Importance of Non-Stand-Replacing Fire for Development of Forest Structure in the Pacific Northwest, USA

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ABSTRACT. Old-growth forests have been the subject of much political concern and forestry research in the 20th century. Evidence that many old-growth stands of the western Oregon Cascade Range have experienced multiple low- to moderate-severity fires has led to the hypothesis that such fires have sustained structural complexity in certain temperate coniferous forests. Multiple regression analysis was used to assess the role of historical non-stand-replacing fire for 90 mature and old forest sites on a 450-km^2 landscape of mixed-severity fire regime in western Oregon. The occurrence of non-stand-replacing fire was inferred from the relative frequency of fire scars on *Pseudotsuga menziesii*. Results suggest that in the central western Cascades, the occurrence of non-stand-replacing fire has favored variability in tree diameter sizes, larger trees, and a greater component of shade-tolerant tree species, after accounting for the effects of elevation, slope aspect, and stand age. However, the fire scar variable explained a relatively small percentage of the variance not explained by these effects, with partial R^2 values ranging from 0.05 to 0.16. A path analysis suggested that the effects of stand age on forest structure can be partitioned into direct effects (gap dynamics and successional processes in the absence of disturbance) and indirect effects (older stands have had more time to experience non-stand-replacing fire), with the indirect effects explaining a large component of forest structural attributes that are typically associated with the old-growth seral stage. While the cumulative and long-term effects of non-stand-replacing fire in this region are likely complex, it would seem prudent to include such disturbances as a key ecosystem process, where management practices seek to emulate natural disturbance regimes or facilitate the development of old-growth forest structures. FOR. SCI. 50(2):245–258.

Key Words: Fire regime, forest dynamics, stand structure, old-growth, fire severity.

TWENTIETH CENTURY FRAGMENTATION OF OLD-GROWTH FORESTS, loss of old-growth habitat, and concurrent declines in old-growth-associated plant and animal species have generated much interest in the structure and function of old-growth forests throughout North America (Franklin et al. 1981, Spies and Franklin 1988, Mladenoff et al. 1993, Vora 1994, McCarthy and Bailey 1996, Timoney and Robinson 1996, Taylor and Skinner 1998). To foster development of old-growth habitat structures and ecosystem functions on landscapes dominated by young, managed stands, some have suggested employing forest management practices such as longer rotations, snag creation, thinning, prescribed burning, selection cutting, and leaving residual large trees following harvest (McComb et al. 1993, Vora 1994, Spies and Franklin 1996). Critical to the success of such management activities is a solid understanding of the processes of disturbance and succession leading to the development of various old-growth forest structures now present on the landscape.

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In the western Cascade Range of the Pacific Northwest (PNW), wildfires have played a major role in determining the structure and function of forest ecosystems, patterns of habitat, and patterns of resource availability for human use (Agee 1993). Presettlement landscape-level forest patterns in the widespread Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) forests of the region were greatly influenced by episodic, high-severity fires occurring at average intervals of 200–300 years (Agee 1993). However, overwhelming evidence that many old-growth stands of the western Oregon Cascades have experienced multiple low- to moderate-severity fires (Means 1982, Stewart 1986a, 1986b, Teensma 1987, Morrison and Swanson 1990, Weisberg 1998) has led to the hypothesis that such fires sustained structural complexity at both stand and landscape scales by initiating new cohorts of shade-tolerant or shade-intolerant tree species while maintaining live and dead remnants of the prefire stands. Spies and Franklin (1988) proposed that when such fires burned in young stands, many *P. menziesii* trees were killed and new cohorts of *P. menziesii* established, but that these same fires caused less overstory mortality in old-growth stands, initiating an understory cohort of shade-tolerant species.

The purpose of this study is to assess the role of historical non-stand-replacing fires in forming contemporary stand structures for a large landscape (450 km^2) of mixed-severity fire regime where both stand-initiating fires and low-severity underburns have characteristically occurred over the past half millennium (Weisberg 1998). Fires in this region are generally landscape-level phenomena producing a mosaic of different severity types, only portions of which are stand-replacing (Morrison and Swanson 1990, Kushla and Ripple 1997). In this article, "non-stand-replacing fire" refers to the occurrence of nonlethal fire at the level of stands, patches, or individual trees, irrespective of whether the same fire at the landscape level also included some stand-replacing patches.

In the absence of fire over centuries, *P. menziesii* forests of the central western Cascades are likely to become dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and other shade-tolerant species (Dale et al. 1986, DeBell and Franklin 1987, Huff 1995). Episodic high-severity fires encourage *P. menziesii* establishment, because this species is better able to establish under open conditions and on burned seedbeds than its competitors (Minore 1979). This species is also better adapted for surviving non-stand-replacing fire than *T. heterophylla* and other late-seral species. Mature *P. menziesii* has thicker bark and a deeper root system (Minore 1979), making it a "fire resister" (Agee 1993). However, the influence of non-stand-replacing fires on the development of stand structure in these forests is not clear. Such fires may retard succession by killing understory shade-tolerant species while maintaining overstory *P. menziesii*. Alternatively, they may accelerate succession by killing overstory *P. menziesii* in a patchy manner, creating many small canopy gaps that are too light-limited for *P. menziesii* re-establishment, but open enough for *T. heterophylla* or other species (Spies and Franklin 1988). In mature and old-growth forests of the western Cascades, *P. menziesii* seedlings do not often establish in canopy gaps with diameters less than 0.4 times the canopy tree height, while *T. heterophylla* seedlings survive and grow in gaps with diameters of 0.2 times the canopy tree height (Gray and Spies 1996). Patchy, low-severity fires creating small overstory gaps may facilitate the eventual establishment of shade-tolerant canopy trees, particularly if they reduce competition from surface vegetation (Gray and Spies 1997).

Other potentially important effects of non-stand-replacing fires on forest structure in the PNW do not involve a change in tree species composition. Where large canopy gaps are created, patches of newly established seedlings or surviving advance regeneration can arise as a younger age cohort, which may eventually attain the canopy. An increasing number of age cohorts present in the stand will often result in increased horizontal and vertical heterogeneity, which are critical aspects of old-growth forest structures (Spies and Franklin 1991). Where mortality is more spatially uniform or subdominant trees are preferentially killed, smaller gaps may be created that may or may not allow new tree cohorts to establish. In either case, surviving trees whose neighbors were killed may experience a growth release following the fire, particularly if the stand is dense and in the competitive exclusion stage of development. In the PNW, this stage commonly occurs from canopy closure until about 80–100 years of age (Franklin et al. 2002). Increased growth of surviving trees may lead to increased density of large trees (for stands of a given age) or to increased stand basal area.

In this study, multiple regression analysis is used to evaluate the relative influence of fire history on forest structure at the stand level, given the effects of stand age and topography (as described by elevation and slope aspect). The fire history variable of interest is the frequency of non-stand-replacing fire that has occurred since the establishment of the oldest tree in a stand. This is inferred from a simple fire scar ratio (FSR) index using the relative frequency of fire scars on *P. menziesii*. I discuss the theoretical justification for using the FSR, which does not depend on reconstructing the severity of fire events from the distant past, a difficult if not impossible task. The analysis focuses on three research questions: (Q1) Has non-stand-replacing fire accelerated succession by facilitating regeneration of shade-tolerant trees? (Q2) Has non-stand-replacing fire favored variability in tree diameter sizes, leading to more diverse, heterogeneous stands? and (Q3) Has non-stand-replacing fire favored larger trees, for stands of a given age? Stated as testable hypotheses, these become: (H1) The FSR is positively associated with the relative density or dominance of shade-tolerant trees; (H2) The FSR is positively associated with tree diameter variability; and (H3) The FSR is positively associated with the frequency of large (i.e., $>$100 cm dbh) trees, or with total stand basal area.

Methods

Field Methods

The Blue River study area occupies approximately 450 km^2 in the central western Oregon Cascades (Figure 1) (Weisberg 1998). The H.J. Andrews Experimental Forest occupies 64 km^2 of the area. Elevation ranges from 316 m to 1,645 m, and topography is steep and dissected, with narrow, incised stream valleys and long, sharp ridges. The study area has a temperate, maritime climate with cool, wet winters and warm, dry summers. Nearly 75% of annual precipitation occurs between November and March. A persistent snowpack may form above 1,050 m, although there is much inter-annual variation in snow level (Bierlmaier and McKee 1989). Annual precipitation at the Andrews Forest varied from 1,310 mm to 3,070 mm from 1958 to 1996, averaging 2,300 mm (Greenland 1994, Post and Jones 2001).

Despite abundant annual precipitation, periods of extended drought commonly occur during the summer months. The combination of summer drought, east wind events, and lightning storms leads to a favorable fire climate during certain years. Adiabatic, desiccating east winds occur when thermal low-pressure cells develop along the coast as a high-pressure ridge settles over eastern Oregon, producing warm, dry winds blowing westward across the Cascades. These winds may hasten fuel moisture loss, creating favorable conditions for fires, or may cause existing low-intensity fires to intensify and spread rapidly. Dominant winds during the summer months trend from the southwest and do not have the same drying influence or intensity. Lightning storms, infrequent compared to other mountainous regions of the American West, were sufficient to ignite about 60% of all recorded fires in the central western Cascades from 1910 to 1976 (Burke 1979).

Most of the study area is covered by two major vegetation zones (i.e., forest series): the Western Hemlock zone, between approximately 350 m and 1,000 m; and the Pacific Silver Fir (*Abies amabilis* (Doug) ex. Loud) zone, above approximately 1,000 m (Franklin and Dyrness 1973). Within the Western Hemlock zone, dominant late-seral tree species include *T. heterophylla* and western redcedar (*Thuja plicata* Donn ex D. Don). Occasional tree species include incense-cedar (*Calocedrus decurrens* (Torrey) Florin), western white pine (*Pinus monticola* Dougl. ex D. Don), sugar pine (*Pinus lambertiana* Dougl.), and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.). *P. menziesii*, an early seral species that may persist for a millennium in the absence of major disturbance (Dale et al. 1986), is the dominant tree species. Within the Pacific Silver Fir zone, dominant tree species include *A. amabilis*, *P. menziesii*, noble fir (*Abies procera* Rehd.), and *T. heterophylla* (Franklin and Dyrness 1973). *P. menziesii* and *A. procera* are important early seral tree species.

The dominant tree species in the central western Cascades, *P. menziesii*, often survives fire with small scars, associated with bark furrows (Morrison and Swanson

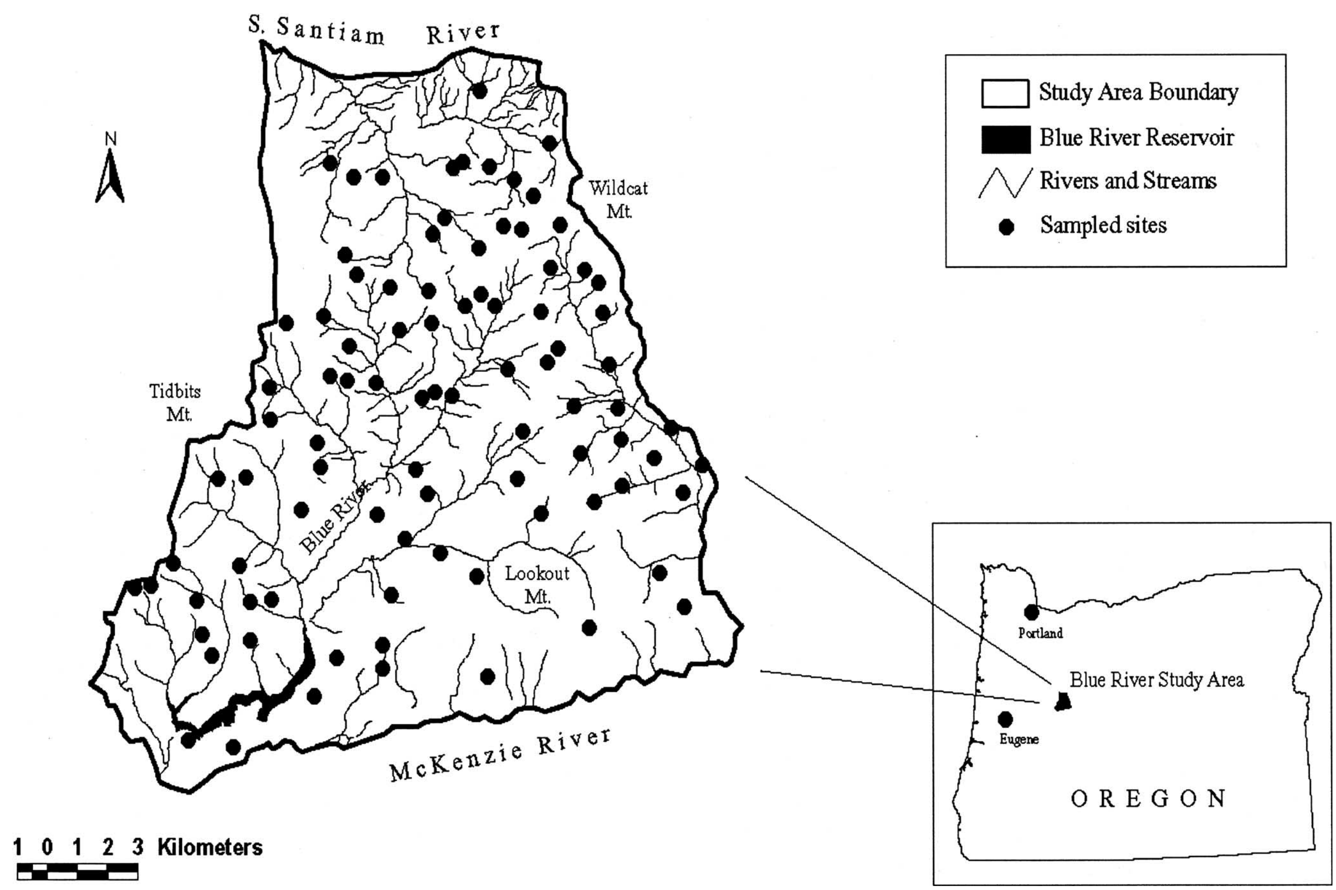

Figure 1. Map of the study area, showing sampled sites.

1990). These small scars can heal rapidly and are often not visible on standing live trees within as early as 20 years following the fire event. Therefore, sites were located in first-rotation clearcuts, where fire scars could be completely and accurately surveyed on cut stumps. One clearcut was randomly sampled in every township and range section for which at least one recent (i.e., less than approximately 12 years old) clearcut was available. Township and range sections form a grid system where cells are typically 2.79 km^2, or 1 mi^2. This sampling scheme allowed extensive coverage of the study area, while preserving an element of randomization.

Within the study area, tree diameters were sampled for 90 4-ha sites for which fire history and environmental information were also collected (Figure 1) (Weisberg 1998). Stand ages at these sites ranged from 108 to 517 years (mean = 390 years), where stand age was estimated as the age of the oldest tree. Each 4-ha square site was subsampled using four 0.1-ha circular plots located at the corners. Within each plot, diameters at stump height were recorded, by species, for all stumps of at least 5-cm diameter. Diameter at breast height (dbh) was measured for all standing trees; this information was aggregated with stump data to describe the diameter structure, by species, for each site. In addition to a suite of ring counting measures used in a related fire history reconstruction of the study area (Weisberg 1998), the number of fire scars was counted for each sampled *P. menziesii* stump of at least 20 cm diameter. Scars were considered to be fire scars if they satisfied a detailed set of morphological and other criteria (Weisberg 1998), including factors such as orientation along a common radius, alignment with a zone of thin bark, temporal synchrony with other scars on nearby trees, occurrence of charcoal on bark predating the scar or partially overlying the scar tissue, presence of an open "cat-face" (rare among *P. menziesii* in the study area), and occurrence on the uphill sides of tree boles (Morrison and Swanson 1990). The purpose of establishing these criteria was to distinguish scars of fire origin from scars created by other processes, such as tree fall injury, antler rubbing, bear damage (Molnar and McMinn 1960), Native American bark-stripping (Swetnam 1984), *Armillaria* infections (Molnar and McMinn 1960), and attacks by insects, such as the bark beetle (Stuart et al. 1983).

Data Analysis

Diameter measurements for each site were aggregated over all plots to calculate tree density (per ha), basal area (m^2 per ha), and mean and standard deviation diameter for each tree species present on each site. Diameters were not corrected to breast height prior to calculating basal area, because not all stump heights were measured. Stump heights varied from 30 to 120 cm, but were usually between 60 and 90 cm. Errors in basal area calculations resulting from variable stump heights probably are randomly distributed among predictor variables. However, the use of stump diameters likely resulted in slightly larger values relative to diameters at breast height, making tree sizes and basal areas reported in this study not directly comparable to those of other studies where dbh was used. Size class histograms suggested that trees of less than 20-cm diameter were underrepresented in the sample, perhaps due to being knocked down during harvest, faster decay rates of small stumps, or greater difficulty locating small stumps in brushy clearcuts. It is likely that trees of at least 20-cm diameter were completely sampled. Therefore, all calculations include only trees of at least 20-cm diameter. This should not significantly influence measurements of basal area, but might greatly influence density measures. Depending on environmental conditions and stand density, *P. menziesii* in the study area requires from 16 to 40 years to reach 20-cm dbh (Nathan Poage, USGS Forest and Rangeland Ecosystem Science Center, Corvallis, OR, March 22, 2003).

To develop a proxy for the frequency of non-stand-replacing fires at each site, I calculated an FSR, the ratio of the number of fire scars found on *P. menziesii* stumps to the number of *P. menziesii* stumps ($\geq$20 cm diameter at stump height) sampled. The FSR would be expected to be greater for sites where the frequency of non-stand-replacing fires has been greater. The concept behind this simple index is clear. The numerator increases with every instance of scar formation, which indicates that a nonlethal fire has occurred (at least at the scale of a single tree). The denominator increases whenever a fire kills a large overstory tree, resulting (over time) in a replacement cohort of smaller, regenerating trees that have had less time to experience scarring fires. Depending on the timing relative to stand self-thinning processes, each such mortality event increases the denominator without increasing the numerator, reducing the FSR. A stand that has experienced a completely stand-replacing fire, and has not experienced another fire since then, will have an FSR of zero. Each "underburn" or completely nonlethal fire may scar trees, increasing the FSR.

Between the two extremes of stand-replacing fires and underburns, what the FSR represents may be less apparent. Figure 2 shows a hypothesized relationship among the FSR, fire frequency, and fire severity. The FSR should have its highest value where numerous fires of relatively low severity have occurred ("H" on Figure 2), scarring many trees but killing relatively few. With increasing fire severity (moving to the right on Figure 2), greater mortality of overstory trees, including those marked by scars from previous fires, would reduce both numerator and denominator of the FSR. Over time, the fire-killed trees would be replaced by higher densities of smaller, regenerating *P. menziesii* trees that would lack fire scars, greatly increasing the denominator term and therefore reducing the FSR. Therefore, the isopleths in Figure 2 show the FSR declining gradually with increasing fire severity, for the portion of the graph to the right of "H." To the left of "H," Figure 2 shows a sharp decline in FSR due to fires burning at such low intensities that scarring may not consistently occur. This decline represents a hypothesized threshold fire intensity (the vertical line above "A" on Figure 2) where scarring of *P. menziesii* becomes unlikely. Such threshold intensities have been

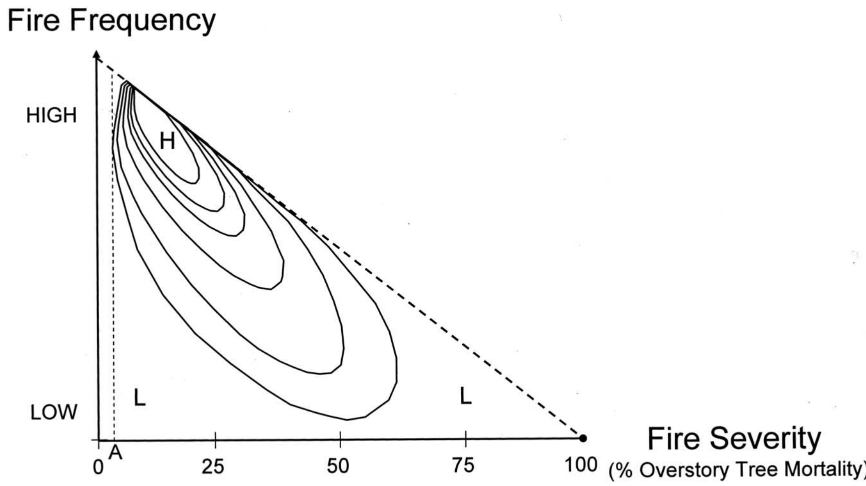

Figure 2. Hypothesized relationship of the fire scar ratio (FSR) (see text for description) with the fire regime parameters severity and frequency. The letters "H" and "L" indicate isopleths of highest and lowest values of the FSR, respectively. The letter "A" on the x-axis refers to the fire severity level corresponding to the minimum fire intensity needed for scarring a *P. menziesii* tree of representative diameter. Fire severity refers to the level of overstory tree mortality occurring for a given fire event and is precisely defined in percentage units on the diagram. Fire frequency refers, in a relative sense, to the number of fires that has been recorded by the oldest trees in the stand. The diagram is truncated so as not to include infeasible combinations of high frequency and high severity. It is assumed that each fire event burns through the entire stand. See the text for further explanation.

modeled for *P. menziesii* of a given diameter and associated bark thickness by Peterson and Ryan (1986).

It is hypothesized in Figure 2 that the FSR is highest where the frequency of non-stand-replacing fires is highest for stands that have generally experienced low fire severity (e.g., <25%). For stands that have typically experienced higher fire severities, a higher fire frequency might be expected to reduce the FSR for reasons already discussed. Therefore, Figure 2 shows a unimodal relationship between fire frequency and the FSR for stands that have been characterized by higher fire severities.

In addition to the FSR, stand structure was predicted as a function of three other variables: stand age, elevation, and northeastness. Stand age was estimated as the age of the oldest tree sampled at the site, where age was estimated using a simple ring count on the stump surface. In a different study in the same area, tree ages determined by simple ring counts in the field were found to be consistently underestimated by a mean of 25 years for trees ranging in age from 90 to 440 years (Weisberg and Swanson 2001). The origin year estimate was corrected by adding the estimated age of the tree at stump height, calculated using an empirical relationship developed for Douglas-fir forests in a nearby study area (Morrison and Swanson 1990). Elevation was estimated from site locations and a 30-m digital elevation model. Slope aspect was measured in the field and converted to a continuous linear variable where high values indicate a northeast aspect using a cosine transformation after converting degrees to radians. Prior to statistical analysis, elevation and northeastness were aggregated to an approximately 4-ha scale using a rectangular moving window averaging filter. This was done so that predictor variables and stand structure response variables would share a common spatial scale.

The FSR, stand age, and the two topographic variables were used to predict four variables describing stand structure: the relative density of shade-tolerant tree species, where shade-tolerant species include *T. heterophylla*, *T. plicata*, *A. grandis*, and *A. amabilis*; total stand basal area; coefficient of variation (cv) of dbh; and the density of large (≥100 cm diameter) *P. menziesii* trees. The shade-tolerant density variable is appropriate for testing the first hypothesis concerning fire-accelerated succession, while the tree diameter variability is suitable for testing the second hypothesis concerning fire effects on creating heterogeneous diameter distributions. The total basal area and density of large *P. menziesii* are appropriate for testing different aspects of the third hypothesis, that the occurrence of non-stand-replacing fires has favored development of larger trees. All four variables are important for distinguishing stand structures of young, mature, and old-growth forests throughout the Pacific Northwest (Spies and Franklin 1991, Acker et al. 1998).

Multiple regression analysis was used to estimate separate statistical models for the four univariate responses as a function of elevation, northeastness, and stand age (i.e., the covariate model). A forward stepwise method was used to help select the covariate model with the smallest Akaike's Information Criterion (AIC) statistic (Hastie and Pregibon 1993). All statistical analyses were conducted using Splus software (MathSoft, Inc. 1999, S-PLUS 2000 Professional).

I then predicted the residuals from the covariate model as a function of the FSR to estimate the independent, direct effect of non-stand-replacing fire given the effects of stand age, elevation, and slope aspect. The FSR was first transformed using an arcsine square root transformation, as is appropriate for highly skewed ratio or percentage data (Zar 1996). The resulting partial R^2 coefficients describe the proportion of variance explained by the FSR, taking into account the effects of the other variables (Sokal and Rohlf 1981).

Spatial patterns of residuals from the full models, where the FSR was added to the covariate models, were examined for autocorrelation using the Moran's I statistic to plot omnidirectional correlograms (Legendre and Fortin 1989). Correlograms were flat and, using 95% confidence intervals for Moran's I as a test for significance (Sokal and Oden 1978), residuals were not spatially autocorrelated over any lag distance for any of the four regression analyses.

In addition to the regression analyses, path coefficient analysis (Sokal and Rohlf 1981, Stohlgren and Bachand 1997) was used to evaluate and graphically illustrate the relative influences of topographic variables, stand age, and the fire scar variable on the four response variables for stand structure. The hypothetical model used for path analyses is shown in Figure 3. Elevation and northeastness are hypothesized to influence stand structure directly, as well as indirectly through correlations with stand age and the FSR. In the study area, higher elevations and more northeasterly aspects generally experience cooler, more mesic conditions and are less susceptible to summer drought. In turn, stand age is hypothesized to influence stand structure both directly (successional processes, gap phase dynamics) and indirectly through its effects on the FSR. Older stands have had more time to experience more non-stand-replacing fires that scar trees and by definition have not recently experienced a stand-replacing fire that would have killed previously scarred trees. "Stand structure" in Figure 3 refers to each of four response variables mentioned above for which different path coefficient analyses were conducted. Path coefficient analyses display the standardized partial regression coefficient (beta weight) for each direct influence (one-headed arrows) and the simple Pearson's correlation coefficient for indirect influences (two-headed arrows) (Sokal and Rohlf 1981). Only significant paths are displayed.

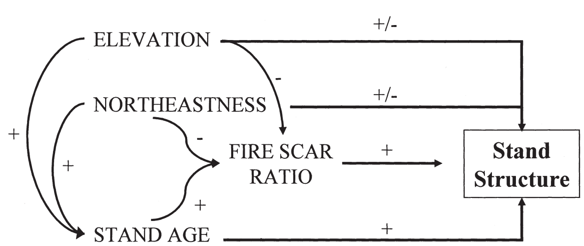

Figure 3. The hypothetical model to be tested using path analysis. The direction of the hypothesized association is indicated using + or - signs. "Stand Structure" may refer to any of the four forest structure variables analyzed in this study: shade-tolerant density, tree diameter variability, total basal area, and density of large *P. menziesii*.

Results

Scatter plots of each of the four stand structure variables against stand age and FSR suggest significant positive relationships of both predictor variables with shade-tolerant density and diameter cv, but weak or nonsignificant relationships with density of large *P. menziesii* and stand basal area (Figure 4). Because the FSR and stand age are correlated ($r = 0.36$), additional analyses were undertaken to partition the proportion of variance in stand structure variables explained by the FSR, after accounting for the effects of stand age. Note that most values of the stand age variable are clustered between about 400 and 475 years, with very few observations between 200 and 400 years, and none below 100 years. This apparent sampling problem is unavoidable given the fire history of the study area, where fire suppression since the early 1900s has been very successful in reducing the frequency and extent of stand-replacing fire (Weisberg 1998). In fact, a regional scale meta-analysis of 10 studies west of the Cascade Crest found the fire history record to be dominated by widespread fire from the late 1400s to ca. 1650, and then again from ca. 1800 to ca. 1925, as is apparent from the distribution of the stand age variable in this study (Figure 4) (Weisberg and Swanson 2003). An additional factor leading to a biased stand age distribution is that clearcuts available for sampling would be less likely to occur in younger forests, due to past forest planning priorities in the study area.

An initial attempt to regress the FSR on the residuals from the four covariate models, one for each stand structure variable, resulted in four sites being identified as outliers consistently for tree diameter variability, the density of large *P. menziesii*, and total basal area (Figure 5). These are high-elevation mesic sites, dominated by shade-tolerant species, within the Pacific Silver Fir and Mountain Hemlock forest types. These sites contain few large *P. menziesii*, but those that are present have survived multiple fires, so that values for the FSR are high. However, the other tree species that dominate these sites (mainly *A. amabilis* and *T. heterophylla*) are less fire resistant than *P. menziesii*, having thinner bark, lower crowns and shallower roots. Therefore, a fire that would be of low severity for *P. menziesii* might be of high severity for most of the trees in these stands. As a result, the ecological interpretation of the FSR for these stands is likely different from elsewhere, and it is not surprising that these stands emerged as outliers in the analysis. The four sites were omitted from all of the statistical analyses described below. Description of these outlier sites suggests that the scope of inference for this study includes stands within the Western Hemlock and Pacific Silver Fir forest types of greater than 10% relative *P. menziesii* density, considering trees at least 20 cm in diameter.

Considering the full regression models, descriptors of stand structure vary according to fire history, stand age, and topography (Table 1). Shade-tolerant density increases with increasing elevation, northeastness, stand age, and non-stand-replacing fires (i.e., FSR). Tree diameter variability decreases with increasing elevation and northeastness, but

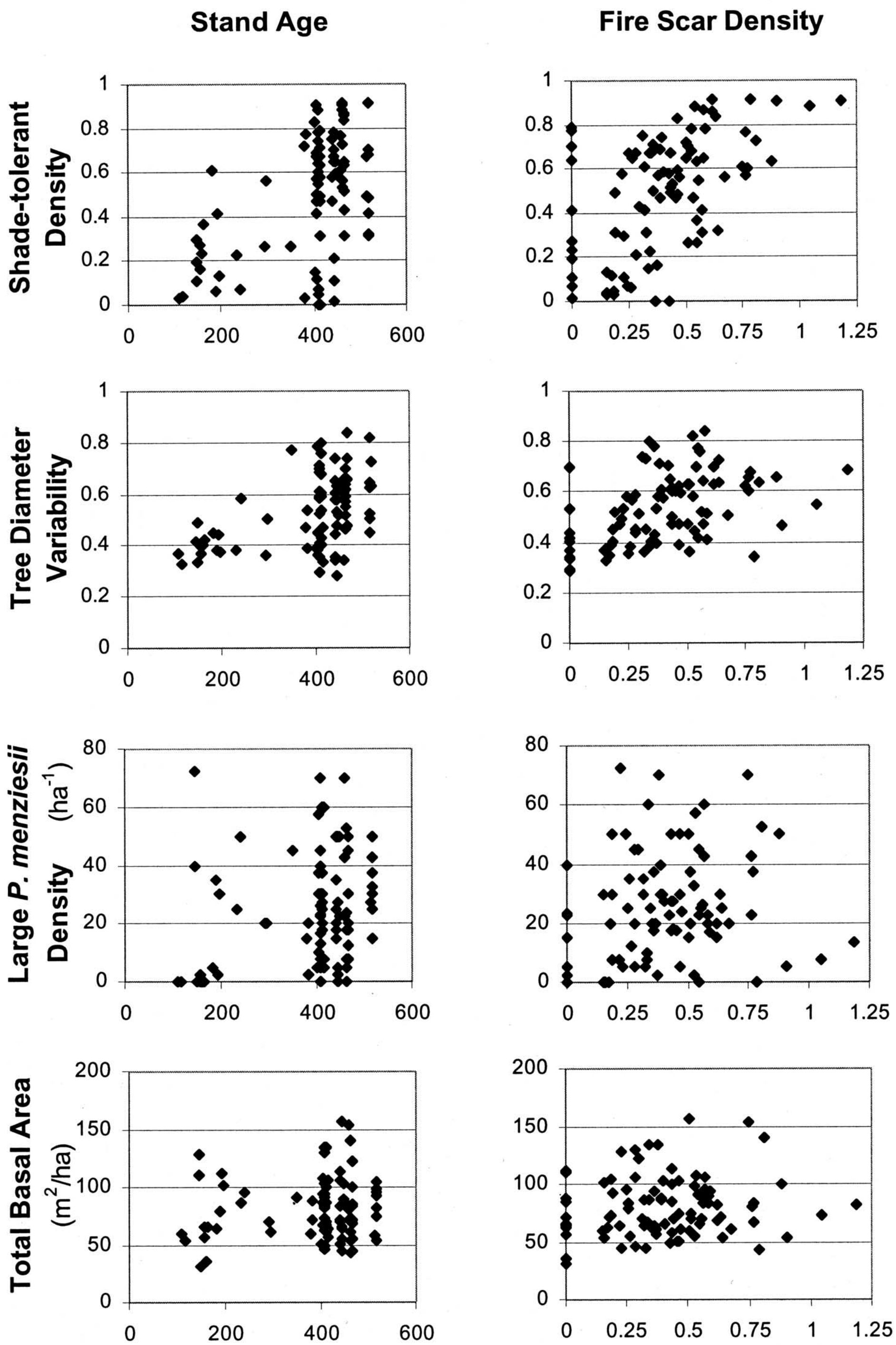

Figure 4. Matrix scatter plot showing the four measures of stand structure (rows) as a function of stand age (years) and the FSR (columns). All variables are shown untransformed. Tree diameter variability represents the coefficient of variation expressed as a proportion, and shade-tolerant density represents the relative density of shade-tolerant tree species, also expressed as a proportion.

increases with stand age and FSR, with the latter being the most important effect (as measured by the slope of the regression relationship). The density of large *P. menziesii* is greater on more southwesterly (drier) slopes, for older stands (a relatively minor effect), and for stands with greater FSR. Total basal area is similarly greater on drier slope aspects and for stands with greater FSR. The proportion of the overall variance explained by the regression models varies from 0.51 for the shade-tolerant density to 0.08 for total basal area (Table 1).

The FSR has a significant positive relationship with each of the four stand structure variables after accounting for the

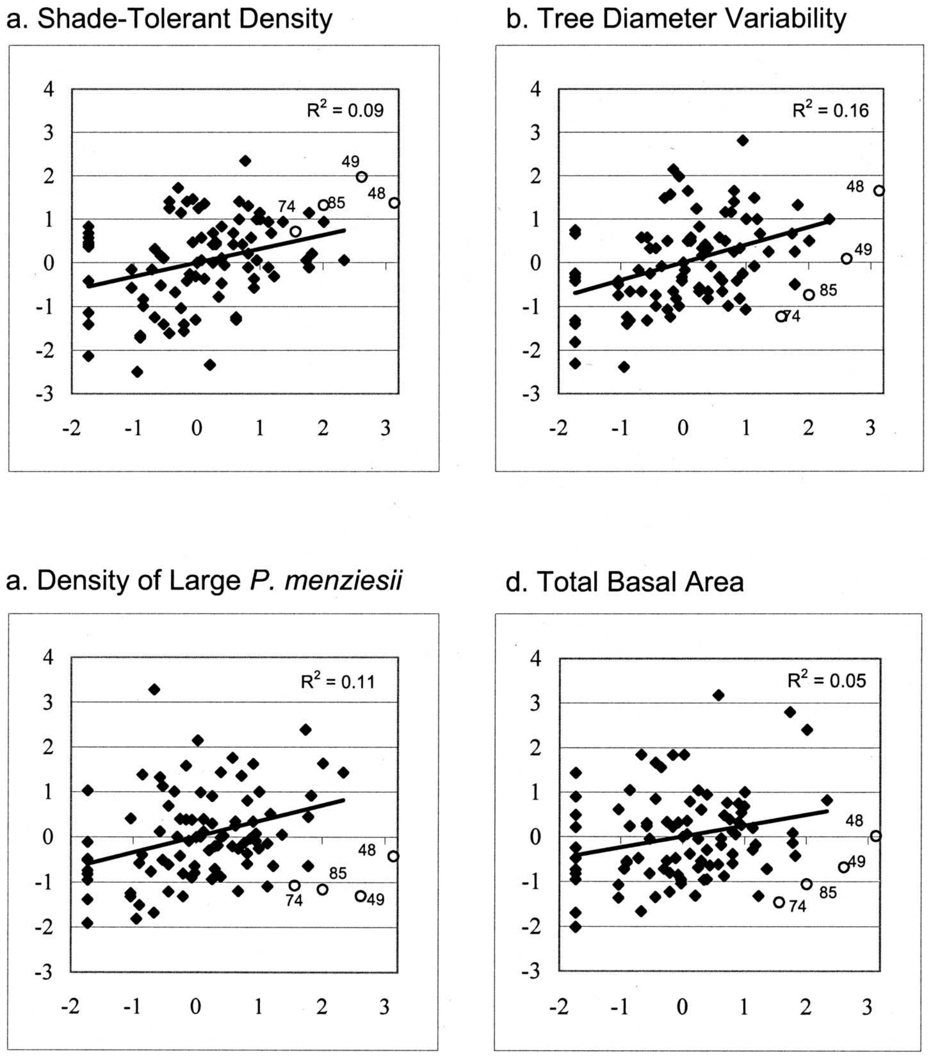

Figure 5. Partial residual plots showing the association between the standardized, arcsine square root transformed FSR (x-axis) and the standardized residuals from the covariate regression models for each of the four stand structure variables (y-axis). The covariate models predict each stand structure variable as a function of elevation, northeastness, and stand age. Outlier sites 48, 49, 74, and 84 are indicated. Also shown are the ordinary least squares regression lines and the partial R^2 values, which represent the proportion of variance explained by the FSR after taking into account the variance explained by the covariate model.

effects of topography and stand age (Table 1, Figure 5). Therefore, all three hypotheses concerning the association between FSR and various aspects of stand structure cannot be rejected. However, the FSR explains a relatively small percentage of the remaining variance, with partial R^2 values of 0.09 (shade-tolerant density), 0.16 (tree diameter variability), 0.11 (density of large *P. menziesii*), and 0.05 (total basal area). A relatively high standardized partial regression coefficient, combined with a relatively low partial R^2 value, indicates a strong effect (steep slope of the regression line) coupled with a high variance (wide scatter around the regression line). Note that Figure 5 uses standardized units for all variables, so that relationships are directly comparable.

Path coefficient analysis shows that the hypothetical model (Figure 3) provides a reasonable structure for analyzing underlying relationships among the variables of interest, except that topographic variables are significant predictors of neither stand age nor the FSR, so those relationships are omitted in all four path analysis diagrams (Figure 6). Every 1-unit increase in standardized FSR is associated with a 0.43-unit increase in standardized stand age, so this relationship is present in path analyses for all four stand structure variables (Figure 6). Other relationships vary depending on the stand structure variable considered.

The path analysis diagrams allow partitioning of the effect of stand age into direct and indirect components. In this case, indirect effects of stand age on stand structure arise from the positive association between stand age and the FSR: older stands have had more time to experience non-stand-replacing fires, which in turn are positively associated with each of the stand structure variables (Table 1). The full effect of stand age on stand structure is the sum of

Table 1. Summary of standardized partial regression coefficients and multiple R^2 values for the four full regression models fit to each stand structure variable. The numbers below the + or − symbols are standardized partial regression coefficients (beta weights), which indicate the relative strength of the relationship between each predictor and response variable (i.e., the steepness of the slope of the regression line) given the effects of the other predictor variables. The + or − signs indicate the direction of the relationship, and the number of + or − symbols is scaled to the beta weight. Multiple R^2 values are for the full regression model, including all four predictor variables (where significant at $\alpha = 0.05$).

Variable	Elevation	Northeastness	Stand age	FSR	Multiple R^2
Shade-tolerant density	+ 0.20	++ 0.37	+ 0.29	++ 0.32	0.51
Tree diameter variability	− 0.12	− 0.21	+ 0.27	+++ 0.51	0.40
Large *P. menziesii* density	NS	−− 0.32	+ 0.11	++ 0.44	0.26
Total basal area	NS	− 0.21	NS	+ 0.26	0.08

direct and indirect effects, with the direct effect being the path coefficient between stand age and the stand structure variable, and the indirect effect being the product of the path coefficients from stand age to the FSR, and from the FSR to the stand structure variable (Sokal and Rohlf 1981). If the path analysis model is adequate, the full effect should be roughly equivalent to the correlation coefficient between stand age and the stand structure variable.

For every model, indirect effects of stand age are significant, and the full effect of stand age is approximately equal to the correlation coefficient. For shade-tolerant density, the indirect effect of stand age is 0.14 (i.e., 0.43 × 0.32), compared to a direct effect of 0.29. The full effect is therefore 0.43 (i.e., 0.14 + 0.29), which approximates the observed correlation coefficient of 0.45. For variation of tree diameters, the indirect effect, direct effect, and full effect of stand age are 0.22, 0.27, and 0.49, respectively (r = 0.42). For density of large *P. menziesii*, these same values are 0.19, 0.11, and 0.30 (r = 0.23). For total stand basal area, there are no significant direct effects of stand age, and the strength of indirect effects is 0.11 (r = 0.13).

Discussion

Utility of the Fire Scar Ratio

While the FSR appears to explain variation in forest structure in a meaningful way, further research is required to see how well it represents the historical frequency of non-stand-replacing fires. For the Blue River study area, the FSR

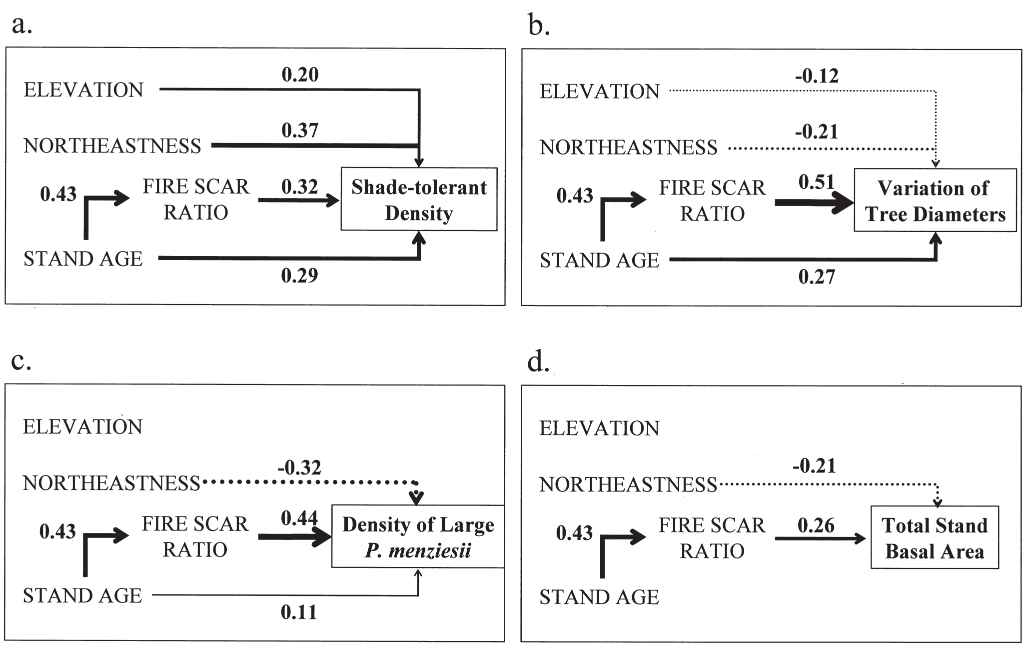

Figure 6. Path analysis diagrams for the hypothetical model shown in Figure 2 applied to each of the four stand structure variables. Nonsignificant influences hypothesized in Figure 2 are not displayed here. The standardized partial regression coefficient (beta weight) is displayed for each influence, and the line width of each arrow reflects the magnitude of the relevant beta weight. Negative influences are displayed as dotted lines.

has a fairly strong correlation ($r = 0.66$) with the frequency of low-severity fires, as estimated using all available fire history and age structure information (Weisberg 1998). For another fire history study in a nearby area (Weisberg 1997), the correlation between the FSR and the estimated frequency of low-severity fires was similarly strong ($r = 0.72$). However, the estimation of fire severity in both studies is approximate at best, because cross-dating procedures were not employed and there may have been cases where multiple low-severity fires were interpreted as occurring at slightly different years when actually there was a single high-severity fire occurring in a single year. For this reason, the FSR was used as a proxy for the frequency of non-stand-replacing fire in this study.

One limitation of the FSR is that it cannot discriminate between sites that have many trees scarred by a single fire from those that have experienced many fires, each scarring few trees. Therefore, fire frequency and severity are integrated within a single metric (Figure 2). Another limitation is that the FSR may represent a comparable proxy for the frequency of non-stand-replacing fire only among sites of similar forest type and overall climate, as indicated by the four outlier sites of this study. However, the FSR has the advantage of not requiring high-resolution dating in fire history reconstruction, including sample collection and cross dating, which is a time-consuming dendrochronological method (Stokes and Smiley 1968) that is essential for accurate fire history reconstruction (Weisberg and Swanson 2001). The FSR can be estimated rapidly and efficiently wherever recent clearcuts are widespread, facilitating its use in landscape-level studies. Nevertheless, it is essential that the specific relationship between the FSR and fire regime parameters be more clearly understood before it is widely applied. It is difficult to directly test the hypothesized relationships shown in Figure 2 because the severity of all but the most recent fire events cannot be reliably reconstructed. However, it would be useful to evaluate scarring and mortality patterns of recent burns in the context of how such burn patterns might, over time, influence the FSR.

Effects of Non-Stand-Replacing Fires on Forest Composition

Non-stand-replacing fires may influence forest composition by either accelerating or decelerating forest succession toward late-seral, shade-tolerant tree species. Disturbance-accelerated succession, where disturbances kill pioneer tree species and create conditions favorable for growth and regeneration of late-seral species, has been described for several North American forests. For example, Abrams and Scott (1989) demonstrate "disturbance-mediated accelerated succession" for two forest types in Michigan. Logging hastened the conversion of sugar maple forest to a northern white cedar community, and clearcutting followed by burning changed a jack pine forest to one dominated by hardwoods.

Alternatively, non-stand-replacing fires may slow succession toward shade-tolerant overstory tree species by killing *Tsuga*, *Thuja*, and *Abies* regeneration in the understory and killing a higher proportion of overstory trees of these species than *P. menziesii* (Morrison and Swanson 1990, Spies 1997). Such fires would maintain a *P. menziesii*-dominated, old-growth forest for a longer period of time. This would be analogous to the role of periodic fires in maintaining *Pinus-Quercus* forest by eliminating shade-tolerant species, such as *Acer rubrum*, *Fagus grandifolia*, and *Tsuga canadensis*, in Appalachian and northeastern US forests (Little 1974, Abrams et al. 1995).

For the Blue River study area, sites with a greater FSR contain a greater component of shade-tolerant tree species, after taking into account the effects of elevation, aspect, and stand age. Assuming the FSR is a useful proxy for the prevalence of non-stand-replacing fire, this result suggests that non-stand-replacing fires have accelerated succession by creating small canopy gaps, which facilitate the regeneration of shade-tolerant trees. However, the effect of the FSR on relative shade-tolerant density is highly variable after taking into account the other effects (partial $R^2 = 0.09$) (Figure 5a). It is likely that low-severity underburns and fires that initiate patchy regeneration within old-growth forests play dual roles, in some cases accelerating succession by facilitating shade-tolerant regeneration and canopy accession, and in other cases retarding succession by killing shade-tolerant regeneration. Fires probably do not accelerate succession toward a shade-tolerant dominated canopy as often or as rapidly as nonfire disturbances such as windthrow, catastrophic windstorms, or insect epidemics, which cause canopy gaps but allow advance regeneration to survive (Spies and Franklin 1988).

Effects of Non-Stand-Replacing Fires on Forest Structure

The results suggest that the occurrence of non-stand-replacing fires has favored variability in tree diameter sizes and has favored larger trees for stands of a given age and topographic setting (Figures 5 and 6). Periodic fires may have reduced tree density and shrub cover, leading to successful tree seedling establishment and creating localized areas where height and diameter growth of surviving trees might be stimulated by release from competition (i.e., a "thinning effect"). Tappeiner and others (1997) have suggested that such fires may have contributed to the historically open stand structures, long regeneration periods, and rapid growth rates reconstructed for *P. menziesii* stands in the Oregon Coast Range and elsewhere in western Oregon (Poage and Tappeiner 2002). Because high variability in tree size, large trees, and high basal area are all important features of old-growth stands in the Pacific Northwest (Franklin et al. 1981, Spies and Franklin 1988, Spies and Franklin 1991) and elsewhere (McCarthy and Bailey 1996, Timoney and Robinson 1996), it is likely that non-stand-replacing fires have fostered the development of old-growth structure in the study area. In this regard, the forests of the central western Oregon Cascades are similar to those of the drier, southern *P. menziesii* forests of the Klamath Mountains, where a mixed fire regime of mostly low- and moderate-severity fires was found to be typical, and to be important for creating the highly variable stand structures now found in that region (Taylor and Skinner 1998). However, the role of episodic stand-replacing fires has clearly not been as important in the Klamath Mountains as for most of the central Oregon Cascades.

Vertical stand structure was not explicitly considered in this study, although the vertical component of forest structure appears to be highly important for a variety of lichen, invertebrate, and vertebrate species (Franklin et al. 2002). However, one would expect that the effects of non-stand-replacing fire on increasing diameter class heterogeneity would be strongly associated with increased vertical heterogeneity as well.

Topographic Influences on Stand Structure

Stands of the same age and of similar fire history, as inferred from the FSR, were observed to have different structures. Much of this variation was explained by differences in simple topographic predictor variables. Over the elevational range of sites used in the statistical analysis (575–1,361 m), the association of slope aspect with stand structure was much greater than that of elevation (Table 1, Figure 6). Differences in elevation and slope aspect reflect underlying spatial patterning of factors influencing tree growth, establishment, mortality, and decomposition. Such factors include: sunlight availability, temperature regime, snowpack, length of the growing season, precipitation, soil moisture, relative humidity, soil depth, and nutrient availability.

The strong influence of wet aspects and high elevations on shade-tolerant density (Table 1, Figure 6) is profoundly important for shaping the structure of forest stands. Detailed study of two sites within the study area, at the transition between the Western Hemlock and Pacific Silver Fir forest series, found little tree regeneration of any species beneath canopies where *T. heterophylla* was a major component (Stewart 1986a, 1988). For hemlock-dominated stands, regeneration was limited to canopy gaps that did not form in large numbers until 300–400 years after stand initiation. Lower tree regeneration and forest forb cover has also been observed under *T. heterophylla* canopies in southeast Alaska (Alaback 1982). Shade-tolerant tree species can occupy a stand at higher densities and continue to grow larger, shading out the understory and resulting in high-density (for their age) stands with high basal area, little structural heterogeneity, and few very big or very small trees. Where shade-tolerant species occupy the overstory, they may inhibit the development of a subcanopy layer by forming a dense upper canopy and so reduce vertical heterogeneity. Understory composition might be limited to the most shade-tolerant species. Higher basal areas of shade-tolerant species on wetter sites have also been observed in a regional study of 196 *P. menziesii* stands in Washington and Oregon (Spies and Franklin 1991) and for the Bull Run watershed in the western Cascades (Sinton et al. 2000).

Wet aspects and higher elevations also have lower total basal area, lower density of large *P. menziesii*, and reduced tree size variability (Table 1, Figure 6). Such environments represent the harshest conditions for *P. menziesii* establishment and growth in the study area (Zenner 1998) due to cold temperatures, persistent snowpack, less sunlight for photosynthesis, and shallow, unstable soils. In addition, the greater overstory component of shade-tolerant species on more northerly slopes might compete with *P. menziesii*, inhibiting its diameter growth and reducing stand basal area. The development of large tree sizes, multiple horizontal and vertical strata, and large snags and logs, characterizing typical old-growth structure for a variety of ecosystems (Franklin et al. 1981, Vora 1994, McCarthy and Bailey 1996), may occur more slowly on moist, snowy sites. However, the tendency for these environments to experience a lower frequency of stand-replacing fires (Weisberg 1998) may counteract this effect.

Stand Age and Forest Structure

The path analysis models suggest the hypothesis that much of the total effect of stand age on different aspects of stand structure may be due to indirect effects as mediated by non-stand-replacing disturbances, such as fire (Figure 6). Older stands may have the structures we observe (increasing heterogeneity with age) mainly because they have had more opportunity to experience low-severity disturbances that open up the forest canopy and allow regeneration in large gaps (Figure 6). For example, a fire history survey of 49 old-growth (age 400–550 years) stands in the same study area estimated that the modal number of non-stand-replacing fires experienced since the last stand-replacing fire was 3 (range: 0–7) (Weisberg 1998).

The direct effects of stand age, apart from fire history as represented by the FSR, are likely due to successional processes or to other non-stand-replacing disturbance types such as windthrow or bark beetle epidemics. Successional processes might include normal gap phase succession, as well as increased accumulation of seeds and seedlings of shade-tolerant species in older stands, even in the absence of discrete gap formation. Such direct effects were more important for shade-tolerant density and tree diameter variability than for the density of large *P. menziesii* and total basal area (Figure 6). This is a logical result, because increasing densities of small shade-tolerant trees establishing in canopy gaps should lead to increases in the former two variables, but would not be expected to greatly influence the two variables that have mainly to do with size of overstory trees.

These results must be interpreted in light of the limited distribution of stand ages available for sampling (Figure 4). There were no sampled stands younger than 100 years, which, in *P. menziesii* forests, typically marks the end of that period of stand structural development when live bole biomass accumulates (Acker et al. 2002, Franklin et al. 2002). Had younger stands been available, it is very likely that there would have been important direct effects of stand age on the two tree-size-related variables. It is also possible that, had I sampled some stands that were 800 years old, a time period approaching the longevity of *P. menziesii*, there might have been greater direct effects of stand age on shade-tolerant density and tree diameter heterogeneity, as old trees die and gap dynamics become even more important.

Scale Dependence of Disturbance Effects on Forest Stand Structure

Most previous studies of the relationships between fire history and stand structure in the western Cascades have focused on a small number of stands. All of these studies have found strong relationships between the frequency and severity of non-stand-replacing disturbances and stand structure, whether in the red fir (*Abies magnifica*) forests of the southern Cascades (Taylor and Halpern 1991), dry forests successional to *P. menziesii* in the central western Cascades (Means 1982), or more mesic *P. menziesii* forests that are successional to *T. heterophylla* or *A. amabilis* (Klopsch 1985, Stewart 1986a, 1986b). Fewer studies have described these relationships over large landscapes, with different forest types and physical environments represented. For a large landscape in the Oregon Coast Range, hillslope forest structures were significantly associated with fire history, while species composition in these same forests was relatively independent of fire history but varied along climatic gradients (Wimberly and Spies 2001). In the Oregon Cascades (this study), both diameter class structure and species composition are found to be significantly influenced by fire history. However, a regional-scale study of Oregon forests found that species composition was strongly related to climatic variables, but only weakly related to disturbance history (Ohmann and Spies 1998).

The extent of the study area appears to be very important for whether the physical environment or disturbance history has played a major role in determining forest structure. It seems likely that disturbance processes dominate at stand scales, while environmental and climatic gradients dominate over regional scales. At watershed or landscape scales (this study; Wimberly and Spies 2001), both disturbance history and environmental variability play important roles.

Cumulative and long-term effects of low- and moderate-severity fires are likely complex. Fires may simplify stand structures by killing shade-tolerant regeneration, or add heterogeneity by killing patches of overstory trees. The effects of fire suppression since the early 1900s are also unclear. For many drier forests of North America, it has been widely documented that suppression of the historically frequent, low-severity fire regime has resulted in unprecedented increases in stand density, surface fuels, and ladder fuels, resulting in an anthropogenic shift in fire regime where the probability of stand-replacing crown fires may now be greater (e.g., Cooper 1960, White 1985, Covington and Moore 1994, Morgan et al. 1994). For more mesic forests, it is less likely that fire occurrence is fuel-limited, so increases in fuel loadings should not be a major factor. Effects on stand structure are likely to be more subtle and difficult to detect and may not become apparent until very long time periods have passed. However, the long-term structural and compositional effects of prolonged fire suppression could have broad ecosystem implications for nutrient cycling and forest productivity. Where the forest management practice is to use information about natural disturbance regimes as a guide for management (Cissel et al. 1999, Landres et al. 1999), it seems prudent to include non-stand-replacing fires as a key ecosystem process, whether by using prescribed fire or allowing naturally occurring non-stand-replacing fires to occur.

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