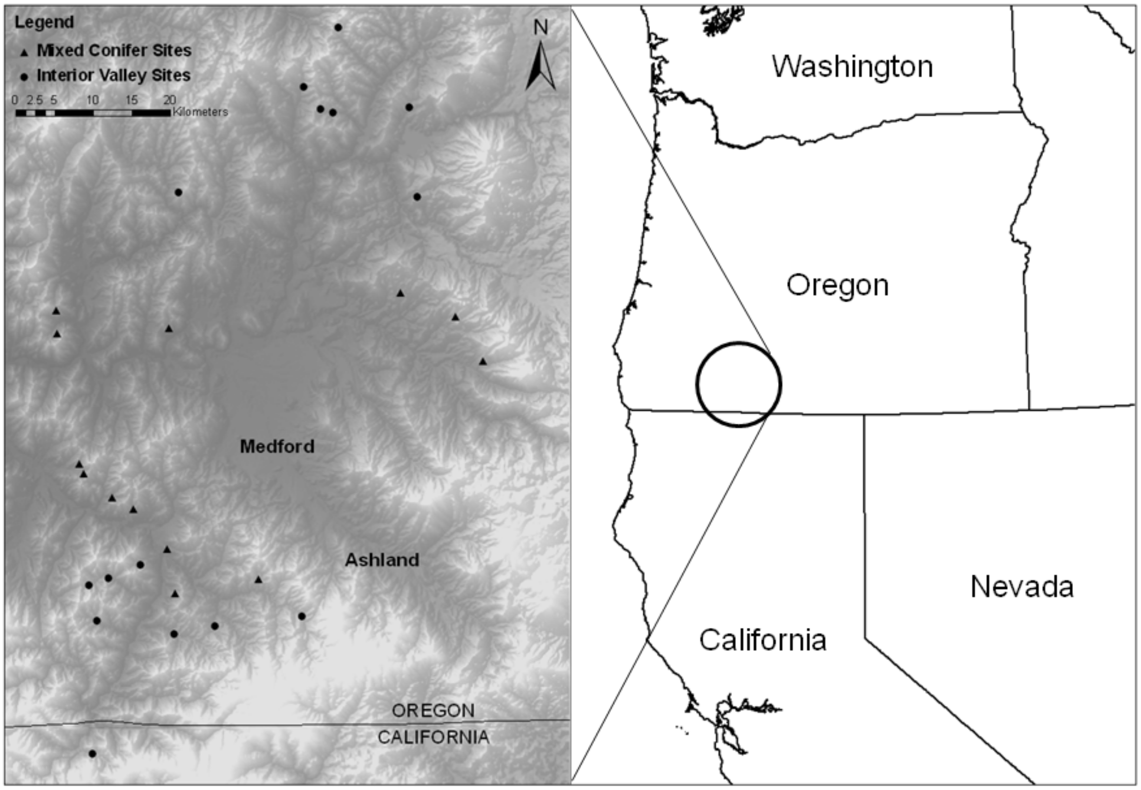
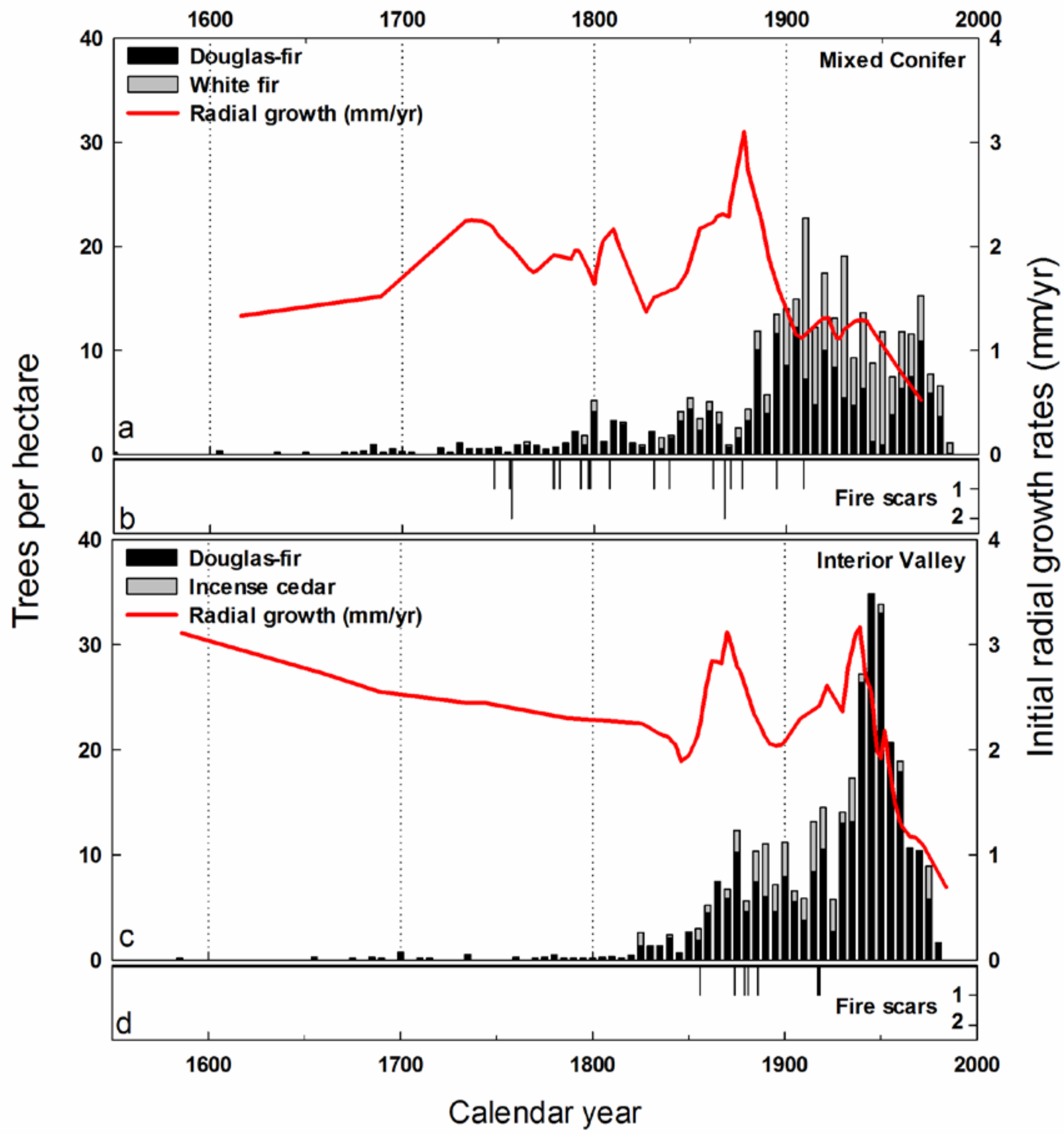

Legend
Mixed Conifer Sites
Interior Valley Sites
0 2.5 5 10 15 20
Kilometers
N
Medford
Ashland
OREGON
CALIFORNIA
Washington
Oregon
California
Nevada

Figure 2.



Douglas-fir
White fir
Radial growth (mm/yr)
Mixed Conifer
a
b
Fire scars
1
2
Douglas-fir
Incense cedar
Radial growth (mm/yr)
Interior Valley
c
d
Fire scars
1
2
1600
1700
1800
1900
2000
0
10
20
30
40
0
1
2
3
4
Trees per hectare
Initial radial growth rates (mm/yr)
Calendar year

Figure 3.

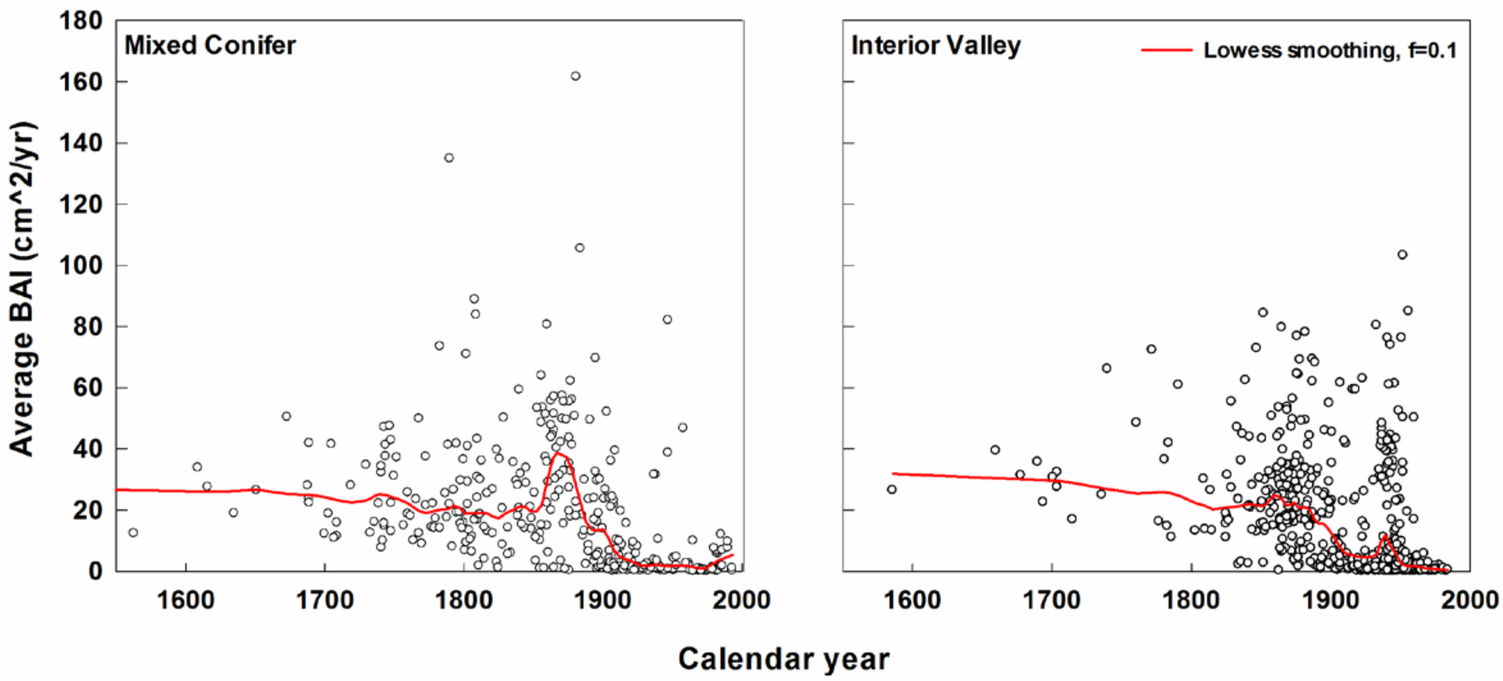

Mixed Conifer
Interior Valley
Lowess smoothing, f=0.1
Average BAI (cm^2/yr)
0
20
40
60
80
100
120
140
160
180
1600
1700
1800
1900
2000
Calendar year

Figure 4.

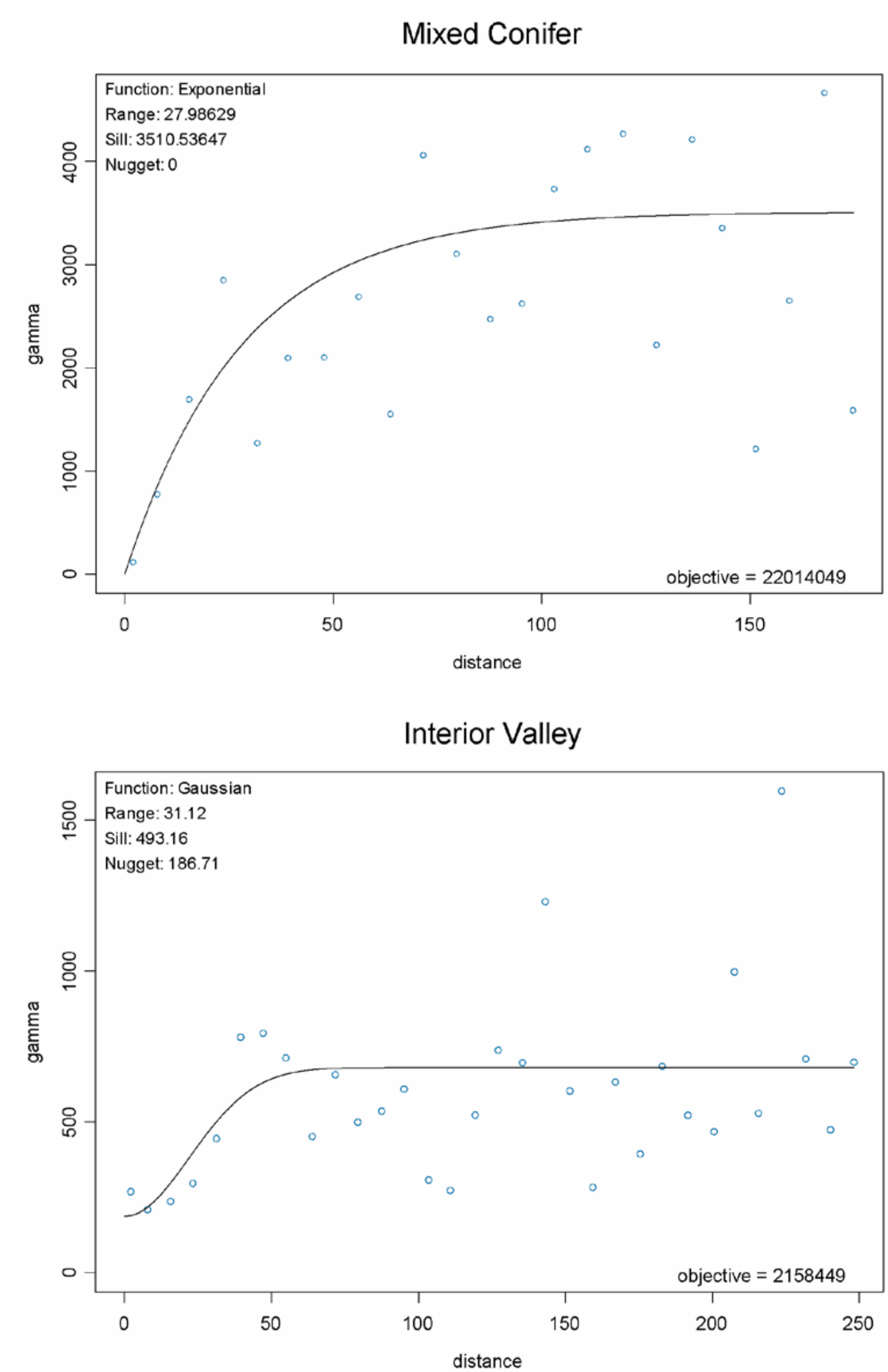
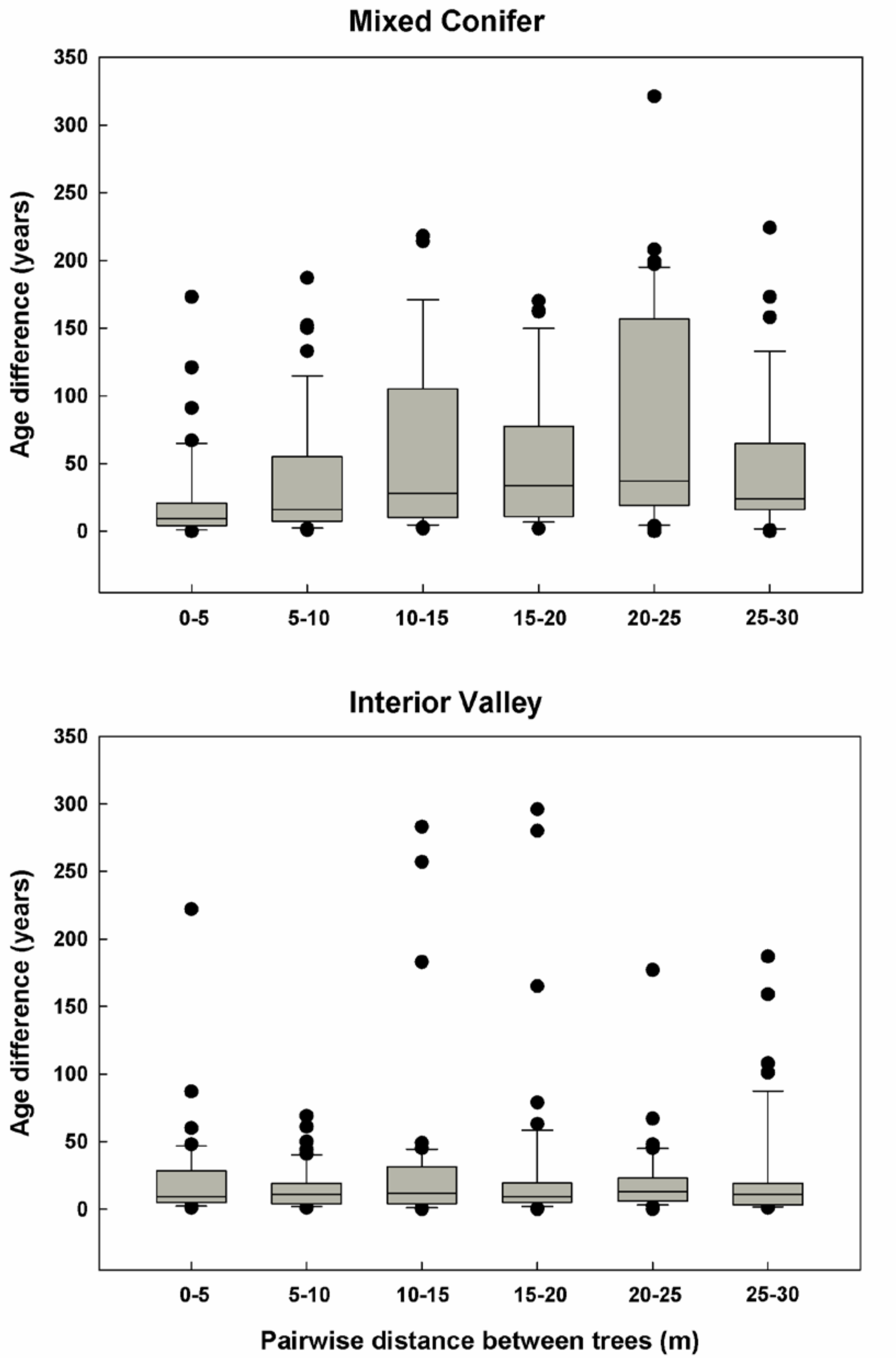

Mixed Conifer
Function: Exponential
Range: 27.98629
Sill: 3510.53647
Nugget: 0
objective = 22014049
gamma
distance
0
1000
2000
3000
4000
0
50
100
150
Interior Valley
Function: Gaussian
Range: 31.12
Sill: 493.16
Nugget: 186.71
objective = 2158449
gamma
distance
0
500
1000
1500
0
50
100
150
200
250

Figure 5.


Mixed Conifer
Age difference (years)
350
300
250
200
150
100
50
0
0-5
5-10
10-15
15-20
20-25
25-30
Interior Valley
Age difference (years)
350
300
250
200
150
100
50
0
0-5
5-10
10-15
15-20
20-25
25-30
Pairwise distance between trees (m)