## AN ABSTRACT OF THE THESIS OF

Matthew N. Goslin for the degree of Master of Science in Forest Science presented on April 14, 1997. Title: Development of Two Coniferous Stands Impacted by Multiple, Partial Fires in the Oregon Cascades: Establishment History and the Spatial Patterns of Colonizing Tree Species Relative to Old-Growth Remnant Trees.

Abstract approved:

Signature redacted for privacy.

Thomas A. Spies

Trees that survive disturbances can form a prominent legacy which may influence post-disturbance successional pathways. The effects of biological legacies on community dynamics is a critical question in ecology. In the present study, I examined two mapped stands in which old-growth remnant trees, survivors of partial fires, emerge above a lower canopy of mature trees which had regenerated after these fires. In the first part of this study, I reconstructed the history and patterns of the most recent fires and the establishment history of the post-fire regeneration. At the Eagle Rock study site, fires occurred in 1848, 1870 and 1892. At the Wolf Rock site, a fire burned in 1892, and fires in 1829 and 1896 appeared likely. Fires burned under the remnant trees, and no area remained unburned during the nineteenth century. Cohorts were layered and interspersed among each other rather than juxtaposed as discrete patches. Regeneration of both early seral Pseudotsuga menziesii and late seral Tsuga heterophylla was initiated by the fire events, and neither displayed continuous recruitment. At both sites, Pseudotsuga regenerated more quickly than Tsuga. The median establishment time for both Pseudotsuga and Tsuga was longer at Eagle Rock (south-facing) than at Wolf Rock (northwest-facing). In the second part of this study, I described the spatial patterns of colonizing tree species relative to the remnant

trees. The spatial patterns of post-fire species were clearly dependent upon the remnant tree pattern. Species were typically dispersed away from remnant trees, but several species, *Castanopsis* and *Cornus nuttallii* at Eagle Rock and *Tsuga* at Wolf Rock, were aggregated around remnant trees. *Tsuga* patterns differed between sites. Consistent with its shade tolerance, *Tsuga* was independent of or aggregated around remnant trees at Wolf Rock, but was unexpectedly dispersed away from remnants at south-facing Eagle Rock. The within-group patterns of remnant trees were clustered, as were the patterns of almost all post-fire species. The clustering of post-fire species may reflect the spatial dependence of each species' pattern upon the clustered remnant tree pattern which ,itself, is the outcome of the patchy pattern of partial fire. The aggregation and dispersion of different post-fire species relative to remnant trees suggests that remnant trees or remnant-associated features from the pre-disturbance community differentially facilitate or inhibit colonizing species, thus influencing the direction of post-disturbance succession. Development of Two Coniferous Stands Impacted by Multiple, Partial Fires in the Oregon Cascades: Establishment History and the Spatial Patterns of Colonizing Tree Species Relative to Old-Growth Remnant Trees.

by

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### Development of Two Coniferous Stands Impacted by Multiple, Partial Fires in the Oregon Cascades: Establishment History and the Spatial Patterns of Colonizing Tree Species Relative to Old-Growth Remnant Trees

#### **Chapter 1: General Introduction**

#### Introduction and literature review

#### Forest management questions

Forest management in the Pacific Northwest has been at the center of intense controversy and is currently in a state of transition. From the 1940s through the 1980s, a focus upon wood fiber production led to the harvest of natural forests and the cultivation Douglas-fir (*Pseudotsuga menziesii*) plantations. Clearcutting, burning woody residue, planting seedlings and suppressing competing vegetation were practiced as a means toward efficient harvest and regeneration. These practices were often perceived and justified as being consistent with prevailing concepts of natural disturbance and succession in the Pacific Northwest (Swanson and Franklin 1992) -- the dominant disturbance being that of catastrophic wildfire with succession typically beginning with the regeneration of an even age, Douglas-fir dominated stand. Currently, however, enhanced understanding of the ecosystems and changing social values have called into question these forest practices.

Revised forest practices, often described as "Ecosystem Management" or "New Forestry," have emerged from studies of disturbance patterns, ecosystem responses to disturbance and the structure and function of natural forest stands. Reconstructions of wildfire histories and landscape patterns have revealed complex fire regimes in which low and moderate severity burns are also a significant component. Residual elements which persist through a disturbance -- coarse woody debris, soil organisms, surviving plant parts -- have been found to be critical for the recovery of disturbed ecosystems (Franklin 1989). Even the most catastrophic disturbances (e.g. Mt. St. Helens' volcanic eruption) are incomplete, leaving behind important legacies from the previous community (Franklin 1989). Studies of old-growth forests have described a structural complexity which may be critical for its ecosystem functions and for its role as habitat for old-growth dependent species. This complexity is in marked contrast to the simplification promoted by previous forest practices (Swanson and Franklin 1992).

The underlying theme of ecosystem management is to promote more natural levels of complexity in managed stands by better mimicking natural disturbance (Swanson and Franklin 1992). Of the practices promoted by ecosystem management, one of the most prominent is the retention of live trees in harvested stands. The retention of live trees is intended to enhance the structural complexity of the regenerating stand, leading to a multi-storied canopy. Retained trees also serve as a future source of snags and coarse woody debris, enhancing habitat for species dependent on these features (F.E.M.A.T. 1993, Hansen et al. 1995). It is also hypothesized that retained trees may serve as refugia and dispersal centers for mycorrhizae, nitrogen-fixing bacteria, epiphytic lichen, arthropods and small mammals (F.E.M.A.T. 1993, Hansen et al. 1995).

While the principles guiding ecosystem management are derived from a wealth of ecological research, less data are available to indicate that the specific practices, such as live-tree retention, will lead to the desired outcomes (DeBell and Curtis 1993, Thomas et al. 1993). Concern remains over the growth loss which will occur in the regenerating stand, the potential loss of retained trees to windthrow and the potential for "negative" biological legacies such as pathogens (DeBell and Curtis 1993, Thomas et al. 1993). Unanswered questions include the appropriate amount and pattern of retained trees and the species mix and management strategy for the regenerating cohort. Ecosystem management practices and their hypothesized outcomes need to be tested experimentally, but reliable results may take decades to accumulate. Alternative avenues of investigation include the use of models and the use of retrospective studies.

Models have been used to predict stand-level growth, economic values and tree species abundance as well as the response of bird species to the modeled habitat (Birch and Johnson 1992, Hansen et al. 1995). Many models, however, were initially derived from studies of even age stands and are limited by the relative lack of data from mixed-species, multiple age class stands.

Retrospective studies suggest possible outcomes of management practices by reconstructing the history of forest stands which experienced disturbances analogous to the proposed harvest practices (at least in severity of tree kill) (Thomas et al. 1993, Acker 1995). Several retrospective studies of two-storied stands have been completed. Wampler (1993) and Hoyer (1993) examined height growth patterns of individual understory trees influenced by residual trees in Washington state. Acker (1995) and Zenner (1995) analyzed a set of 14 paired plots (with and without residual trees) in the Willamette National Forest to assess the impact of residual trees upon stand-level growth and tree species abundance. This set of plots was also used to develop individual tree growth equations, assess lichen abundance and describe understory shrub and herbaceous communities. Rose (1993) assessed residual tree effects on stand-level growth using a large collection of U. S. Forest Service stand inventory plots encompassing the National Forests along the Cascade Mountains from southern Washington to southern Oregon.

#### Study synopsis and ecological questions

In the present study, I complement these retrospective studies of two-tiered stands with a detailed examination of two mapped stands ( $\approx 2$  ha) rather than a larger collection of smaller plots. Both stands are characterized by emergent remnant trees, old (300 - 600 yrs.) survivors of multiple partial fires, intermixed among a lower canopy of mature trees which regenerated after nineteenth century fires. The two stands represent different developmental pathways with the lower canopy of one stand dominated by shade-intolerant *Pseudotsuga* and the other by shade-tolerant *Tsuga*. Complementing previous retrospective

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studies which focused upon growth impacts, the present study emphasizes developmental history and species patterns. In the first part of the study, I reconstruct the recent history (<200 yrs.) of fire and regeneration in each stand. In the second part, I describe withinstand species and crown class patterns relative to the remnant trees using point pattern analysis. The study was motivated by both management and ecological questions. The practice of live-tree retention harvests has raised questions about the proper application of this practice and its potential outcomes. Successional patterns after partial fire are not well known relative to those after catastrophic fire, leading to questions about the distinctive characteristics of vegetation change and patterns after partial fire. Specifically, are the species patterns and the direction of vegetation change after a partial fire dependent upon the pattern of residual elements which survive from the previous community?

Most studies of post-disturbance succession in the Pacific Northwest have not focused on partial disturbances, but on the extremes of large-scale catastrophic disturbances and small-scale disturbances in an undisturbed matrix. The abundance of clear-cuts and the occurrence of catastrophic fires in this century has led to many studies of early succession after such large, catastrophic disturbances (Isaac 1940, Munger 1940, Isaac 1943, Agee and Huff 1987, Halpern 1988, Halpern 1989, Halpern and Franklin 1990, Huff 1995). Furthermore, chronosequences of successional trends have typically used stands which developed after single catastrophic fires, allowing straightforward age categories (Schoonmaker and McKee 1988, Halpern and Spies 1995, Huff 1995). Interest in the processes driving old-growth forest development has led to investigations of regeneration in small canopy gaps (Stewart 1986a, Spies and Franklin 1989, Canham et al. 1990, Spies et al. 1990, Moeur 1991, Wilson 1991, Gray 1995). Between the extremes of large catastrophic fires and small canopy gaps lies a range of intermediate disturbances, one of the most prevalent being partial-mortality fires which create multiple cohort stands. With the exception of Means (1982) and Stewart (1986b), little attention has been given to the history and patterns of communities which developed after partial fire.

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#### Reconstruction of forest stand history

In the first part of this study, I describe the size structure and reconstruct the recent history (<200 yrs.) of fire and establishment for the two stands. Reconstructions of stand history and descriptions of population structure have been critical in understanding vegetation change, species' life history strategies and the interaction between disturbance and vegetation change.

Stand reconstructions have led to revised concepts about vegetation change and its interaction with disturbance. Techniques of detailed stand reconstruction were pioneered by Henry and Swan (1974) and Oliver and Stephens (1977) in northeastern hardwood forests. These reconstructions found no evidence for gradual, autogenic succession in these forests. Instead, disturbance-initiated species change was suggested by discontinuous age distributions and establishment dates clustered around fire and hurricane disturbances. Furthermore, species changes occurred individualistically (Henry and Swan 1974, Oliver and Stephens 1977).

In addition to investigating patterns of whole stand development, age distributions have been used to investigate particular species' life history strategies. *Thuja plicata* age structure in old-growth *Thuja* stands suggest that this species' low mortality rates and great longevity allow its persistence in spite of remarkably low regeneration rates (Daniels 1994). In late successional *Abies amabilis* stands, *Abies* age structures are highly variable, continuous recruitment is rare and regeneration is highly correlated with low canopy or herbaceous cover. These patterns suggest that this species persists without continuous seedling establishment, opportunistically occurring where canopy and herbaceous cover has been opened (Wilson 1991). Stewart and Rose (1990) describe how differing life histories (low recruitment/ low mortality versus high recruitment/ high mortality) in a New Zealand *Nothofagus* stand promote the coexistence of two species which apparently lack strong differences in shade tolerance or regeneration niches.

In the Pacific Northwest, reconstructions of stands have indicated that species can play multiple successional roles depending on environmental conditions and disturbance history. On dry sites in the Oregon Cascades, size distributions suggested continuous regeneration of shade-intolerant Pseudotsuga menziesii and an absence of the typical Tsuga heterophylla understory regeneration. Reconstructions of age distributions and fire history indicated that Pseudotsuga's dominance of all size classes resulted from frequent partial fires which opened up small areas of the stand (Means 1982). In the wet Olympic Mountains, an area characterized by large, infrequent catastrophic fires, shade-tolerant Tsuga heterophylla can be an important invader, with discontinuous regeneration occurring immediately after fire. A second period of Tsuga regeneration typically begins much later (>100 yrs.), presumably after its preferred seedbed, decayed coarse woody debris, has accumulated (Huff 1995). In the Oregon Cascades, age distributions of Pseudotsuga and Tsuga in unburned old-growth stands indicated that the abundance and timing of Tsuga regeneration later in the stand's history was linked to the abundance of Tsuga in the initial regeneration (Stewart 1986a). If Tsuga made up a large proportion of the initial regeneration, subsequent regeneration of Tsuga beneath the canopy was significantly delayed, presumably due to greater density of Tsuga crowns relative to Pseudotsuga crowns (Stewart 1986a).

## Point pattern analysis in forest ecology

In the second part of this study, I describe the spatial relationship between firesurviving remnant trees and post-fire individuals of different species and size classes. The guiding question in this analysis is whether the patterns of the post-fire regeneration are dependent upon the patterns of the surviving trees. I assessed these patterns using two different methods of point pattern analysis: Hamill-Wright refined nearest neighbor analysis and Ripley's K(t). A detailed discussion of point pattern analysis theory and methodology is presented in the second part of this chapter.

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Point pattern analysis has been applied to many questions in forest ecology, with particular emphasis upon changes in pattern that occur with stand development. One of the most frequently observed patterns in forest stands is the clustering of smaller individuals and the regular spacing of larger individuals (Cooper 1961, Christensen 1977, Bonnicksen and Stone 1981, Good and Whipple 1982, Turner and Franz 1985b, Sterner et al. 1986, Stewart 1986b, Stewart and Rose 1990, Moeur 1991). This trend toward increasing uniformity with increasing size has been hypothesized to be the product of competitive interactions and non-random thinning mortality which left greater spacing between the larger, surviving individuals. Such processes should yield changes in pattern with time, not just changes with size at a given point in time. Several authors have indeed documented a shift with time from clustered or random patterns toward regularity (Laessle 1965, Christensen 1977, Ghent and Franson 1986, Kenkel 1988, Rebertus et al. 1989, Duncan 1991), and a few have demonstrated that this pattern change differs from that expected under random mortality (Ghent and Franson 1986, Kenkel 1988, Duncan 1991). The spatial relationship between living and dead individuals has also suggested that there are two phases in the establishment of a uniform pattern (Ghent and Franson 1986, Kenkel 1988). In the first phase, "two-sided" competition produces patches of mortality in areas of high density or stressful environmental conditions, such that surviving trees are dispersed away from clusters of dead trees. In the second phase, "one-sided" competition leads to vigorous individuals surviving and suppressing less vigorous neighbors, such that surviving and dead trees are adjacent to each other (Ghent and Franson 1986, Kenkel 1988). All of these studies have used relatively large plot sizes and began with trees at least the size of saplings. Leemans (1991), however, describes pattern change in a cohort of natural Picea abies germinants in small plots (1 \* 1 m) during a two year period. At this scale and point in development, an initial random pattern of germinants developed toward a clustered pattern of seedlings, a directional change differing from that observed for established trees (Leemans 1991). Generalizations about pattern change must also be

qualified by the fact that most studies have been conducted in non-clonal, often conifer, populations. Recent studies have suggested that mortality processes in clonal populations do not lead toward regular spacing, producing instead greater clustering (Peterson and Squiers 1995).

It is rare for studies to address whether point patterns may differ between sites with similar species composition, but different environmental features. Contrary to their expectations, Collins and Klahr (1991) found that the degree of clustering in Oklahoma oak-dominated forests was greater where soils were poorer in quality. They hypothesized that trees in the poor conditions had not reached sizes sufficient for competitive interactions to increase inter-plant distances via non-random mortality. In direct contrast to this finding, Padien and Lajtha (1992) documented random patterns in xeric, nutrient-poor juniper-pinyon forests and clustered patterns in similar forests at higher elevations with richer soils and more moisture.

While most stands exhibit a directional change toward greater uniformity with increasing size or time, the most commonly detected pattern is that of clustering, whether for all individuals in a stand or for individuals of a given species or age class. Clustered patterns have been attributed to a variety of processes depending on the context of the study. When each species is clustered in the context of a heterogeneous environment, a suggested causal agent has been niche differentiation across distinct environmental patches, particularly when each species is dispersed away from each other or when clustering increases with time or size class (Good and Whipple 1982, Hamill and Wright 1986, Padien and Lajtha 1992). Small-scale clustering has been attributed to microsite heterogeneity and regeneration niches (Stewart 1986b, Stewart 1986a, Stewart and Rose 1990, Leemans 1991, Duncan 1993), while large-scale clustering has been attributed to large-scale environmental gradients and features such as swamps or riparian areas (Whipple 1980, Good and Whipple 1982, Briggs and Gibson 1992). Clustering of cohorts has been attributed to regeneration in disturbance patches initiated at different times (Cooper 1961,

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Bonnicksen and Stone 1981, Stewart 1986b, Duncan and Stewart 1991, Duncan 1993). Fire and other disturbances have been described as producing a mosaic of even-age aggregations (Cooper 1961, Bonnicksen and Stone 1981, Stewart 1986b). Clustering of species or age classes may also be produced by limited dispersal of juveniles away from adults (Hatton 1989, Briggs and Gibson 1992, Burns 1993). Cluster size may be linked to the mode and potential distance of dispersal (Stamp and Lucas 1990, Briggs and Gibson 1992). Hatton (1989) detected clustering of each species in an Australian subalpine heath community across a homogeneous study area with no detectable environmental gradient. Hatton (1989) cites the computer simulations of Green (1989) which demonstrate that limited dispersal can produce intra-species clustering and negative associations between species without invoking disturbances or environmental heterogeneity and competition.

The role of canopy gaps in producing forest patterns has also been addressed with point pattern techniques. In Idaho coniferous forests, Moeur (1991) makes a case for gapphase regeneration: regenerating individuals were strongly dispersed from large trees, weakly dispersed from standing dead trees and aggregated around down, fallen trees. In New Zealand, younger (<80 yrs.) *Nothofagus* were often aggregated around snapped or uprooted trees and dispersed from older individuals, suggesting regeneration in windthrow-created gaps (Stewart and Rose 1990). In a novel spatial analysis of point patterns relative to patches, large saplings and subcanopy trees were positively associated with gaps in a Swedish boreal forest (Leemans 1991).

Few studies have explicitly assessed the affects of fire or other large-scale disturbances upon point patterns within a forest stand. As mentioned earlier, several studies have noted the clustering of different age classes in fire-impacted forests and have attributed this clustering to regeneration in fire-opened patches. Rebertus et al. (1989), however, used an experimental approach to assess fire effects upon pattern in the Florida sandhills. In unburned plots, oaks, pines and all individuals (both species) became less clustered with time, consistent with established observations of increasing regularity with

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time. In contrast, clustering intensity increased in burned plots, and the dispersion between the two species increased. Rebertus et al. (1989) suggest that fire's effect on pattern operates in opposition to the tendency of communities to become less clustered during disturbance-free periods of competitive interactions. In a case study of stands affected by floods of different severity, Duncan (1993) described the spatial interactions after a moderate severity flood between flood survivors and post-flood establishment by species. While some post-flood species were dispersed away from surviving trees, other species were aggregated around the survivors and another species was independently distributed. Duncan (1993) suggests that moderate severity floods may promote species diversity as a result of the differing spatial interactions between each species and the flood survivors.

## Point pattern analysis: theory and methodology

Classical statistics are founded upon a number of assumptions, including the assumption that observations are independent of each other. Geographic data violates this assumption. Processes in geographic space give rise to events and observations which are dependent upon each other -- soil samples, nesting sites, city locations and forest trees, for example. This problem has given rise to the field of spatial statistics. Spatial methods allow for dependence between events and characterize the degree and nature of this dependence.

A spatial point pattern is a set of "events," such as trees, represented by point locations  $(x_i, y_i)$  distributed within a finite planar region. Such events have been generated by some unknown mechanism, described as a spatial point process (Diggle 1983, Andersen 1992). Point pattern analysis begins by testing the null model of point patterns, that of complete spatial randomness. Complete spatial randomness is generated by a Poisson point process defined by two conditions: 1) "each location in the study area has an equal chance of receiving a point (uniformity)" and 2) the location of a point does not influence the location of any other point (independence) (Boots and Getis 1988). The alternative to these conditions is that of environmental heterogeneity (a non-uniform study area) and interaction between points. Points may interact by either attracting or repulsing each other. The alternative hypotheses to complete spatial randomness are either clustered or regular patterns (Figure 1.1) (Boots and Getis 1988).

Pattern has been described as "the zero-dimensional characteristic of a set of points which describes the location of these points in terms of the relative distances of one point to another" (Hudson and Fowler 1966 in Upton and Fingleton 1985). While a variety of statistics have been developed to describe point pattern, they are all derived from inter-event distances. Univariate or within-group patterns are described by the distances between points of the same type (Figure 1.1). Bivariate (or multivariate) patterns are described by distances between points of different type. Analogous to the null and alternative univariate patterns, bivariate patterns may be independent, aggregated or dispersed, the latter two cases reflecting attraction or repulsion between two different types (Figure 1.2).

Spatial point processes may be described in terms of their first-order and secondorder properties, analogous to the classical statistic properties of mean and variance (or covariance), respectively. First-order properties are described by  $\lambda(x, y)$ , the intensity function of the process, where  $\lambda(x, y)$  is "the limit of the expected number of events per unit area in an arbitrary small region centered on point (x, y) as the area of the region goes to zero" (Andersen 1992).  $\lambda(x, y)$  can be estimated by  $\hat{\lambda} = n/A$  where *n* is the number of points within the study region and *A* is the area of the region. In the case of complete spatial randomness, the intensity function must be constant over the entire region,  $\lambda(x, y) = \lambda$  (Andersen 1992). First-order analysis of point patterns include nearest neighbor analyses, in which the statistic is derived from the distance of each point to only its nearest neighboring point. Second-order analyses focus upon the variance of inter-event distances. They are dependent upon the spacing between all pairs of events, rather than the frequency of events (Boots and Getis 1988, Andersen 1992).



Figure 1.1. Examples of random, clustered and uniform univariate point patterns. Mapped plots are 100 \* 100 m. To the right of each map, the observed values (—) of Ripley's L(t) for that plot are tested against 90% confidence envelopes (----) from random simulations.

## independent 5 - (t) 0 -5 aggregated 10 0.00 S 0 ģ 8 5 0.0 L (t) 0 $^{\circ}$ o -5 00 -- 10 dispersed 5 ° P ିଚ 0 0 0 -5 Ð -10 00 $\circ$ -15 5 15 20 25 10 0 Distance (m)

Figure 1.2. Examples of independent, aggregated and dispersed bivariate point patterns. Mapped plots are 100 \* 100 m and show two different point types (•) and (•). To the right of each map, the observed values (---) of Ripley's L(t) for that plot are tested against 90% confidence envelopes (----) from random simulations.

In the present study, I analyzed bivariate patterns with both a first-order statistic, the Hamill-Wright statistic, and a second-order statistic, Ripley's K(t). Univariate patterns were described only with Ripley's K(t). Thorough discussions of the secondorder Ripley's K(t) and first-order statistics are provided by Diggle (1983), Upton and Fingleton (1985), Boots and Getis (1988), Moeur (1991), Andersen (1992) and Moeur (1993). Second-order theory and procedures were developed by Ripley (1977, 1979) with extensions contributed by Besag and Diggle (1977), Lotwick and Silverman (1982) and Diggle (1983). The first-order Hamill-Wright statistic was developed by Hamill and Wright (1986).

#### Ripley's K(t): univariate analysis

Because Ripley's K(t) incorporates all inter-event distances, it is a powerful technique that can potentially yield more information about point patterns than other analyses. Many point patterns are the product of processes operating at different scales. For example, at a small scale, natural thinning typically creates a minimum distance between mature forest trees, but, at a larger scale, these trees may be clumped in response to environmental patchiness. Ripley's K(t) distinguishes patterns which differ at different scales. While the statistic, K(t) is not easily interpreted on its own, it has a straightforward explanation when it is multiplied by the intensity parameter,  $\lambda$  (Upton and Fingleton 1985).

$$\lambda K(t) = \mathbf{E} [N(t)] \tag{1.1}$$

where N(t) is the number of points within a distance t of an arbitrary point. Since  $\lambda = n/A$ ,

$$K(t) = \frac{1}{\lambda} E[N(t)] = \frac{A}{n} E[N(t)] = \frac{\pi t^2}{n} E[N(t)]$$
(1.2)

Remembering that constant intensity is a requirement of complete spatial randomness, it becomes evident that, for a random pattern,  $K(t) = \pi t^2$ . That is, K(t) would be equivalent to the area of a circle with radius t from a randomly chosen point.

The estimator of K(t) is calculated as

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$$\hat{K}(t) = A \sum_{i=1}^{n} \sum_{j=1}^{n} I_{ij}(t) / n^2 \text{ where } I_{ij}(t) = 1 \text{ if } d_{ij} \le t$$

$$= 0 \text{ if } d_{ij} > t$$
(1.3)

 $I_{ij}(t)$  is an indicator function, and  $d_{ij}$  is the distance between point *i* and point *j*. In essence,  $\hat{K}(t)$  is a cumulative function. In testing whether a pattern is random, the number of observed pairs of point is summed at all test distances. At each distance, the number of observed point pairs is compared with the expected number of paired points, an expectation dependent on the point density and sample size for the study region. The summation of point pairs,  $I_{ij}(t)$ , is illustrated in Figure 1.3. For t = 5 m, each point falling within a circle of 5 m radius is paired with the center point of that circle. For example, when i = 2

(1 1)



Figure 1.3. Example plot demonstrating the calculation of Ripley's K(t). Plot includes 8 points with circular radii, t, of 5 m drawn around each point and plot dimensions of 40 \* 30 m.

and j = 3, their inter-event distance,  $d_{ij}$ , is less than t, such that they are counted as a pair. They are counted as a pair again when i = 3 and j = 2.  $I_{ij}(t)$  increases by 1 with each pairing, and it is this number of pairs that forms the data (Boots and Getis 1988). In Figure 1.3, there are four pairs of points, each counted twice, such that  $I_{ij}(5) = 8$ .

A problem is posed by the summation's exclusion of unobservable points that may exist beyond the plot boundary but within distance t. If no allowance is made for edge effects,  $\hat{K}(t)$  will be biased downward (Moeur 1993). This bias can be corrected by a method proposed by Ripley (1977).  $I_{ij}(t)$  is replaced by a weight,  $w_{ij}(t)$ , which increases the value of point pairs for which the distance apart,  $d_{ij}$ , is greater than the distance between point i and the boundary,  $d_{ib}$ . The weight,  $w_{ij}(t)$ , is the inverse of the proportion of the circumference of the circle centered on tree i and passing through tree j the circle lies outside the plot,  $w_{ij}(t) > 1$ . For rectangular plots, the calculation of  $w_{ij}(t)$  follows one of three possible cases.

1. 
$$w_{ij}(t) = 1$$
 (1.4)

if the circle is wholly within the plot (  $d_{ij} \leq d_{ib}$  ).

2. 
$$w_{ij}(t) = \left[1 - \cos^{-1}\left(\frac{d_{ib}}{t}\right) \cdot \frac{1}{\pi}\right]^{-1}$$
 (1.5)

if only one border is intersected (Figure 1.4a).

3. 
$$w_{ij}(t) = \left[1 - \left\{\cos^{-1}\left(\frac{d_{ib1}}{t}\right) + \cos^{-1}\left(\frac{d_{ib2}}{t}\right) + \frac{\pi}{2}\right\} \cdot \frac{1}{2\pi}\right]^{-1}$$
 (1.6)

if two borders are intersected (Figure 1.4b), and where  $d_{ib1}$  and  $d_{ib2}$  are the distances from point *i* to the two nearest borders.

Because the weights can become unbounded as t increases, it is necessary to restrict maximum t to one-half the shortest boundary. Ripley (1977) recommends that  $w_{ij}(t)$  be limited to  $\leq 4$  for point pairs.

Incorporating the edge correction weights, the estimator for K(t) becomes

$$\hat{K}(t) = A \sum_{i=1}^{n} \sum_{j=1}^{n} w_{ij}(t) / n^2$$
(1.7)

for all pairs of points with  $d_{ij} \leq t$ .



Figure 1.4. a) Case 2 and b) case 3 in the calcuation of the weight variable,  $w_{ij}(t)$ , used to account for edge bias in the calculation of Ripley's K(t) as discussed in the text.

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Ripley's  $\hat{K}(t)$  is often replaced by its transformation,  $\hat{L}(t)$ , proposed by Besag [in the discussion of Ripley (1977)]:

$$\hat{L}(t) = \sqrt{\frac{\hat{K}(t)}{\pi}} - t.$$
(1.8)

 $\hat{L}(t)$  is a square root transformation that makes  $\hat{K}(t)$  a linear expression and stabilizes its variance (Moeur 1993). Since  $\hat{K}(t) = \pi t^2$  for a Poisson point pattern,  $\hat{L}(t)$  is expected to be zero under the Poisson assumption. This transformation facilitates interpretation of  $\hat{K}(t)$ . If points occur farther away from each other than expected under randomness,  $\hat{L}(t)$  is negative and the observed pattern is described as regular or uniform. If points occur closer to each other than expected under randomness,  $\hat{L}(t)$  is positive and the pattern is described as clustered.

Pattern is typically described as occurring at a particular scale. For example, if points are described as clustered at a distance of 10 m, points occur in clusters with average radii of 10 m (Figure 1.1). If points are described as uniform (or regular) at a distance of 10 m, then points are evenly spaced with average distances of 10 m between them (Figure 1.1). Point patterns may exhibit different patterns at different scales. For instance, clusters with radii of 5 m may have distances of 20 m between clump centers, resulting in uniformity at 20 m. Alternatively, Ripley's K(t) may exhibit increasing clumping over all the scales examined. This indicates that smaller clumps are organized into progressively larger clumps and is described as hierarchical clumping. At some scale within the study region, clustering intensity must decline to random. However, since the scales examined must be limited to one half the smallest boundary length, the window of examined scales may not be large enough to show the decline in clumping. Ripley's K(t) analysis can be extended to analyze bivariate patterns, the spatial interaction between two different types of points. The method for estimating the bivariate  $K_{12}(t)$  is analogous to the method used for estimating the univariate K(t). The bivariate  $K_{12}(t)$  is defined by a set of functions,

$$\lambda_j K_{ij}(t) = \text{E}[\text{number of type } j \text{ points within a distance } t \text{ of an}$$
(1.9)  
arbitrary type  $i \text{ point}]$ 

where  $\lambda_j$  is the intensity of type *j* points in the study area (Diggle 1983). In the univariate case,  $\hat{K}(t)$  is derived from the distances between all points, and each point serves as both a "from" point (*i*) and a "to" point (*j*). In the bivariate case,  $\hat{K}_{12}(t)$  is calculated in the same manner, but the statistic is derived from the distances between points of different type only, and points serve as either a "from" point or a "to" point (not both) in the summation. By definition, the statistic is "symmetric"  $K_{12}^*(t) = K_{21}^*(t)$ . Therefore, it is appropriate to combine the two component estimators,  $\hat{K}_{12}^*(t)$ , the distribution of distances from type 1 to type 2 points, and  $\hat{K}_{21}^*(t)$ , the distribution of distances from type 2 to type 1 points, into a single estimator,  $\hat{K}_{12}(t)$ .

$$\hat{K}_{12}^{*}(t) = \frac{A}{n_{1}n_{2}} \sum_{i=1}^{n_{1}} \sum_{j=1}^{n_{2}} w_{ij}(t)$$
(1.10)

$$\hat{K}_{21}^{*}(t) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ji}(t)$$
(1.11)

for all pairs of points with  $d_{ij} \le t$ , where  $n_1$  and  $n_2$  are the number of type 1 and type 2 points.

Lotwick and Silverman (1983) show that the most efficient estimator is the linear combination

$$\hat{K}_{12}(t) = \frac{n_2 \hat{K}_{12}^*(t) + n_1 \hat{K}_{21}^*(t)}{n_1 + n_2}.$$
(1.12)

If the two point sets are independent of each other, the expected value of  $\hat{K}_{12}(t) = \pi t^2$ . The expected value of the square root transformation,  $\hat{L}_{12}(t) = \sqrt{\hat{K}_{12}(t)/\pi} - t$ , is 0. If  $\hat{L}_{12}(t)$  is positive, then the two point types are located at distances closer to each other than would be expected with spatial independence. This is described as an aggregated pattern. If  $\hat{L}_{12}(t)$  is negative, the pattern is dispersed, meaning the two point types are farther from each other than expected.

## Tests of significance for univariate and bivariate Ripley's K(t)

Testing the significance of a spatial statistic, such as Ripley's K(t), is problematic, because the underlying distribution of the statistic is unknown. An alternative method for assessing significance is through the use of Monte Carlo simulations. Observed values of  $\hat{L}(t)$  are compared to those of multiple realizations of  $\hat{L}(t)$  generated from a Poisson point process. In addition to circumventing the statistical distribution theory problem, the Monte Carlo approach offers other advantages. It provides an approximate test for randomness (or independence in the bivariate case) at any scale t, and it provides an excellent visual tool for comparing observed to hypothesized patterns (Moeur 1993).

In the present study, I compared observed values of  $\hat{L}(t)$  with the upper and lower boundaries of a Monte Carlo confidence envelope generated with procedure outlined by Moeur (1993) which is a variation on the procedure proposed by (Besag and Diggle 1977). In this procedure, a set of *n* random point coordinates is generated within the study area boundaries, *n* being equal to the number of points in the set being tested.  $\hat{L}(t)$  is then calculated for the set of random coordinates. These first two steps are repeated a specified number of times *s*. At each value of *t*, the values of  $\hat{L}_i(t)$  for all iterations (i = 1, ..., s) are ordered, and the smallest and largest 5% of the values are discarded. The remaining minimum and maximum values define a two-sided 90% confidence envelope.  $\hat{L}(t)$  is compared with the confidence envelope at each distance, *t*. Wherever  $\hat{L}(t)$  is greater than the envelope's upper boundary (clustered) or less than the envelope's lower boundary (regular), the observed point pattern is deemed nonrandom at that scale using a 10% acceptance level. In this study, I used 100 Monte Carlo iterations for point sets with  $n \ge$ 100 and 200 Monte Carlo iterations for point sets with n < 100. This number of iterations was based upon observations of multiple sample runs with different numbers of iterations. With large sets of points ( $n \ge 100$ ), confidence envelopes showed little change in stability when the number of iterations was increased from 100 to 200. For smaller point sets, 200 iterations were necessary for stable confidence envelopes that did not change with multiple sample runs for a given point set.

Significance of the bivariate  $\hat{K}_{12}(t)$  was also evaluated with Monte Carlo approach, but with an added twist. In the first step of the procedure, a reasonable approach might be to generate sets of  $n_1$  and  $n_2$  random point coordinates,  $n_1$  and  $n_2$  being equal to the number of type 1 and type 2 points. This approach, however, is not valid if the separate processes underlying the type 1 and type 2 patterns are non-random. If the separate processes are not random, the possibility of spurious significance is introduced. An alternative approach is the use of toroidal shifts as proposed by Lotwick and Silverman (1982). Type 1 points are held in place, while type 2 points are all shifted the same random distance, adding  $\Delta x$  and  $\Delta y$  to all x and y coordinates. To avoid shifting points to locations outside the study region, the study region is wrapped into a torus such that opposite edges are adjoined. A point that would be shifted outside the study region ends up instead in the opposite corner of the region (Upton and Fingleton 1985). The strength of the toroidal shift approach is that the structure of the separate observed processes is preserved, and the simulated type 1 and type 2 patterns are independent of each other, providing a valid test of the hypothesis of independence between the two observed patterns (Lotwick and Silverman 1982).

#### Hamill-Wright statistic

The Hamill-Wright (1986) statistic is a bivariate first-order spatial statistic conceived for describing the dispersion of juvenile plants relative to adults. It may be categorized as a refined nearest neighbor analysis. All nearest neighbor analyses have their root in the Clark-Evans (1954) statistic which assesses the univariate pattern of a point set by measuring the distance from each point to its nearest neighboring point. The statistic is the ratio of the observed mean nearest neighbor distance to the mean nearest neighbor distance expected under the random hypothesis. The statistic yields a global index of pattern rather than a measure of pattern as a function of distance. *Refined* nearest neighbor distances as a function of scale. The observed cumulative distribution function is compared with that expected for a random pattern, permitting measures of pattern as a function of distance (Moeur 1991).

The Hamill-Wright statistic applies the refined nearest neighbor approach to bivariate patterns. The first step is to construct the null cumulative distribution, that is, the probability that a type 1 (juvenile) point will be within a given distance t of a type 2 (adult) point under the random hypothesis. This probability is equal to the proportion of the total area that is within the given distance of any type 2 point.
For a rectangular plot, the random cumulative distribution is calculated by

$$F(t) = \frac{1}{A} \int_{x=0}^{x_{\text{max}}} \int_{y=0}^{y_{\text{max}}} I(t) \, dy \, dx \tag{1.13}$$

where 
$$I(t) = 1$$
, if Min  $\{d_{(x,y)j} : j = 1, 2, ..., n\} \le t$   
= 0, if Min  $\{d_{(x,y)j} : j = 1, 2, ..., n\} > t$ .

The plot dimensions are defined by  $x_{\max}$  and  $y_{\max}$ . Min  $\{d_{(x,y)j}\}$  is the smallest distance between any (x, y) value and a type 2 (j) point. I(t) is an indicator function which equals 1 for all (x, y) values which have a nearest type 2 neighbor distance  $\leq t$ . The integral calculates the area in the plot for which all points are within a distance t of the nearest type 2 point. Dividing by the total area yields the random probability. It should be emphasized that the null distribution is dependent only on the dimensions of the study region and the locations of type 2 points (Hamill and Wright 1986).

The next step is calculating the observed cumulative distribution of distances from type 1 to type 2 points. This straightforward calculation is the proportion of type 1 (*i*)points which have a distance to nearest type 2 neighbor (*j*) within the given distance t.

$$\hat{F}(t) = \frac{\sum_{i=1}^{n} I_i(t)}{n_1} \quad \text{where} \quad I_i(t) = 1, \text{ if } \min\{d_{ij}: j = 1, 2, ..., n\} \le t \quad (1.14)$$
$$= 0, \text{ if } \min\{d_{ij}: j = 1, 2, ..., n\} > t$$

The construction of the observed cumulative distribution is illustrated graphically in Figure 1.5 and Table 1.1.

Since the theoretical cumulative distribution for the random process is known, the hypothesis that type 1 points are located randomly relative to type 2 points can be tested with a standard non-parametric statistic, the Kolmogorov-Smirnov (K-S) test. The K-S



Figure 1.5. Example plot with type 1 ( $\bullet$ ) and type 2 ( $\circ$ ) points used in Table 1.1. for the construction of the bivariate nearest neighbor statistic. Plot is 50 m \* 30 m and radii, *t*, of 5 m are drawn around type 1 points. Lines are drawn from type 1 points to nearest neighboring type 1 points within 5 m.

Table 1.1. Construction of bivariate nearest neighbor distribution using point locations and
highlighting the distance, t, shown in Figure 1.5. The expected proportion depends on the
plot area (50 * 30 m) and the number of type 2 ("to") points (20). The observed proportion
reflects the number of nearest type 2 points within a given distance of type 1 ("from")
points. The total number of nearest neighbors is the number of type 1 points (10).
•

Distance	nearest neighbors encountered	observed cumulative distribution	expected cumulativ distribution	e
<i>t</i> (m)	$d_{ii} < t$	$\hat{F}(t)$	$\_\_F(t)\_\_$	difference
1	0	0.0	.040	040
2	Õ	0.0	.169	169
3	3	0.3	.337	037
4	4	0.4	.534	134
5	6	0.6	.688	088
6	7	0.7	.812	112
7	9	0.9	.903	003
8	10	1.0	.953	.047
9	10	1.0	.979	.021
10	10	1.0	.995	.005
11	10	1.0	1.000	.000

test uses the maximum difference M between the observed and theoretical proportions of nearest neighbor distances across the range of distances examined.

$$M = \max_{\text{all } t} \left| \hat{F}(t) - F(t) \right|$$
(1.15)

The difference M is compared with a critical value based upon the number of samples (type 1 points) used in calculating the observed distribution (Moeur 1991).

If the maximum difference exceeds the critical value, the hypothesis that type 1 points are located randomly and independently of type 2 points is rejected. If this difference is positive (the observed proportion is greater than the theoretical proportion), type 1 points are aggregated relative to nearest type 2 points. If the difference is negative, type 1 points are dispersed relative to nearest type 2 points. The K-S test provides a global statistic relevant to whether the overall distribution is different from random. Nevertheless, the distances over which the difference between observed and null distribution is greater than the critical value can provide an indication of the pattern's scale.

The Hamill-Wright statistic has several advantageous features that compliment Ripley's K(t). Because a standard statistical test may be used, the strength of a given pattern may be objectively assessed on the basis of a statistically valid p-value. Another feature is that type 2 points need not be confined within the boundaries of the study region. This was particularly important in the present study, given that remnant trees had been mapped up to 25 m from the edges of the plot boundaries. Since 25 m exceeds all nearest neighbor distances to remnants, the problem of unknown type 2 points did not exist and edge corrections were unnecessary. In this regard, the Hamill-Wright statistic allowed us to incorporate information that Ripley's K(t) did not.

While the Hamill-Wright statistic is straightforward in its interpretation, care must be taken with its use. Where Ripley's K(t) can indicate a general pattern, e.g. aggregation, of all points, Hamill-Wright indicates only the pattern of the nearest



Figure 1.6. Identical example plots a) and b) with two point types, demonstrating the asymmetry of the bivariate nearest neighbor analysis. In plot a), (•) serve as type 1 points, and lines are drawn to nearest neighboring type 2 (•) points. In plot b), (•) serve as type 1 points with lines drawn to nearest neighboring type 2 (•) points. The distribution of distances clearly differs depending on which set of points serves as the type 1 "from" points.

neighbors. Since Hamill-Wright provides no information regarding distances to further neighbors, it yields less insight concerning subtleties of pattern and no insight regarding larger-scale patterns.

Another important feature is that Hamill-Wright is "asymmetric" or "directional" (Figure 1.6). Given two sets of points, the observed cumulative distribution of distances from type 1 ("from") points to type 2 ("to") points is not the same as the distribution from

type 2 to type 1 points. The designation of points as "from" or "to" point sets can yield different results. In some cases, this designation is clearly provided by the study question. When studying the pattern of juvenile dispersion, the juveniles are clearly the "from" (type 1) points, because their pattern relative to adults is the key question. In the present study, the relevant question was whether post-fire trees were located randomly relative to nearest remnant trees, clearly allowing the designation of "from" (post-fire trees) and "to" (remnant trees) points.

# Chapter 2: Fire History and Post-fire Establishment Patterns in Two Coniferous Stands Impacted by Partial Fires, Oregon Cascades

# Introduction

Severe disturbances return plant communities to earlier stages of succession, but moderate disturbances may direct communities toward earlier or later stages of succession (Martin et al. 1976). A moderate-severity fire may remove established late seral species and open space for the regeneration of early seral species. Alternatively, a moderateseverity fire may thin a forest sufficiently for enhanced growth of dominants and establishment of late seral understory species, but insufficiently for the re-establishment of early seral species (Martin et al. 1976). Forests impacted by multiple, partial fires might also be described as a mosaic of patches, each cycling through different stages of development and destruction (Isaac 1940, Watt 1947, Bonnicksen and Stone 1981, Remmert 1991). The mosaic concept originates from the observed clustering of cohorts in many forests, leading to the description of forest communities as a patchwork of even-age aggregations, each occupying different disturbance-opened patches (Isaac 1940, Cooper 1961, Bonnicksen and Stone 1981, Stewart 1986b).

This study investigates the fire patterns and establishment history at two sites in the Oregon Cascades, both impacted by partial fires but differing in post-fire composition of early and late seral species. I chose sites characterized by old-growth remnant trees (>200 yrs.) emergent above a lower canopy of mature and young trees ( $\approx 100$  yrs.). The two-tiered canopy and the scarring of remnant trees indicated the occurrence of at least one partial fire, but the fire history of each site was unknown when sites were selected. Early seral *Pseudotsuga menziesii* dominated the lower canopy at one site, and late seral *Tsuga heterophylla* dominated the lower canopy at the other.

The first objective was to assess the model of forests as a mosaic of fire-opened patches by describing the fire history and the spatial arrangement of cohorts. Specific questions were:

- 1) Did the partial fire leave old-growth remnants in unburned patches or did the fire burn under the remnants?
- 2) In the case that the lower mature canopy was initiated by multiple, recent (nineteenth century) fires, are the different recent cohorts found in distinct patches?
- 3) During the most recent fire (in the case of multiple recent fires), was the survival pattern of old-growth remnant trees associated with the survival patches of younger, recently established trees?

The second objective was to describe establishment history after the partial fire and how post-fire development became dominated by either early or late seral species. Specific questions were:

- 1) Did *Pseudotsuga* and *Tsuga* establish concurrently at both sites, or did *Tsuga* regenerate later and grow into the canopy, as general successional theory might predict? If both species established concurrently, current species composition may reflect initial post-fire composition.
- 2) Did sites differ in the rate at which they regenerated? Canopy species composition may be linked to differences in overall regeneration rates (and, thus, degree of canopy infilling) and to differences in environmental conditions which regeneration rates may reflect.
- 3) In the case of multiple fires within each stand, did patches associated with different fires develop with similar or differing species compositions?

After a partial fire, the developmental pathway may be influenced by a variety of factors: underlying environmental conditions, disturbance history, establishment history, and the pattern and composition of survivors from the previous community. In Chapter 3, I explicitly assess the relationship between post-fire species patterns and the spatial pattern

of old-growth survivors. In the present study, I evaluate the influence of surviving trees in only a general manner, focusing instead upon the importance of environment, fire history and establishment history.

The simplified model of succession in the Pacific Northwest has been that of complete stand destruction by infrequent catastrophic fires and subsequent invasion by shade-intolerants, particularly *Pseudotsuga menziesii* (Isaac 1940, Munger 1940, Isaac 1943). Understory re-initiation takes place beneath the even-age canopy as shade-tolerants, such as *Tsuga heterophylla*, regenerate and then enter the canopy via gap-phase replacement. With time, the multi-tiered features of a *Pseudotsuga-Tsuga* old-growth forest emerge. Potentially, development could lead to a self-replacing *Tsuga* forest, but catastrophic fires typically re-initiate the cycle prior to this stage.

Stand reconstructions and fire chronologies have revealed that the simplified cycle may be a useful starting point, but wide variations on this pattern, if not radically different patterns, are prevalent (Morrison and Swanson 1990, Agee 1991). Infrequent catastrophic fire regimes are characteristic of the Olympic Mountains, northern Washington Cascades and Oregon Coast Range; a 465 year natural fire rotation has been estimated for Mt. Rainier National Park, Washington Cascades (Hemstrom and Franklin 1982). Although the catastrophic fire regime of the Olympic Mountains may fit the simplified model, *Tsuga* frequently outnumbers *Pseudotsuga* as an invader of burned sites in this wet environment (Huff 1995). In the Oregon Cascades, dry sites have a mean fire return interval of only 103 years (Means 1982). On such sites, *Pseudotsuga* is self-replacing, and *Tsuga* is excluded (Means 1982). Across the region, community composition and structure are closely linked to fire histories, and the interaction between environmental gradients and fire patterns has resulted in a diversity of successional pathways (Agee 1991, Huff 1995).

In the central western Oregon Cascades, a wide range of fire histories has created a patchwork of stands across a predominantly mesic environment (Morrison and Swanson 1990). Burned patch sizes can range from .2 - >100 ha, and site fire frequencies can range

from 20 - 400 years (Morrison and Swanson 1990). A large proportion of sites with oldgrowth trees have been impacted by at least one fire, with remnant trees persisting through such fires (Morrison and Swanson 1990). The development and persistence of old-growth characteristics through a regime of partial fires differs from the classic conception of uninterrupted developmental cycles between catastrophic fires (Morrison and Swanson 1990). With the exception of a few studies (Means 1982, Stewart 1986b), little attention has been given to the development of older stands through repeated, partial fires. Such stands in the Oregon Cascades offer a unique opportunity to assess the patch dynamics/ mosaic conception of forest development and the relationship between successional pathways, environmental conditions and fire history.

## Methods

#### Site description

I chose two stands characterized by distinctly two-tiered canopies in which oldgrowth trees (> 200 yrs.) emerged above a lower canopy of mature trees (80 - 200 yrs.) which had presumably regenerated after a recent fire event(s). I chose one site in which *Pseudotsuga menziesii*, a shade-intolerant, dominated the post-fire cohort and one in which *Tsuga heterophylla*, a shade-tolerant, dominated the post-fire cohort. I selected sites with relatively uniform topography. Where topographic variation existed, remnant tree locations did not appear to be associated with topographic features.

The Eagle Rock stand is located east of the town of Detroit, Oregon, in the Detroit Ranger District of the Willamette National Forest (latitude 44°47' N, longitude 122°2' W). The Wolf Rock stand is located adjacent to the H.J. Andrews Experimental Forest northeast of the town of Blue River, Oregon, in the Blue River Ranger District of the Willamette National Forest (latitude 44°17' N, longitude 122°10' W). Both stands are located within the *Tsuga heterophylla* zone (Franklin and Dyrness 1973) of the west side of the central Oregon Cascade Mountains (see Table 2.1 for site characteristics). Climatic regimes are typical of the Pacific Northwest with cool, wet winters interrupted by summer drought and high temperatures from June through September. Winter snowpacks occasionally exceed 1 m in depth and are often transient at 500-1000 m elevation in the Cascades. Eagle Rock is characterized by the *Tsuga heterophylla / Berberis nervosa* plant association, typical of warm, well-drained, moderately productive sites (Hemstrom et al. 1987). Wolf Rock is characterized by the *Tsuga heterophylla / Rhododendron macrophyllum / Linnea borealis* plant association, common on gentle terrain in cooler areas, where deeper winter snowpacks and summer frost may occur (Hemstrom et al. 1987). The central portion of the 2 ha Eagle Rock stand is a relatively homogeneous slope, but a southeast-facing riparian slope covers .27 ha along the east end and a seep (.13 ha) and ridge (.24 ha) cover the west end. The topography at Wolf Rock is subtle with few distinguishable features.

# Stand mapping

At Eagle Rock, I mapped 2 ha (100 \* 200 m) and at Wolf Rock, 2.25 ha (100 \* 225 m). I tagged, mapped and measured -- recording species, diameter at breast height (dbh, at 1.4 m), and crown (relative height) class -- all live trees with diameter  $\geq$  5 cm at breast height. I also mapped and measured dead remnant trees which were judged to have died after the most recent fire. I mapped all remnant trees which were located within an additional 25 m of the mapped stand perimeter (making remnant mapped area 3.75 ha at Eagle and 4.125 ha at Wolf). At Wolf, within this additional 25 m, I also mapped live individuals which belonged to a cohort intermediate in age between the remnant trees and the youngest cohort.

33

		Eagle Rock	Wolf Rock
Elevation		700 m	850 m
Aspect		S	W/NW
Slope		20° - 30°	< 5°
Annual precipi	itation	1903 mm	2181 mm
June - Aug. pr	ecipitation	125 mm	155 mm
Mean July ten	perature	≈ 17° C	≈ 15.9° C
Mean January	temperature	≈ l° C	≈ l° C
Lower canopy	: primary species	Pseudotsuga menziesii	Tsuga heterophylla
	density, basal area	1113 t/ha, 43.9 m <sup>2</sup> /ha	1431 t/ha, 38.6 m <sup>2</sup> /ha
Emergents:	primary species	Pseudotsuga menziesii	Pseudotsuga menziesii
-	density, basal area	28 t/ha, 30.2 m <sup>2</sup> /ha	43 t/ha, 39.6 m <sup>2</sup> /ha

Table 2.1. Site characteristics of Eagle Rock and Wolf Rock reference stands.

A detailed description of the mapping procedure is reported in Chapter 3. Topography was generated in ARC/INFO, a GIS software (E.S.R.I. 1995). At Eagle Rock, I constructed topography for the 25 m beyond the 2 ha stand perimeter, since this was necessary to present key topographic features. I defined boundaries for the topographic features at Eagle Rock -- riparian slope, wet seep, and dry ridge -- based upon my field observations of these features. At Wolf Rock, I constructed topography for only the 2.25 ha stand.

# Fire chronology

I dated fire scars and fire-associated ring structures using increment cores. Because both stands were established as permanent reference plots, destructive sampling within each stand was not possible. I cored charred remnant trees with bark furrowed from scarring. Due to the low severity of the most recent fires and to the passage of time, such furrows were not always distinct, making it difficult to locate buried fire scar in the increment core. Given this difficulty and my primary interest in the most recent fires, I attempted to date only the most recent events (< 200 yrs. b.p.) with increment core data. While I dated several scars prior to this time period, I did not build a sufficient sample for analysis.

Fire scars were dated using methods outlined by (Means 1989). Scarred increment cores were compared with unscarred cores from the same tree. Distinctive ring sequences older than the fire scar were identified in both cores. After dating the ring sequence in the uninterrupted core, ring counts were made from this date up to the scar. For each remnant tree, I obtained two uninterrupted cores and at least two cores with fire evidence. If multiple events scarred the trees, for each event, I obtained at least one core (two where possible) in which only the scar from that event was present. I mounted increment cores individually in core mounts and sanded them with successively finer grits up to 400 grit. Increment cores were examined with a dissecting scope with maximum magnification of 100.

I supplemented the evidence from fire scars with evidence from pitch rings, which appeared to be fire-associated ring structures (cf. Brown and Swetnam 1994). Pitch-rings are common in *Pseudotsuga menziesii*; fire, wind stress and insect attacks have been suggested as causes. Pitch-rings are characterized by a delamination between two annual rings which is filled with a layer of pitch. Pitch-rings can extend over a large proportion of the tree's circumference. At both of my study sites, almost all pitch-rings coincided with dates for which fire events had been documented in the surrounding landscape. Furthermore, pitch-rings were often found in trees with a fire scar occurring in the same year. Fire scars were small and localized, whereas the pitch-ring extended over a much greater proportion of the same tree's circumference. Given the synchronicity of pitch-rings with known fire events and collected scars, I treated them as fire-associated ring structures.

In addition to dating fire scars within the two study sites, I examined landscapelevel data compiled by other investigators. These studies permitted an approximation of the fire history for the two sites prior to the most recent 200 years. Morrison and Swanson (1990) and Teensma (1987) both collected fire history data for the Blue River Ranger District where the Wolf Rock site is located. Garza (1995) collected similar data for the Detroit Ranger District in which the Eagle Rock site is located. These data consist of tree ages and scar dates collected from stumps in clear cuts and thinnings. Scar dates were used in conjunction with tree ages to identify cohorts across the landscape and the fire episodes leading to these cohorts. Having been given access to the original data, I built fire chronologies based upon evidence from the immediate and adjacent topographic units in which the stands were located. Evidence-providing sites within the immediate topographic units were no more than 1.5 km from my sites and the closest sites were less than .5 km.

# Post-fire establishment patterns following the most recent fires

In order to describe the regeneration patterns following the most recent fires, I cored 171 *Pseudotsuga menziesii*, 69 *Tsuga heterophylla* and 30 *Castanopsis chrysophylla* at Eagle Rock and 60 *Pseudotsuga menziesii* and 134 *Tsuga heterophylla* at Wolf Rock. While *Thuja plicata* was also an important species, the extensive occurrence of pith rot in this species made dating problematic, consequently I did not systematically sample this species.

I used a hierarchical stratified random sampling scheme that was designed to collect age data for both the present study and for a growth model of the younger individuals as a function of remnant tree and within-cohort competition (Goslin 1993). The sampling scheme insured that all possible competitive and environmental (represented by geographic blocks) conditions within the stand were adequately and independently sampled. A minimum distance (5 m) was maintained between sampled trees in order to reduce autocorrelation effects. A computer program written by B. Marks selected trees according to the sampling rules. I obtained at least two cores from each tree. I prepared and examined cores in the same manner described for remnant tree cores. For trees with suppressed ring series, I used signature years to compare ring sequences across cores and account for locally missing rings. For 80% of the sampled trees, I obtained a core which included the pith. For the remaining trees, I derived the distance to the pith from measurements of the earliest ring's arc and added years-to-pith based upon the growth rate of the earliest five rings. All trees were cored as close to their base as possible. Most trees were cored within 0.25 m (many as close as 0.05 m) and all were cored within 0.5 m of their base. I did not add years for growth to the core height or make adjustments for differences in coring height. While this decision added error to my age estimates, I judged that the alternative approach would add more error as a result of the wide variation in growth rates within the stands. Trees cored at higher points were larger (preventing the use of small-handled borers) than trees cored closer to the ground. These size differences were typically due to dramatic differences in growth rates which are not taken into account when years are added on the basis of average age-to-height relationships.

I tested for differences in median age and establishment time (the difference between fire date and tree origin date) between species within a site and for each species between sites using the Wilcoxon rank sum test (NPAR1WAY procedure in SAS 6.10 [SAS Institute Inc. 1987]). In describing age-to-size relationships, I fit least squares linear, logarithmic, and power function regression models to the age and diameter data for each species (REG procedure in SAS 6.10 [SAS Institute Inc. 1987]). I also fit other dependent variable transformations, if they were suggested by the Box-Cox method. Only the best fit models are presented.

# Spatial patterns of the most recent fires

I reconstructed the spatial pattern of those fires which initiated the lower canopy (< 200 yrs. b.p.) using the establishment dates of these trees. The reconstructed fire

chronologies indicated that a series of multiple fires occurred during this time period. Trees which established after one of the initial nineteenth century fires would have been very young and particularly vulnerable to the later fires. Using the locations of trees which established after an earlier nineteenth century fire but which predated subsequent fires, I delineated those areas which burned during the most recent fire and those patches which survived (i.e. the fire was of negligible severity). It is important to note that these patches reflect severity relative to young trees and not the relatively fire-resistant remnant trees. I subjectively drew boundaries around those areas which survived later fires. I took a conservative approach in estimating survival patches, assuming an area was burned unless there was evidence otherwise. In drawing patch boundaries, I accounted for the presence of fire scars in remnant trees and for size structure differences (within the younger cohort) between burned and surviving patches.

I supplemented my systematic sample of the younger cohorts with non-systematic "reconnaissance coring" from a preliminary attempt to identify fire patches. Twenty reconnaissance cores were collected at Eagle Rock and 55 at Wolf Rock. Reconnaissance cores included a broad range of species, including *Thuja*, since the goal was not precise dating, but assigning trees to cohorts defined by the fire dates.

### Associations between regenerating species and fire patches

In Chapter 3, I describe spatial associations between species in the younger cohort and the remnant trees. In the present chapter, I determined whether species were associated with particular fire patches, that is, areas which burned in 1892 versus areas which burned in an earlier fire (1870 at Eagle and 1829 at Wolf) but survived the later fire. At Wolf Rock, I used a simple chi-square test to test the association between fire patches and the following species: *Pseudotsuga*, *Tsuga*, *Thuja*, *Abies amabilis* and *Taxus brevifolia*. At Eagle Rock, I defined four topographic blocks -- wet seep, riparian slope, central mesic slope and dry ridge -- and used a Cochran-Mantel-Haenszel Chi-Square test to test for an association between species and fire patches after accounting for any association with the topographic blocks (FREQ procedure in SAS 6.10 [SAS Institute Inc. 1987]). I tested this association for *Pseudotsuga*, *Tsuga*, *Thuja*, *Castanopsis* and *Cornus nuttallii*.

# Results

# Fire chronology

At Eagle, there was scar evidence for fires at 1892, 1870-1873 and 1848-1850 (henceforth referred to as the 1892, 1870 and 1848 fires) (Figure 2.1). At Wolf, withinstand scar evidence points to a major fire in 1892 (Figure 2.2). A reburn in 1896 at Wolf is suggested by two trees marked by either a pitch ring or scar, an absence of tree establishment dates between 1892-1896 and data from the landscape fire chronologies. A fire event in 1829-1835 is also highly probable at Wolf. Within the Wolf stand, a cohort of shade-intolerant *Pseudotsuga* predated the 1892 fire, but was substantially younger than the remnant trees. Estimated pith dates from these trees (six of which are the first trees shown in Figure 2.2) and scars on nearby clear cut stumps were consistent with an 1829-1835 fire episode. Nevertheless, I was unable to locate any scars at this date within the stand. Field-conducted ring counts of an additional 12 cored remnant trees indicated that 10 were scarred around 1892, but none were scarred around 1829. At both sites, scars and pitch rings occurred at other dates, but were not consistent enough (no more than one instance at a date) to presume the occurrence of fire.

# Fire spatial pattern

At both sites, I did not find any areas which escaped all of the nineteenth century fires. Across the south-facing slope at Eagle, the upper portion was burned most



Figure 2.1. Eagle Rock fire chronologies from cored trees within the reference stand. Horizontal lines represent dated time spans for individual trees derived from multiple cores for each tree. Scars or pitch rings are shown at the dates they were observed. Undateable scars (typically preceded by rot) are shown at approximate locations, but are not counted in the scar index.



Figure 2.2. Wolf Rock fire chronologies from cored trees within the reference stand. Horizontal lines represent dated time spans for individual trees derived from multiple cores for each tree. Scars or pitch rings are shown at the dates they were observed. Undateable scars are shown at approximate locations, but are not counted in the scar index.

completely in 1892 (Figure 2.3). This burned area included the stand's largest cluster of remnant trees, many of which exhibited 1892 fire scars. Large areas downslope experienced negligible severity of very young (post-1870) individuals during the 1892 fire and, in the southeast corner of the mapped stand, two trees (post-1848) survived both the 1870 and 1892 fires. Within the southeast-facing riparian slope, a small east-facing draw survived the 1892 fire. At the west end of the mapped stand, areas along the ridge crest and at the head of the seep survived the 1892 fire and, in places, the 1870 fire as well. Survival patches ranged in size from single trees to >1730 m<sup>2</sup> (the largest patches extended beyond the mapped stand's borders). Of the trees which established after 1870, but survived the 1892 fire, only one contained an 1892 pitch ring and none contained fire scars. Of the trees which established after 1848 and survived later fires, those in the seep did not exhibit fire evidence, but all those which survived as isolated individuals (e.g. in the southeast corner) contained 1892 fire scars.

Since it was not possible to differentiate the pattern of the 1892 and 1896 fire at Wolf, the pattern is described as that of the 1892 fire. Islands of young tree survival ranged from single trees to a large patch (2390 m<sup>2</sup>) in the central portion of the Wolf stand (Figure 2.4). This central patch coincides with the high density cluster of remnant trees in the center of the plot, but the remnant tree cluster extends beyond the survival patch into areas that were more severely burned. In the eastern third of the plot, several small to moderately sized patches survived the fire, but the majority of the area burned. The western third of the plot appeared to burn most completely with only one small patch and one isolated tree surviving the 1892 fire. Young trees (post-1829) which survived inside the central survival patches or as isolated individuals typically contained 1892 fire scars.

An examination of Figures 2.3 and 2.4 reveals that trees which regenerated after 1892 (< 100 yrs.) are sometimes located within patches that are designated as having survived the 1892 fire. These individuals were typically small trees which were



Figure 2.3. Eagle Rock: map of topography, remnant trees, age class of sampled trees and pattern of the nineteenth century fires.



Figure 2.4. Wolf Rock: map of topography, remnant trees, age classes of sampled trees and pattern of the nineteenth century fires.

surrounded by larger mature trees (not cored) similar in size to nearby large (cored) that predated the 1892 fire. I assumed that the large uncored trees also predated the 1892 fire and that the smaller trees were cases of delayed regeneration after the earlier fire, thus including these trees within the survival patch. The maps also show boundaries of survival patches extending into areas where no trees were sampled. These boundaries were drawn between areas where sharp differences in codominant/dominant tree size were evident, with the larger codominants (similar in size to nearby cored codominants which predated the 1892 fire) included within the survival patches.

## Size distributions

Diameter distributions of *Pseudotsuga* were somewhat bimodal at both sites with distinct, but small populations of remnant trees at large diameters and younger non-remnant trees at smaller diameters (< 70 cm) (Figures 2.5a, 2.6a). At Wolf, the small-diameter population displayed a bell-shaped distribution with a distinct peak at 15-20 cm dbh, whereas, at Eagle, a much greater percent of this population was found in the smallest size classes with a peak at 10-15 cm dbh.

Individuals of *Thuja* at Eagle decreased in number with increasing size class, but the distribution did not resemble a negative exponential distribution (Figure 2.5b). Indeed, the distribution of the younger population was relatively flat and a secondary peak was suggested at 30-35 cm dbh. The *Thuja* population included one remnant tree. At Wolf, the diameter distribution of *Thuja* resembled a negative exponential distribution with a long tail consisting of large-diameter remnant trees (Figure 2.6b). Remnant trees of *Thuja* were smaller than those of *Pseudotsuga*. The diameter distribution displayed overlaps in size between age classes, particularly between the youngest (<100 yrs.) and intermediate (100 -163 yrs) age class.



continued

d. Castanopsis

e. Libocedrus



Figure 2.5. Diameter (at 1.4 m) distributions at Eagle Rock for a) *Pseudotsuga*, b) *Thuja*, c) *Tsuga*, d) *Castanopsis* and e) *Libocedrus*.

*Tsuga* displayed a negative exponential diameter distribution at both sites (Figures 2.5c, 2.6c). There were no remnant trees in either *Tsuga* population and no individuals larger than 65 cm.

At Eagle, *Castanopsis* displayed a strong unimodal distribution with a peak at 10-15 cm dbh (Figure 2.5d). *Libocedrus* was the one other species which included largediameter remnant trees (Figure 2.5e). These remnant trees were smaller than those of *Pseudotsuga* as well as those of the Wolf Rock *Thuja*.

## Crown class distributions

The *Pseudotsuga* population at Eagle included a much greater proportion of individuals in the suppressed crown class than the population at Wolf (Table 2.2).

# a. Pseudotsuga







continued

c. Tsuga



Figure 2.6. Diameter (at 1.4 m) distributions at Wolf Rock for a) *Pseudotsuga*, b) *Thuja*, c) *Tsuga*. All individuals > 35 cm dbh have been positively differentiated between young, intermediate and remnant age classes, but smaller size classes of *Tsuga* and *Thuja* may include individuals of intermediate age which have not been identified.

a. Lagie Rock	Crown Class	<u> </u>			
Species	Suppressed	Intermediate	Codominant	Dominant	Emergent
Pseudotsuga menziesii	528	438	393	84	52
Tsuga heterophylla	269	39	63	14	0
Thuja plicata	70	20	11	0	1
Castanopsis chrysophylla	a 88	45	0	0	0
Cornus nuttallii	105	6	0	0	0
Acer macrophyllum	7	17	2	0	0
Libocedrus decurrens	10	1	0	0	3
Taxus brevifolia	13	0	0	0	0
Other	2	0	0	0	0
b. Wolf Rock					
Tsuga heterophylla	834	369	403	149	0
Thuja plicata	462	195	167	39	26
Pseudotsuga menziesii	30	155	251	115	70
Abies amabilis	11	6	4	4	0
Taxus brevifolia	11	2	0	0	0
Castanopsis chrysophylla	ı 2	7	2	1	0
Other	1	2	0	0	0

Table 2.2. Number of trees ( $\geq$  5 cm dbh) in crown classes (relative height) at each site

Whereas *Pseudotsuga* numbers decreased with crown class at Eagle, *Pseudotsuga* was most abundant in the codominant class at Wolf. *Tsuga* and *Thuja* decreased with increasing crown class at both sites. This decrease was more precipitous at Eagle, where both species had a greater proportion of their population in the suppressed class than at Wolf. At both sites, the codominant and dominant trees which define the canopy included *Pseudotsuga*, *Tsuga* and *Thuja*. *Tsuga* and *Thuja*, however, made up a much smaller proportion of this canopy layer at Eagle (16%) than at Wolf (67%). The density of remnant trees was greater at Wolf and included a greater proportion of *Thuja* remnant trees.

### Post-fire establishment history

The age distributions of *Pseudotsuga*, *Tsuga* or *Castanopsis* regenerating after the nineteenth century burns each displayed a strong peak in origin dates and a date after which little regeneration occurred (Figures 2.7, 2.8).

At Eagle, *Pseudotsuga* regeneration occurred in small numbers immediately after both the 1870 and 1892 fires and then gradually increased with peaks at 16 yrs. after 1870 and 9 yrs. and 18 yrs. after 1892 (Figure 2.7a). No trees established later than 41 yrs. when the first regenerating between the 1848 and 1870 fire, but two individuals are known to have regenerated in this time period. The *Tsuga* age distribution included individuals which regenerated after each of the three burns (Figure 2.7b). After the 1892 burn, regeneration of *Tsuga* was initially more sporadic than that of *Pseudotsuga*, including several years without regeneration, but regenerated to the theory of the period, ending 61 yrs. after 1892. No *Castanopsis* regenerated before 1892 (Figure 2.7c). Regeneration peaked immediately after the 1892 burn, declined rapidly and ended within 22 yrs. Median ages of the post-1892 populations differed significantly between *Pseudotsuga*, *Tsuga* and *Castanopsis* (Table 2.3). *Castanopsis* median age was the oldest, and *Tsuga* median age the youngest.

At Wolf, no *Pseudotsuga* establishment dates were found within the first six years after the 1892 fire (Figure 2.8a). For *Tsuga*, a gap of four years followed the 1892 fire (Figure 2.8b). The one individual that originated between 1892-1896 (99 yrs. old) is located within a patch that burned in 1829 but escaped the 1892 fire. The regeneration gap after the 1892 fire for both *Pseudotsuga* and *Tsuga* supports the 1896 fire suggested by the scar data and landscape chronologies.

Regeneration of *Pseudotsuga* at Wolf proceeded rapidly after 1896 with a strong peak 8 yrs. afterwards. Establishment then declined rapidly with only three individuals later than 18 yrs. after 1896, the last originating 36 yrs. after 1896. The sample included one individual 155 yrs. old, establishing 8 yrs. after 1829. Several *Tsuga* individuals



Figure 2.7. Sampled age distributions and dates of major fires at Eagle Rock for a) *Pseudotsuga*, b) *Tsuga* and c) *Castanopsis* in the lower canopy. Establishment time since immediately previous fire is shown along upper x-axis.



Figure 2.8. Sampled age distributions and dates of major fires at Wolf Rock for a) *Pseudotsuga* and b) *Tsuga* in the lower canopy. Establishment time since immediately previous fire is shown along upper x-axis.

Table 2.3. a) Median age and b) median establishment time after fire for sampled *Pseudotsuga*, *Tsuga* and *Castanopsis* less than 100 years of age at Eagle and Wolf sites. Age is years before 1992. Establishment time is calculated as years after most recent fire (1892 at Eagle, 1896 at Wolf). Median age is used to make comparisons among species within sites. Median establishment time is used to make among site comparisons for each species (*Castanopsis* is shown for reference only).

## a. Median age

	Site	
Species	Eagle Rock	Wolf Rock
Pseudotsuga menziesii	85 b	88 b
Tsuga heterophylla	83 a	83 a
Castanopsis chrysophylla	97 c	

a Letters indicate <u>among species</u> differences (p < .05) in age within a site.

#### b. Median establishment time

	Site	
Species	Eagle Rock	Wolf Rock
Pseudotsuga menziesii	15 b	8 a
Tsuga heterophylla	17 b	13 a
Castanopsis chrysophylla	3	

Site

<sup>a</sup> Letters indicate <u>among site</u> differences (p < .05) in establishment time for a given species.

originated between the 1829 and 1892 fires. One individual seems to predate the 1829 fire (at 163 yrs. old, dated from 1992), but this is likely due to an erroneous estimation of the origin date, since this core did not hit the pith and several years were added to the inside date. After 1896, regeneration of *Tsuga* gradually increased and then decreased slowly, continuing for a longer time period than *Pseudotsuga* and ending within 54 yrs. As at Eagle, the median age of *Pseudotsuga* was significantly greater than that of *Tsuga* (Table 2.3a).

There were significant differences between sites in the time it took for regeneration to establish after the fire, assuming the occurrence of the 1896 reburn at Wolf. For both *Pseudotsuga* and *Tsuga*, the median establishment time was shorter at Wolf than at Eagle

(Table 2.3b). However, median ages of post-1892 *Pseudotsuga* and *Tsuga* did not differ between sites.

### Age-diameter relationships

Tree diameters (non-remnant) were poorly correlated with age (Figures 2.9, 2.10). The strength of association was greatest for *Castanopsis* and was greater for *Pseudotsuga* than for *Tsuga* at both sites. The association was stronger at Eagle than at Wolf for both *Pseudotsuga* and *Tsuga*. If only the post-1892 trees are used in the regression, the strength of association decreased at Eagle ( $r^2 = .32$  and  $r^2 = .22$  for *Pseudotsuga* and *Tsuga*, respectively), but increased at Wolf ( $r^2 = .31$  and  $r^2 = .33$ , respectively).

The nature of the age-size relationship differed between *Pseudotsuga* and *Tsuga*. At Wolf, *Pseudotsuga* established within a short period and individuals which established immediately after 1896 (within 8 yrs.) were among the largest size classes and did not occur within the smallest classes (Figure 2.10a). Small-diameter *Tsuga*, however, were spread out over a large range, including many individuals which established immediately after 1896 but remained suppressed (Figure 2.10b). Furthermore, *Tsuga* which established prior to 1892/1896 were not necessarily bigger than those *Tsuga* which established after the 1892/1896 fires. A broad range of small-diameter *Tsuga* was also seen at Eagle, but individuals which established prior to 1892 were generally larger in diameter than those which established afterwards (Figure 2.9b).

# Associations between regenerating species and fire patches

After accounting for associations with topography at Eagle, *Thuja* and *Castanopsis* were found to be associated with particular fire patches (Table 2.4). *Castanopsis* was associated with those areas which burned in 1892, while *Thuja* was associated with patches







continued





Figure 2.9. Diameter-age relationships at Eagle Rock for a) *Pseudotsuga*, b) *Tsuga* and c) *Castanopsis* regenerating after the nineteenth century fires.

which burned in 1870 but survived the 1892 fire. *Pseudotsuga*, *Tsuga* and *Cornus* were not associated with particular fire patches.

At Wolf, *Pseudotsuga* was associated with areas burned in 1892, while *Thuja*, *Abies amabilis* and *Taxus brevifolia* were associated with areas which burned in 1829, but survived the 1892 fire (Table 2.5). *Tsuga* was not associated with either fire patch, being abundant across both.

# Distribution of the intermediate age class at Wolf

No intermediate age (100-163 yrs.) *Pseudotsuga* were located in the large central patches which survived the 1892 fire (Figure 2.11). Rather, they occurred as isolated individuals or in small survival patches removed from the central high density remnant cluster. In contrast, most intermediate age *Tsuga* were located in the large central survival







Figure 2.10. Diameter-age relationships at Wolf Rock for a) *Pseudotsuga* and b) *Tsuga* regenerating after the nineteenth century fires.

The Cochran-Mantel-Haenszel (CMH) tests for the association between two variables in a stratified population after accounting for any association with the strata. Contingency tables are shown for a) *Thuja* and b) *Castanopsis*, the two species with significant CMH statistics. In each topographic block, value of the species which is greater than expected for a fire patch is in bold. Contingency tables are not shown for *Pseudotsuga*, *Tsuga* and *Cornus*, species for which the test was conducted, but not significant. Table 2.4. Contingency tables for association between species and fire patches after accounting for topographic blocks at Eagle Rock.

а.	Topographi Fire patch	ic block						
Species	Dry ridge		Seep		Central hillslo (aspect: south	) )	Riparian slope (aspect: east/s	s outheast)
Actual (Expected)	burned 1892	burned 1870, escaped 1892	burned 1892	burned 1870, escaped 1892	burned 1892	burned 1870, escaped 1892	burned 1892	burned 1870, escaped 1892
Thuja plicata	2 (3.4)	2 (.6)	2 (13.1)	<b>25</b> (13.9)	20 (28.9)	<b>16</b> (7.1)	22 (25.6)	<b>9</b> (5.4)
Other	268 (266.6)	43 (44.4)	65 (53.9)	46 (57.1)	1144 (1135.1)	268 (276.9)	222 (218.5)	43 (46.6)
<u>Column Totals</u> <u>Row Totals</u> Thuja Other	270 4 311	45	67 27 111	17	1164 36 1412	284	244 31 265	52
	X2 = 4.2 p = .04		X2 = 22.7 p < .001		X2 = 14.4 p < .001		X2 = 3.14 p = .076	
CMH = 40.4 p < .001	-	-	-	-		-		

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Table 2.5. (continued)

b.	Topographi Fire patch	ic block		·				
Species	Dry ridge		Seep		Central hillslo (aspect: south	) )	Riparian slope (aspect: east/s	e outheast)
Actual (Expected)	burned 1892	burned 1870, escaped 1892	burned 1892	burned 1870, escaped 1892	burned 1892	burned 1870, escaped 1892	burned 1892	burned 1870, escaped 1892
Castanopsis chrysophylla	<b>17</b> (16.3)	2 (2.7)	0 (0)	0	<b>97</b> (81.9)	5 (20.1)	<b>12</b> (9.9)	0 (2.1)
Other	253 (253.7)	43 (42.3)	67 (67)	71 (71)	1057 (1072.1)	279 (263.9)	232 (234.1)	52 (49.9)
Column Totals Row Totals Castanopsis Other	270 19 296	45	67 0 138	71	1164 102 1336	284	244 12 284	52
CMH = 17.1	X2 = .23 p = .63		$\begin{array}{l} X2 = N/A \\ p = N/A \end{array}$		X2 = 15.3 p < .001		X2 = 2.7 p = .10	

MH = 17.1p < .001 60

Table 2.5. Contingency tables for associations between species and fire patches at Wolf Rock: a) *Pseudotsuga*, b) *Thuja*, c) *Tsuga*, d) *Abies* and e) *Taxus*.

Actual (Expected)	burned in 1892	escaped in 1892, burned in 1829	Total
Pseudotsuga menziesii	<b>543</b> (503)	8 (48)	551
Other	2401 (2441)	270 (230)	2671
Total	2944	278	$X^2 = 43.4$ p < .001

# a. Species Fire Patch

# b. Species Fire Patch

Actual (Expected)	burned in 1892	escaped in 1892, burned in 1829	Total
Thuja plicata	770 (789)	<b>93</b> (74)	863
Other	2174 (2155)	185 (204)	2359
Total	2944	278	$X^2 = 6.9$ p < .009

# c. Species Fire Patch

Actual (Expected)	burned in 1892	escaped in 1892, burned in 1829	Total
Tsuga heterophylla	1604 (1604)	151 (151)	1755
Other	1340 (1340)	127 (127)	1467
Total	2944	278	$X^2 = .003$ p < .957

Actual (Expected)	burned in 1892	escaped in 1892, burned in 1829	Total
Abies amabilis	9 (23)	<b>16</b> (2)	25
Other	2935 (2921)	262 (276)	3197
Total	2944	278	$X^2 = 98.0$ p < .001

### d. Species Fire Patch

### e. Species Fire Patch

Actual (Expected)	burned in 1892	escaped in 1892, burned in 1829	Total
Taxus brevifolia	3 (12)	<b>10</b> (1)	13
Other	2941 (2932)	268 (277)	3209
Total	2944	278	$X^2 = 77.2$ p < .001

patch. Only one *Tsuga* survived as an isolated individual and this individual was located within the high density remnant cluster. A few *Tsuga* survived in small and medium survival patches in the eastern portion of the stand. Intermediate age *Thuja* were found in both the central survival patches and as isolated individuals, often in areas of low remnant tree density. *Thuja* also survived in small and medium patches in both the eastern and western portions of the stand. *Thuja* which survived outside the central survival patch were typically marked by large fire scars, in contrast to typically unscarred *Thuja* within the patch.



Figure 2.11. Wolf Rock: map of intermediate age class trees (100-163 yrs.) by species, remnant trees and fire survival patches.

### Discussion

### Fire temporal and spatial pattern

The Eagle and Wolf stands illustrate the complexity of fire patterns in the Oregon Cascades across both space and time. These stands did not arise from a single, catastrophic fire nor from regularly recurring low severity fires. Rather, they were impacted by multiple fire events which were episodic in nature, occurring at highly variable intervals. At Eagle, two intervals of 22 years and, at Wolf, 63 and 4 years elapsed between the nineteenth century fires. In addition to corroborating my evidence for these recent fires, the landscape chronologies (Figure 2.12) provided a larger temporal context in which to place the fires (Teensma 1987, Morrison and Swanson 1990, Garza 1995). The relatively small inter-fire periods between the three nineteenth century fires at Eagle were likely preceded by longer fire-free intervals, with over 100 years between the 1848 fire and a possible early eighteenth century fire(s) and another >100 year period between this fire and a cluster of possible fires between 1555 and 1602 (Figure 2.12a). The area around Wolf also appears to have had a long fire-free interval ( at least >150 yrs.) after an initial cluster of much earlier possible fires (1470-1556) (Figure 2.12b). A long fire-free interval at some point in the stand's history may be necessary to establish the bimodal diameter distribution and the strong vertical stratification between emergent remnants and the younger post-fire canopy.

The reburns which followed at 22 year intervals after the initial 1848 fire at Eagle resulted in a broad range of overlapping origin dates for the early seral *Pseudotsuga*. This range spanned 60 years for the sampled *Pseudotsuga*. If this distribution had included the entire population, the two individuals originating between 1848-1870 would have lengthened this range to nearly 80 years. The *Pseudotsuga* distribution is suggestive of a single cohort and, without fire scar evidence, might lead to the conclusion that only one partial fire impacted the stand. This broad range of origin dates suggests the possibility that

- scars and regeneration (cohort origin dates) in same topographic unit as Eagle or Wolf Rock
- 9 scars or regeneration in topographic unit and complimentary evidence in adjacent unit
- scars or regeneration in adjacent topographic unit
- \* scars found at Eagle or Wolf Rock in the present study
- + cohort origin dates (but not scars) found at Wolf Rock in present study





multiple reburns may have been a factor in the broad age distributions (≈ 100 years) documented for old-growth *Pseudotsuga* in many stands across the Pacific Northwest (Franklin and Hemstrom 1981, Means 1982, Stewart 1986b). Multiple reburns are not uncommon in the Pacific Northwest, being facilitated by a rapid accumulation of fine fuels after the initial burn (Agee and Huff 1987). Fire-killed trees deposit dead needles and branches, and shrubs and herbs which proliferate in the open conditions contribute  $\pm 0$  additional fine fuels. In a chronosequence of stands in the Olympic Mountains, fine fuels were highest in the first year following fire and litter depth peaked in a 19-year-old stand (Agee and Huff 1987).

In contrast with Eagle, the large gap between the 1829 and 1892 fires at Wolf resulted in an age distribution with a clear break between trees establishing after the different fires. Wolf may also be distinguished by an even shorter reburn interval with a possible reburn only four years after 1892. An 1896 reburn would account for the apparent post-1892 regeneration delay in an age distribution which -- with a sharp incline and peak skewed toward the fire event -- would otherwise suggest rapid establishment. The question mark surrounding the 1896 reburn illustrates the difficulties encountered in fire reconstructions. Such immediate reburns are not uncommon but are difficult to document. An immediate reburn may have been a light surface fire, leaving little evidence of scarring on mature trees. In landscape fire chronologies, the broad ranges given to fire episodes may be due, in part, to an inability to detect immediate reburns or to differentiate between initial fires and reburns in field-conducted ring counts which are not cross-dated (Brown and Swetnam 1994). The result may lead to an underestimate of fire return intervals and an incomplete picture of the temporal fire pattern. The landscape chronology around Wolf indicates that much of the 1892 burn area subsequently reburned in 1899-1907 with scars found on stumps < 500 m from my site. Although this date range is not exactly synchronous with my 1896 scars, it does indicate that reburns were prevalent. The difference in dates may stem from less precise field counts. (It is also possible that scars from an 1896 fire event were imprecisely counted in the opposite direction, being grouped with the 1888-1895 episode).

Scars from the 1892 fire at Wolf were highly variable in direction (Figure 2.4). The lack of directionality may explain my inability to find scar evidence for the earlier 1829 fire. Unless there are external visual clues, locating scars in trees of this size is akin to "looking for a needle in a haystack." Almost all of the external scar features at Wolf were associated with the 1892 fire; those of the 1829 fire appear to have completely healed. This suggests that the direction of the 1829 burn (or the pattern of fuel accumulation) differed from that of the 1892 burn or, like the 1892 burn, was variable. The Wolf site is relatively flat; fires would not have been slope-driven, nor would fuel be consistently accumulated on the uphill side of trees. This contrasts with the sharply sloped Eagle site, where scars were "stacked" behind each other, and multiple scars were encountered using a single external cue.

The most recent fire (1892) did not burn evenly across either stand, but was heterogeneous in its spatial pattern. Survival islands varied in shape and size, ranging from isolated trees to the 2390 m<sup>2</sup> escaped patch at Wolf. At Eagle, escaped patches often corresponded with topographic features such as the seep, ridgeline and riparian slope. Escaped patches were not associated with any topographic features at Wolf.

The fire patterns demonstrate the critical point that remnant trees do not indicate an absence of fire. Remnant trees did not persist in unburned patches juxtaposed with burned patches. Rather, the entire area of each stand was burned at some point during the nineteenth century. Remnant trees survived amidst this burned area, survival made possible by the elevated crowns and thick bark of mature *Pseudotsuga* (Martin et al. 1976). Where fire intensity was greater or trees more vulnerable (e.g. smaller in size) remnant trees may not have survived. This interspersion of large survivors amidst the burned area is an essential feature in the development of a two-layered or multi-layered canopy, making possible the maintenance and emergence of old-growth characteristics within a context of repeated burns (Morrison and Swanson 1990).

Although it may be apparent that remnant trees do not indicate an absence of fire, it is tempting to assume that their locations reflect areas of low intensity during the most recent fire. The 1892 fire pattern at Eagle suggests that this is not a valid assumption.

While it was not possible to reconstruct the pattern of fire intensity, per se, the pattern of severity for young trees (post-1848, 1870) suggests that many remnant trees were located where the fire's intensity was likely greater and few were located where intensity was likely lower. The upper slope contained the highest density of remnant trees, but remnant trees typically contained 1892 fire scars and few individuals from the recently established cohorts (1848, 1870) survived the fire. Fire intensity may have been lower in patches where vulnerable, young trees survived and fire scars were absent, but few remnant trees were located in these patches. Remnant tree patterns are the cumulative outcome of all previous fires and mortality. At Eagle, the dislocation of remnant tree clusters relative to young tree survival patches suggests that the remnant tree pattern was established primarily by the severity pattern of a fire or fires prior to the 1892 event. Differences in vulnerability between cohorts and differences in fire patterns and intensity makes possible complex, unaligned patterns of severity between cohorts.

Survival patterns left by a fire are a complex interaction between the pattern of fire intensity and that of vegetation with differing susceptibility. For instance, a striking feature at Eagle is the relative lack of remnant trees in the seep, an area where fire intensity would be expected to be lower. The absence of remnants may be because this area was occupied by fire sensitive species. The wet conditions are favorable for *Tsuga* and *Thuja*, two species which currently dominate the seep and which are more vulnerable to fire than *Pseudotsuga* (Minore 1979). Survival patterns reflect not only fire intensity, but also the pattern of species with differing vulnerability.

The case of the 1829 cohort at Wolf, the intermediate age class, further illustrates the interaction between fire pattern and species traits (Figure 2.11). Intermediate age *Tsuga* were found primarily in large patches which escaped the 1892 fire and were located in areas of high remnant density. In contrast, *Pseudotsuga* survived as isolated individuals or in escaped patches in areas of low remnant tree density. *Pseudotsuga*'s shade-intolerance explains its absence from the high remnant density patches, and its fire resistance permitted

survival as isolated individuals outside these patches. The pattern of *Thuja* survival shared aspects of both the *Pseudotsuga* and *Tsuga* pattern. *Thuja* survived the 1892 fire in the large escaped patches, in small escaped patches and as isolated individuals. Like *Tsuga*, *Thuja* is shade-tolerant and was abundant in the large patches coincident with high remnant tree density. *Thuja*, however, is more fire-resistant than *Tsuga*. *Thuja* is thin-barked, but remarkably resilient, capable of surviving with large portions of cambium-kill (Minore 1983). Reflecting this resilience, *Thuja* survived the 1892 fire as isolated individuals and in the small patch in the more severely burned western region.

The nineteenth century fires not only left a patchwork of differing cohorts, these fires also left different balances of species within the surviving and regenerating patches. At Eagle, *Thuja* was strongly associated with those patches which burned in 1870 but escaped in 1892 (Table 2.4). The paucity of *Thuja* in the 1892 burn area suggests successful regeneration after the earlier fire and poor regeneration after the later fire. Poor regeneration may have resulted from any of several possible factors: insufficient exposure of mineral soil by the 1892 fire, poor seed years, a prior reduction in seed source across the landscape or an increase in *Thuja*-preferring herbivores (deer) (McCune and Allen 1985). At Wolf, *Pseudotsuga* was associated with the patches burned in 1892, being largely absent from the largest survival patches (Table 2.5). In contrast, *Taxus brevifolia*, an extremely shade-tolerant and fire-sensitive associated with old-growth forests, was strongly associated with patches which survived the 1892 fire, suggesting that the existence of older patches was critical to its presence within the stand. The association of species with particular fire patches suggests the potential for cohorts or patches of differing age to include differing proportions of species, enhancing the heterogeneity of the stand.

Forest communities have been described as "mosaics of more or less even-aged aggregations" (Isaac 1940, Cooper 1961, Bonnicksen and Stone 1981, Stewart 1986b). Mosaic models describe the forest as consisting of patches or gaps which proceed through cycles of initiation, development and destruction (Watt 1947, Remmert 1991), and partial fires have been described as a gap process maintaining such mosaics (Bonnicksen and Stone 1981, Means 1982, Stewart 1986b). The mosaic model appropriately emphasizes the importance of disturbance in initiating cohorts which compose the forest. However, the conception of a mosaic may not adequately capture the complexity of stands in which cohorts are layered and interspersed rather than juxtaposed in discrete patches. In the Eagle and Wolf stands, the most recent fire left identifiable patches of young survivors and regenerating cohorts, but young survivors were also interspersed as isolated individuals among the regenerating cohort. In addition, the patterns established by the most recent fires were overlaid by interspersed remnant trees, surviving members of much older cohorts. Remnant trees did not survive in discrete, unburned patches. Furthermore, the remnant tree pattern was not aligned or associated with the pattern of young survivors of the most recent fire. In a regime of episodic, partial fire, each fire event opens space for a new cohort, but the residual patterns created by all previous fires are overlaid upon and interspersed among these patches.

#### Size structure and post-fire establishment history

Despite the strong differences in post-fire species composition between sites, the establishment timing of species relative to each other was remarkably similar. At both sites, *Pseudotsuga* regenerated more quickly than *Tsuga*, and *Tsuga* regeneration continued for longer periods. However, like *Pseudotsuga*, *Tsuga* regeneration was clustered soon after the fire event. *Tsuga*'s reverse-J size distribution -- most of the population occurred in the smallest size classes and declined rapidly with increasing size class -- cannot be attributed to continuous recruitment. Rather, this distribution was produced by size differentiation among concurrently establishing individuals and by *Tsuga*'s ability to survive indefinitely in a suppressed state. As shown by its age-to-diameter relationship, the smallest size classes included *Tsuga* of all ages.

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When size distributions are used as a surrogate for age distributions, all-sized populations with a reverse-J distribution have often been interpreted as all-aged populations with continuous recruitment (cf. Oliver and Stephens 1977, Stewart 1986b). As illustrated by the *Tsuga* populations and demonstrated by several other studies, this interpretation is not always correct. Even if regeneration is initiated by a particular event and ceases after a limited time period, the population may display a reverse-J size distribution despite having a bell-shaped age distribution.

A reliance on size distributions in past studies led to an emphasis on forest composition as being driven by continual recruitment and gradual species replacements (Oliver and Stephens 1977). The role of disturbance events was underemphasized. Later reconstruction of forest history and age structure demonstrated the importance of disturbance in initiating the cohorts which composed the canopy. These studies lent support to Egler's (1954) contention that initial floristic composition after a disturbance may be more important than sequential replacements in determining a community's composition. In the Pacific Northwest, early general descriptions of succession emphasized the occupation of disturbed sites by intolerant *Pseudotsuga* with shade-tolerant *Tsuga* and *Thuja* following later in succession (Isaac 1940, Munger 1940). Accumulated studies, however, have shown that each species can play multiple successional roles and that *Tsuga* and *Thuja* can be important pioneers (Franklin and Hemstrom 1981, Huff 1995). At the Eagle and Wolf stands, *Tsuga* remained an important canopy species as a result of its initial abundance in the cohort.

The sequence of species establishment reflected differences in species' life history traits and regeneration niches. At Eagle, the median age of *Castanopsis* was significantly greater than that of both *Pseudotsuga* and *Tsuga*. Fifty percent of its population originated within the first 3 years after the 1892 fire at Eagle. The ability of *Castanopsis* to resprout vigorously after fire (Kauffman and Martin 1990, McKee 1990) gave it a head start over its competitors. While it cannot equal the potential size of its competitors, a smaller percent of

its population was left in the smallest size class. The more rapid establishment of *Pseudotsuga* relative to *Tsuga* may be explained by its tolerance of drought and exposure, conditions to which *Tsuga* is particularly susceptible (Larsen 1940, Haig et al. 1941, Livingston and Black 1987, Livingston and Black 1988). The shade-tolerance of *Tsuga* (Carter and Klinka 1992) may account for its ability to regenerate for a longer time period after the fire.

Although the sequence of species establishment was similar at both sites, the median establishment time for both *Pseudotsuga* and *Tsuga* was longer at Eagle than at Wolf, possibly reflecting important site differences. This difference assumes an 1896 reburn at Wolf, but even without this assumption, early regeneration of *Pseudotsuga* can be described as tighter at Wolf. The earliest 50% of the population regenerated within a 5 year time period at Wolf, whereas the first 50% spanned 14 years at Eagle. In the hot, dry summers of the Pacific Northwest, regeneration can be significantly delayed on south-facing slopes such as that of Eagle (Means 1982).

Given that both *Pseudotsuga* and *Tsuga* regenerated soon after the fire and that the order of establishment was similar at both sites, the differences in species composition may be attributed to other two sources: differences in the initial abundance of each species and differences in density-dependent mortality. The exposed conditions which may have delayed regeneration of both species at Eagle may have inhibited *Tsuga* regeneration, in particular, limiting recruits across its establishment period. In contrast, moderate conditions at Wolf may have allowed *Tsuga* to regenerate in abundance. Furthermore, numerous post-1829 *Tsuga* survived the 1892 fire in the large survival patch and, being reproductively mature, would have served as a seed source. Initially, it is possible that *Pseudotsuga* abundance was similar between sites. Subsequent suppression mortality, however, was likely more intense at Wolf. Few *Pseudotsuga* (5%) have persisted in the suppressed crown class, whereas, at Eagle, a large proportion of *Pseudotsuga* (40%) has persisted in this class (Table 2.2). At Wolf, *Pseudotsuga* which fell behind the canopy's

growth would have been shaded by dense *Tsuga* crowns in addition to those of *Pseudotsuga*. Survival may have been impossible for *Pseudotsuga* which did not regenerate immediately after the fire, compressing the age distribution (Figure 2.8a). At Eagle, slow, incomplete regeneration and the initial scarcity of *Tsuga* has left a relatively open canopy, possibly allowing *Pseudotsuga* to regenerate in greater numbers over a longer period and to persist in a suppressed state.

The size distribution of *Thuja* at Wolf was distinctive in that it differed from *Thuja* size distributions in *Thuja* old-growth stands elsewhere in the Pacific Northwest. In these stands, *Thuja* size distributions are typically flat, extending to large size classes but including few individuals in small classes (Schmidt 1955, Gregory 1957, Keenan 1993, Daniels 1994). This distribution reflects *Thuja*'s restricted ability to regenerate under a closed canopy. *Thuja* regeneration may be particularly dependent on mineral seedbeds such as those exposed by root-throw or large-scale disturbance (Parker 1986, Minore 1990, Daniels 1994). In contrast to the flat distributions, the population at Wolf included large numbers of small individuals with numbers declining rapidly with size. These large numbers reflect *Thuja*'s successful regeneration after partial fire, a recruitment opportunity that would not typically occur in *Thuja* old-growth stands, since such stands tend to be located in moist environments or protected topographic positions (Parker 1986, Keenan 1993, Daniels 1994).

The size distribution of *Thuja* was also distinguished by its differences with both the *Tsuga* and *Pseudotsuga* distributions. Unlike *Tsuga*, the size distribution of *Thuja* displayed a long tail extending to the large (remnant tree) size classes, reflecting *Thuja*'s low mortality rate and, compared with *Tsuga*, lower fire-susceptibility. In contrast with *Pseudotsuga*, *Thuja*'s shade tolerance permitted a large proportion of the population to persist in smaller size classes. Furthermore, whereas few *Pseudotsuga* were present in the intermediate age class, *Thuja* was relatively abundant in this cohort. The abundance (relative to other species) of *Thuja* within each of the age classes (young, intermediate, remnants) may be attributed to a suite of traits unique among the species at Wolf: shade tolerance, successful regeneration after fire and tolerance of moderate fire damage. The low-severity fire history and moderate conditions at Wolf may provide a particularly advantageous habitat for *Thuja*.

At Eagle, the moderate decline in *Tsuga* with increasing size class and the secondary peak at 30-35 cm might be explained by successful regeneration after the 1870 fire followed by poor regeneration after the 1892 fire, as suggested by the scarcity of *Thuja* within the 1892 burn area, an observation confirmed by *Thuja*'s strong association with those areas which burned in 1870 but escaped in 1892.

In natural stands, size-to-age relationships are typically poor, but those at the Eagle and Wolf stands were at the lower end of reported r<sup>2</sup> values for stands in the central western Cascades. Stewart (1986a) reports r<sup>2</sup> values of .53-.82 for *Tsuga heterophylla* in unburned old-growth stands. In a stand with an emergent *Pseudotsuga* cohort ( $\approx$ 450 yrs.) above a single cohort arising after a fire  $\approx$ 1890 AD, the r<sup>2</sup> value for post-1890 *Tsuga* was .50 (Stewart 1986b). In a two-cohort stand with fires at  $\approx$ 1860 and  $\approx$ 1890, Stewart (1986b) reports an r<sup>2</sup> of .45 for *Pseudotsuga*. The relationships described for these stands may give meaning to the high degree of variance at the Eagle and Wolf stands. Stands impacted by partial fire may have greater variance in the size-to-age relationship than unburned stands. Although the two stands described by Stewart (1986b) were both impacted by partial fire, the Eagle and Wolf stands included additional cohorts and, accordingly, had somewhat weaker relationships.

The complexity of interactions at Eagle and Wolf may break down the relationship between age and size. A 95-year-old tree in the middle of a patch initiated 122 years ago would likely experience greater competition than a tree of similar age in the most recent patch initiated 100 years ago. Whether a tree survived fire as an isolated individual or in the center of patch should significantly impact that tree's growth. In addition to its temporal and spatial position within recently initiated patches, a tree's growth should also

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be influenced by its position relative to the remnant trees which were unevenly distributed across each stand (Chapter 3).

The Eagle and Wolf stands were characterized by alternate pathways, but describing the pathways as moving succession either "forward" or "backward" is problematic. At Eagle, partial fires were followed by an abundance of early seral Pseudotsuga and the persistence of resprouting Castanopsis. But these fires have also created the multi-tiered canopy typically associated with later stages of development. At Wolf, late seral Tsuga dominated the post-fire cohort numerically, suggestive of an advance in succession. But Tsuga may have been prevalent previously, and the fires' first effect was the elimination of Tsuga from the previous community. The fires also initiated new cohorts of Pseudotsuga. While less abundant overall, Pseudotsuga made up a large proportion of the dominant crown class and Pseudotsuga dominants were larger than those of Tsuga. Before the forest can transition to a self-replacing Tsuga forest, death must first overtake the post-fire Pseudotsuga dominants in addition to the Pseudotsuga remnant trees. Morrison and Swanson (1990) have suggested that partial fires may extend the duration over which a Pseudotsuga old-growth stand occupies a site by delaying the transition to a self-replacing Tsuga forest. Even at a site where Tsuga dominates the post-fire cohort numerically, sufficient numbers of Pseudotsuga may establish to insure a continual recruitment and presence of old-growth Pseudotsuga dominants.

Where repeated, partial fires have been an ongoing component of development, multiple cohorts with differing species compositions may have  $be_{\Lambda}^{QV}$  consistent characteristic of the community, and the potential for any successional end point illusory. While the Eagle and Wolf stands present two alternate paths of development, both suggest that notions of moving succession forward or backward may not be applicable to a community impacted by repeated partial fires. Furthermore, fire-opened patches are not discrete, but are overlaid by a complex pattern of survivors, such that concepts of mosaics and patchwise development cycles are also problematic. Both stands also suggest the potential for partial fires to create developmental cycles which extend the lifetime of forests with the oldgrowth characteristics.

## Chapter 3: Spatial Patterns of Colonizing Tree Species Relative to Surviving Trees after Partial Fires in Two Coniferous Stands, Oregon Cascades

### Introduction

Successional theory has traditionally emphasized colonization following standreplacing disturbances (Franklin et al. 1985b). However, disturbance does not typically leave a blank slate for successional processes. Even after catastrophic disturbances, legacies of the previous community may persist: soil patterns, fine and coarse dead organic matter, seed banks, mycorrhizae and belowground perenating structures. Although they are not always taken into account, these biological legacies can strongly influence rates of recovery and successional pathways (Franklin et al. 1985b, Franklin and Halpern 1987, Halpern 1988). After a moderate disturbance, aboveground survivors form a prominent legacy, raising a critical question: to what extent are post-disturbance successional pathways influenced by survivors from the previous community?

Until recently, most models of succession treated disturbance in only a general manner, with disturbance serving simply as the initiator of the replacement sequences upon which emphasis was placed (Cattelino 1979). Models such as those of Noble and Slatyer (1980) have demonstrated that disturbance characteristics and the adaptive traits of species relative to disturbance are essential in predicting successional pathways. Different pathways can result from disturbances of different size, magnitude, frequency or timing (Sousa 1984; Noble 1980; Pickett 1987). Surviving individuals -- whose abundance, composition and pattern is an outcome of disturbance characteristics -- may influence vegetation patterns by either facilitating or inhibiting those species available to repopulate a site. While catastrophic disturbances generally reverse succession, being followed by the establishment of early seral species, moderate severity disturbances may modify the direction of vegetation change in a variety of case-specific ways (Martin et al. 1976, Walker and Chapin 1987).

In the Pacific Northwest, where wildfire is the primary stand-replacing disturbance, moderate severity fires can leave a prominent pattern of surviving remnant trees. Remnant trees may interfere for light, intercept precipitation and compete for water and nutrients. Remnant trees may also alter microclimate: for instance, providing cool, shaded microsites in an otherwise exposed environment. The remnant tree pattern may also be associated with other legacies which make up the post-fire residual pattern, such as substrate patterns of litter and mineral soil.

In this study, I examine the spatial relationship between old-growth remnant trees (>200 yrs. age) left by a partial-mortality fire and mature post-fire trees (≈100 yrs. age) in two stands in the Oregon Cascades. The two stands differed in environmental conditions and in the mature cohort's species composition; one stand, strongly sloped and south-facing, was dominated by early seral *Pseudotsuga menziesii*, and the other stand, flat and northwest-facing, was dominated by late seral *Tsuga heterophylla*. The broad question of how post-disturbance succession may be influenced by surviving individuals was framed in terms of the more specific question of spatial dependence. That is, are the species patterns of the post-fire cohort spatially independent of remnant trees, or do significant spatial interactions (aggregation, dispersion) exist between colonizing species and surviving trees? Aggregation of a species around remnant trees may suggest that remnant trees (or other remnant tree-associated residual features) facilitate the presence of that species, dispersion may suggest an inhibitory effect, and spatial independence may suggest a neutral net effect.

Several secondary questions are nested within the overarching question of spatial dependence between the remnant trees and species of the post-fire cohort.

First, for each post-fire species, are size class patterns spatially dependent upon the remnant tree pattern? Trends in pattern across size classes may suggest a remnant tree effect upon that species' growth and mortality patterns.

Second, do the spatial interactions between post-fire species and remnant trees differ with the species of the remnant tree? Such differences would suggest that the species composition of survivors, not just the density of survivors, is an important factor in postfire successional pathways.

Third, at short distances from remnant trees (i.e. within the remnant's projected crown area) are post-fire species positively or negatively associated with areas to the north or to the south of remnant trees? On south-facing slopes during the hot, dry summers of the Pacific Northwest, remnant tree shade to the immediate north may facilitate the establishment of exposure-sensitive species. To the immediate south, remnant effects upon these same species may be neutral or, if remnant tree interception and uptake of water is significant, inhibitory.

Fourth, are the within-group spatial patterns of remnant trees, post-fire species and post-fire species' size classes different from random? Fifth, do significant spatial interactions exist between species within the post-fire cohort? The last two questions do not explicitly address the interaction between remnant trees and the post-fire cohort. However, these patterns -- within-group patterns and interactions between species within a cohort -- can be compared to those described for forests which have not been impacted by partial fires. Distinctive patterns might be an outcome of the spatial interactions with remnant trees.

Although descriptions of pattern are often used to generate hypotheses about the processes driving patterns (Leps 1990, Levin 1992), patterns are an important feature of a community or landscape, in and of themselves. The details of spatial pattern at small scales (i.e. within a stand) may have critical consequences to important higher-level functions, such as biodiversity and productivity (Pacala and Deutschman 1995). Therefore, I will discuss the observed patterns as distinctive features of these communities, in and of themselves, and with regard to characteristics of diversity.

Point pattern analysis, the method I use to describe spatial interactions, has been applied to many issues in forest ecology. Particular emphasis has been given to changes in point patterns with stand development and those pattern changes (i.e. increasing uniformity) which are expected to result from density-dependent processes such as competition (Laessle 1965, Christensen 1977, Whipple 1980, Good and Whipple 1982, West 1984, Ghent and Franson 1986, Sterner et al. 1986, Kenkel 1988, Duncan 1991, Szwagrzyk 1992). Point pattern investigations have tested for spatial associations between subcanopy regeneration and the small-scale openings of canopy gaps (Szwagrzyk 1990, Leemans 1991, Moeur 1991, Moeur 1993). In forests with large fire-created openings, clustered within-group patterns (of size or age classes) have been interpreted as the signature of even-age groups regenerating in fire patches (Cooper 1961, Bonnicksen and Stone 1981, Stewart 1986b). Although disturbance effects upon point pattern have been investigated, much greater attention has been given to pattern development during disturbance-free periods. Furthermore, with the exception of Duncan's (1993) description of patterns after a moderate-severity flood, few accounts of disturbance-associated pattern have thoroughly assessed the spatial interaction between surviving trees and those which established afterwards.

In the Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest, infrequent, stand-replacing fires were thought to be the paradigmatic disturbance regime until recent work, particularly in the Oregon Cascades, provided numerous examples of higher frequency, partial-mortality fires (Agee 1991). However, despite their prevalence, multiple cohort stands arising from partial fires have received little attention (notable exceptions being Means [1982], Stewart [1986b] and Zenner [1995]). Chronosequences used to assess successional trends have avoided multiple cohort stands, focusing instead on stands which developed after a single, catastrophic fire and permitted straightforward age categories (Schoonmaker and McKee 1988, Spies and Franklin 1991, Halpern and Spies 1995, Huff 1995). Studies of early successional patterns have typically been conducted in the aftermath of severe fires or clear cuts (Isaac and Meagher 1936, Isaac 1940, Dyrness 1973, Agee and Huff 1987, Halpern 1988, Halpern 1989, Halpern and Franklin 1990, Huff 1995). Recent modeling and retrospective studies have suggested that partial fires or harvests which leave remnant trees may lead to greater proportions of late seral *Tsuga heterophylla* and *Thuja plicata* in the regenerating cohort (Hansen et al. 1995, Zenner 1995). However, after reconstructing two stands on dry sites, Means (1982) proposed that frequent, partial fires on such sites promoted the regeneration of early seral *Pseudotsuga menziesii* to the exclusion of *Tsuga heterophylla*. Successional pathways after partial fires are not well understood, and no studies have thoroughly examined within-stand species patterns. Determining whether the spatial relationship between remnant trees and regenerating species is facilitory, inhibitory or neutral in the context of different environmental conditions may permit a better understanding of successional pathways following partial fire.

### Methods

### Site description

I chose two stands characterized by two-tiered canopies in which remnant trees, survivors of at least one partial fire, emerged above a mature lower canopy which had regenerated after the most recent fire events. Remnant old-growth trees were 200-600 years in age and 60-165 cm in diameter. Most individuals in the lower canopy were less than 100 years in age, and mean diameters (quadratic) were 22 cm and 19 cm at the two sites. I chose one site at which *Pseudotsuga menziesii*, a shade-intolerant, dominated the lower canopy and one at which *Tsuga heterophylla*, a shade-tolerant, dominated the lower canopy (Table 3.1- 3.3).

	Eagle Rock	Wolf Rock
Elevation	700 m	850 m
Aspect	S	W/NW
Slope	20° - 30°	< 5°
Annual precipitation	1903 mm	2181 mm
June - Aug. precipitation	125 mm	155 mm
Mean July temperature	≈ 17° C	≈ 15.9° C
Mean January temperature	≈ l° C	≈ l° C
Most recent fires	1848, 1870, 1892	1831, 1892, ?1896

Table 3.1. Site characteristics of Eagle Rock and Wolf Rock reference stands

The Eagle Rock stand is located east of the town of Detroit, Oregon, in the Detroit Ranger District of the Willamette National Forest (latitude 44° 47' N, longitude 122° 2' W). The Wolf Rock stand is located adjacent to the H.J. Andrews Experimental Forest northeast of the town of Blue River, Oregon, in the Blue River Ranger District of the Willamette National Forest (latitude 44° 17' N longitude 122° 10' W).

Both stands are located within the *Tsuga heterophylla* zone (Franklin and Dyrness 1973) of the west side of the central Oregon Cascade Mountains. The climate is typical of the Pacific Northwest with cool, wet winters interrupted by summer drought and high temperatures from June through September. Winter snowpacks occasionally exceed 1 m in depth and are often transient at 500-1000 m elevation in the Cascades. Eagle Rock is characterized by the *Tsuga heterophylla / Berberis nervosa* plant association, typical of warm, well-drained, moderately productive sites (Hemstrom et al. 1987). Wolf Rock is characterized by the *Tsuga heterophylla / Rhododendron macrophyllum / Linnea borealis* plant association, common on gentle terrain in cooler areas, where deeper winter snowpacks and summer frost may occur (Hemstrom et al. 1987).

The mapped areas at each site were located within stands -- that is, a relatively continuous area of similar age structure, species composition and topography -- of much

greater area. The 2.25 ha mapped area at Wolf Rock was located within a stand of  $\approx 14.5$  ha. A road separates this area from forest of similar age and composition, which would extend the stand to a total of  $\approx 80$  ha. The 2 ha mapped area at Eagle Rock was located within a stand of  $\approx 70$  ha.

Sites were selected to minimize topographic variation. Where topographic variation existed, remnant tree locations did not appear to be associated with topographic features. At Eagle Rock, the central portion of the 2 ha mapped stand is a relatively homogeneous hillslope (S aspect), but a riparian slope (E/SE aspect) covers .27 ha along the east end of the stand and a seep (.13 ha) and ridge (.24 ha) cover the west end of the stand. The topography at Wolf Rock is subtle with few distinguishable features.

At Eagle Rock, the most recent fire events occurred at 100 yrs. (1892), 122 yrs. (1870) and 144 yrs. (1848) before present (present being 1992, the year the stand was mapped). A majority of the lower canopy regenerated after the 1892 fire, but a large minority originated after the 1870 fire. Only a few individuals remained from regeneration after the 1849 fire (Chapter 2). At Wolf Rock, the most recent fire events occurred at 100 yrs. (1892) and 163 yrs. (1829) before present. The majority of the lower canopy regenerated after the 1892 fire. Regeneration after the 1829 fire, however, dominated almost a third of the stand and was clustered in the center of the stand (Chapter 2).

At Eagle Rock, remnant trees were almost all *Pseudotsuga menziesii*, but included several *Libocedrus decurrens* (Table 3.2). At Wolf, *Pseudotsuga menziesii* was the dominant remnant species, but *Thuja plicata* made up 25 % of all remnants (Table 3.3). At both sites, the most important post-fire species were the three conifers, *Pseudotsuga menziesii*, *Tsuga heterophylla* and *Thuja plicata*, but, at Eagle, two hardwoods, *Castanopsis chrysophylla* and *Cornus nuttallii*, were also abundant (Tables 3.2, 3.3).

<u>2 ha plot (100 * 200 m)</u>	<u>density (#/ha)</u>	basal area (m <sup>2</sup> /ha)	<u>quadratic mean diameter (cm)</u>
Total Live	1140.5	74.07	28.8
Remnant age class			
Live	28.0	30.20	117.2
Pseudotsuga menziesii Libocedrus decurrens Thuja plicata	26.0 1.5 .5	29.32 .69 .19	119.8 76.3 70.3
Dead	6.5	7.33	119.9
Pseudotsuga menziesii	6.5	7.33	119.9
Post-fire age class			
Total	1112.5	43.87	22.4
Conifers	977.0	41.53	23.3
Pseudotsuga menziesii Tsuga heterophylla Thuja plicata Libocedrus decurrens Taxus brevifolia Abies grandis	721.5 192.5 50.5 5.5 6.5 .5	33.45 6.50 1.38 .05 .03 .002	24.3 20.7 18.7 10.3 7.6 8.3
Hardwoods	135.5	2.33	14.8
Castanopsis chrysophylla Cornus nuttallii Acer macrophyllum Alnus rubra	66.5 55.5 13.0 .5	1.49 .43 .42 .001	16.9 9.9 20.2 5.5
<u>3.75 ha extended plot (150 * 25</u>	0 m)		
Remnant age class			
Live	32.3	32.61	113.4
Pseudotsuga menziesii Libocedrus decurrens Thuja plicata Tsuga heterophylla	30.1 1.6 .3 .3	31.69 .73 .10 .08	115.7 76.2 70.3 63.6
Dead	5.9	5.75	111.7
Pseudotsuga menziesii Tsuga heterophylla	5.6 .3	5.67 .07	113.6 59.8

Table 3.2. Measurements of stand structure at Eagle Rock reference stand within 2 ha plot (all age classes) and within 3.75 ha extended plot (remnants only).

<u>2.25 ha plot (100 * 225 m)</u>	density (#/ha)	<u>basal area (m²/ha)</u>	quadratic mean diameter (cm)
Total Live	1473.4	78.19	26.0
Remnants			
Live	42.7	39.64	108.8
Pseudotsuga menziesii Thuja plicata	31.1 11.6	31.94 7.70	114.3 92.1
Dead	7.1	5.79	101.8
Pseudotsuga menziesii Thuja plicata Tsuga heterophylla	5.8 .9 .4	4.54 1.16 .09	100.0 129.1 51.2
Post-fire age class			
Total	1430.7	38.55	18.5
Conifers	1424.8	37.98	18.4
Tsuga heterophylla Thuja plicata Pseudotsuga menziesii Abies amabilis Taxus brevifolia Abies grandis Pinus monticola	781.3 382.7 243.1 11.1 5.8 .4 .4	17.99 10.52 9.48 .36 .06 .002 .01	17.1 18.7 22.3 20.3 11.6 7.2 17.4
Hardwoods	5.8	.14	17.7
Castanopsis chrysophylla Cornus nuttallii	5.3 .4	.13 .01	17.9 15.7

Table 3.3. Measurements of stand structure at Wolf Rock reference stand within 2.25 ha plot (all age classes) and 3.875 ha extended plot (remnants only).

## <u>3.875 ha extended plot (150 \* 275 m)</u>

## Remnant age class

Live	35.4	31.66	106.8
Pseudotsuga menziesii	26.1	25.65	111.9
Thuja plicata	9.3	6.01	90.8
Dead	6.5	5.51	104.3
Pseudotsuga menziesii	4.9	4.32	105.9
Thuja plicata	1.3	1.14	105.9
Tsuga heterophylla	.3	.05	51.2

### Stand mapping

I established reference stands of 2 ha (100 \* 200 m) at Eagle Rock and 2.25 ha (100 \* 225 m) at Wolf Rock. I tagged, mapped and measured all live trees with diameter  $\geq$ 5 cm at breast height (dbh, at 1.4 m). I also mapped all remnant trees which were located within 25 m of the mapped stand perimeter, such that remnant trees were mapped within "extended plots" of 3.75 ha (150 \* 250 m) and 4.125 ha (150 \* 275 m), respectively. In addition, I mapped dead remnant trees which were judged, on the basis of their decay class (Cline et al. 1980), to have died after the most recent fire.

I initiated stand mapping by surveying a grid with reference posts at 25 m intervals. As tree mapping progressed, additional reference posts were surveyed because of poor visibility in areas of high stem density. I mapped most trees using double-station surveys: azimuth measurements (only) from two known reference points. Cartesian coordinates were then calculated via triangulation. I mapped remaining trees with single-station surveys: azimuth, distance and vertical slope measurement from a single reference post. Azimuths were measured with staff compasses. Protocol followed Pabst et al. (1993) and coordinates were calculated with a SAS code (SAS Institute Inc. 1987) written by R. Pabst. I checked the completed stem maps for errors by visiting all mapped trees. Tree location errors are not greater than .5 m.

Trees were classified by crown classes representing their relative height within the canopy: emergent, dominant, codominant, intermediate and suppressed. Remnant oldgrowth trees were classified as an emergent class above the mature lower canopy. For all remnant trees, I constructed crown projections by estimating crown edge with vertical clinometer sightings and measuring crown radii in each cardinal direction. All other classes represent relative height within the mature lower canopy. This lower canopy layer is defined by the codominant crown tops. Dominant crowns lie within the canopy, but their tops rise above and are unshaded by the codominants. Intermediate crowns also lie within the canopy, but their tops are positioned below the codominant tops. Suppressed crowns

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are positioned entirely below the lower canopy. The crown classifications of mature lower canopy trees make **no** reference to a tree's height relative to remnant trees, but only relative to other mature trees. That is, a mature tree immediately adjacent to an old-growth remnant tree could be classified as either suppressed or dominant, even though it is dwarfed by the remnant tree; its classification depends **only** on its height relative to surrounding mature trees.

I input all tree coordinate and attribute data into a Geographic Information System (GIS), creating point coverages joining tree attributes and locations. GIS facilitated the analysis of additional coverages (e.g. polygon coverages representing remnant tree crowns) in conjunction with the stem maps.

### Point pattern analysis: statistics

Univariate spatial patterns (those of a single group) were analyzed using the function L(t), a transformation of Ripley's K(t) function. Ripley's K(t) function uses all tree-tree distances to provide a measure of spatial pattern at various distances t. It is defined as the expected number of trees within a distance t of an arbitrarily chosen tree. The unbiased estimator of K(t) for an observed pattern is

$$\hat{K}(t) = \frac{A}{n^2} \sum_{i=1}^{n} \sum_{j=1}^{n} w_{ij} I_{ij}(t)$$

where *n* is the number of trees in a rectangular plot of area, *A*;  $I_{ij}(t)$ , the counter variable, equals 1 if  $d_{ij}$  (the distance between trees *i* and *j*)  $\leq t$  and 0 if not;  $w_{ij}$  is a weight which accounts for edge bias. Under the null hypothesis of complete spatial randomness  $K(t) = \pi t^2$ .  $\hat{L}(t)$  is a square-root transformation of  $\hat{K}(t)$  which stabilizes the variance. Since  $\hat{L}(t) = \sqrt{\hat{K}(t)/\pi} - t$ , a value of  $\hat{L}(t) = 0$  indicates that the spatial pattern of trees at a given distance *t* is random. Positive values of  $\hat{L}(t)$  indicate a clumped distribution and negative values indicate a uniform (regularly spaced) distribution. Bivariate spatial interactions between two different groups of trees were analyzed with two different methods: the  $L_{12}(t)$  transformation of the Ripley's  $K_{12}(t)$  function and the Hamill-Wright (1986) refined nearest neighbor statistic.  $K_{12}(t)$  is a generalization of the univariate function K(t) to a bivariate point process:  $K_{12}^*(t)$  is determined from the number of type 2 trees within a distance t of an arbitrary type 1 tree, and  $K_{21}^*(t)$  is determined from the number of type 1 trees within a distance t of an arbitrary type 2 tree. The estimator,  $\hat{K}_{12}(t)$ , is calculated from a linear combination of  $K_{12}^*(t)$  and  $K_{21}^*(t)$ described by (Lotwick and Silverman 1982). When two groups are spatially independent,  $\hat{K}_{12}(t) = \pi t^2$ . Since  $\hat{L}(t) = \sqrt{\frac{\hat{K}(t)}{\pi}} - t$ , a value of  $\hat{L}_{12}(t) = 0$  indicates that two groups of trees are spatially independent. Positive values of  $\hat{L}_{12}(t)$  indicate aggregation (positive association) and negative values indicate dispersion (negative association).

While the bivariate Ripley's  $K_{12}(t)$  takes into account all distances between two groups of trees, the Hamill-Wright statistic takes into account only the distances between type 1 trees and the type 2 tree nearest to each type 1 tree. The Hamill-Wright statistic compares the observed cumulative distribution of nearest neighbor distances to the null cumulative distribution. The null distribution is the probability that a type 1 tree will be within a given distance t of a type 2 tree under the random hypothesis, a probability equal to the percentage of the total area that is within the given distance of any type 2 tree. This probability depends only on the plot area and the locations of type 2 trees. The observed cumulative distribution is the percentage of type 1 trees within the given distance t of a type 2 tree. The null hypothesis is tested with a Kolmogorov-Smirnov (KS) test for continuous data which compares the maximum difference between the observed and null distribution with a critical value based on the number of distances (type 1 trees) used to calculate the observed distribution. If the maximum difference is positive and greater than the critical value at p = .05, type 1 points are aggregated around type 2 points. If the difference is negative and significant, type 1 points are dispersed away from type 2 points.

For the univariate and bivariate Ripley's K(t), the theoretical statistical distribution is unknown. Therefore, Monte Carlo simulations were used to assess significance following the procedure outlined by Moeur (1993), a variation of that proposed by Besag and Diggle (1977). For the univariate case, L(t) was calculated for a set of n random coordinates (n equal to the number of trees in the observed group). After 100 iterations, the values of L(t) for all iterations were ordered and the smallest and largest 5% of values at each value of t were discarded. The remaining minimum and maximum values defined a two-sided 90% confidence envelope. Significant clustering or uniformity was indicated where observed values of L(t) were greater or less than the envelope's upper or lower boundary. For the bivariate case, the locations of type 1 trees were maintained at each iteration. Type 2 trees were all shifted the same random distance across a toroidal region such that points were not shifted outside the study area. The toroidal shift method makes the type 1 and type 2 patterns independent of each other, but maintains the underlying structure of each point pattern (Lotwick and Silverman 1982). I used 200 iterations to generate confidence envelopes for the bivariate  $L_{12}(t)$ . Significant aggregation or dispersion was indicated where observed values of  $L_{12}(t)$  were greater or less than the envelope's upper or lower boundary.

I used both the bivariate Ripley's  $K_{12}(t)$  and the Hamill-Wright nearest neighbor analysis to assess bivariate patterns with the intent that the two tests would complement each other. Ripley's  $K_{12}(t)$  is the more powerful test, incorporating all tree-tree distances, and can detect different patterns at different scales. The Hamill-Wright method uses only nearest neighbor distances, but interpretation was often more straightforward. By yielding a statistically valid *p*-value for each pattern, this test permits an objective assessment of a pattern's strength. The Hamill-Wright method also allows type 2 trees to occupy an area larger than, but including, the area occupied by type 1 trees. (For Ripley's  $K_{12}(t)$ , the two groups of trees must occupy the same area). In the present study, the nearest neighbor analysis offered the important feature of accounting for remnant locations (within the extended plots) beyond the borders of the area in which post-fire trees were mapped.

The univariate and bivariate calculations of Ripley's K(t) were calculated with the FORTRAN programs, RIPK and KTOR, written by and obtained from M. Moeur. Both programs transform  $\hat{K}(t)$  to  $\hat{L}(t)$  and run Monte Carlo simulations following the methods outlined here. The Hamill-Wright statistic was calculated with a BASIC program, FASTNAD, written by D.N. Hamill and S.J. Wright and made available to me by R. Busing and L. Lopez-Mata.

### Point pattern analysis: structure of the data analysis

The primary objective of this study was to describe the relationship between the remnant tree pattern and the species and size class patterns of post-fire canopy. I included both live and dead remnant trees in the remnant point set, since post-fire species patterns were likely associated with remnant trees present at the time of establishment and not just currently live remnant trees. In analyzing size class patterns, I used crown classes rather than absolute size classes. Since the height of the lower canopy varied greatly across each stand, crown classes were a better measure of a tree's competitive status within the post-fire canopy than was absolute size.

At Eagle, I used the entire 2 ha plot for each spatial analysis. At Wolf, fire patterns resulted in differing canopy structures among the western, central and eastern portions of the stand (Chapter 2). The western and eastern portions burned in 1892, leaving distinct two-tiered canopies of remnant trees and mature post-fire trees. In contrast, large patches within the central portion were not burned in 1892, being burned earlier in 1829, and unburned patches were intermixed with burned patches. The resulting patchwork of canopy structures, with post-1829 trees and post-1892 trees intermixed, was not comparable to the distinct two-tiered system of the eastern and western areas. Therefore, I divided the 2.25 ha mapped stand into three .75 ha (75 \* 100 m) plots: west, central and

east. I conducted spatial analyses for the west and east plots only. Although the Eagle stand also burned more than once in the nineteenth century, differences in tree ages were relatively small, such that the two-tiered canopy was distinct and consistent across the stand.

An inter-type point pattern consists of four elements: 1) the within-group (univariate pattern) of type 1 points alone; 2) the pattern of type 2 alone; 3) the combined pattern of type 1 and type 2 when treated as a single univariate pattern; 4) the interaction (bivariate pattern) between the type 1 points and the type 2 points (Upton and Fingleton 1985).

Following this structure, I first used Ripley's K(t) to describe the univariate pattern of the remnant trees. Remnant tree pattern was described in the standard plot (100 \* 200 m) at Eagle and the west and east plots (100 \* 75 m) at Wolf, the plots within which the post-fire trees were confined and analyzed. Remnant pattern was also described for the extended plots (150 \* 250 m at Eagle and 150 \* 275 m at Wolf), the plots which provided the largest scale of analysis for the remnant trees.

Second, I assessed the univariate pattern of post-fire trees by species and then by crown classes within selected species. At both sites, I analyzed the major conifers by species: *Pseudotsuga menziesii*, *Tsuga heterophylla* and *Thuja plicata*. At Eagle, I also analyzed two hardwoods, *Castanopsis chrysophylla* and *Cornus nuttallii*. In the crown class analysis, I described *Pseudotsuga menziesii* and *Tsuga heterophylla* at both sites as well as *Thuja plicata* at Wolf.

Describing the third element of an inter-type pattern -- that is, the univariate pattern of the two point sets combined -- can provide additional information and may be necessary to adequately model the underlying spatial processes (Upton and Fingleton 1985). Nevertheless, the combined pattern is less informative than the separate univariate patterns and the bivariate interaction. In this study, I analyzed the univariate pattern of remnant trees combined with each post-fire species and species-crown class. With one exception, I do not report these results, as they did not generally add any information to the analysis. However, I do report the univariate patterns of the remnant trees combined with each of the post-fire *Pseudotsuga* crown classes at Eagle Rock, since these patterns were particularly revealing.

Finally, I used both Ripley's  $K_{12}(t)$  and the Hamill-Wright nearest neighbor analysis to describe the bivariate interaction between all remnant trees and each post-fire species and species-crown class. In the east Wolf plot, over a third of the remnant trees were *Thuja plicata* (the rest being *Pseudotsuga*). Therefore, in this plot, I also described the bivariate interaction between each post-fire species and each remnant tree species.

In addition to the post-fire trees to remnant tree interaction, I used Ripley's  $K_{12}(t)$  to describe the bivariate interaction between species within the post-fire canopy. I did not use the nearest neighbor analysis, because it is an asymmetric statistic and is more appropriate when a relationship is inherently asymmetric -- e.g. juveniles "to" adults, or post-fire species "to" remnant trees.

Values of L(t) and  $L_{12}(t)$  were calculated over a range of distances t from 0 to 30 m at .5 m intervals. However, for the univariate analysis of remnant trees in the extended plots, L(t) was calculated over a range of distances t from 0 to 50 m.

In reporting bivariate results, unqualified statements regarding pattern are made if both methods, Ripley's K(t) (RK) and the Hamill-Wright nearest neighbor analysis (NNA), were in general agreement. Where a discrepancy in the overall pattern exists, it is noted. When the scale of a pattern is noted, the statistical source (RK or NNA) is cited. "Small" distances are generally <10 m, "intermediate" distances 10 - 20 m and "large" distances > 20 m.

### Species patterns within remnant tree crowns: Eagle Rock

At Eagle Rock, field observations suggested that species patterns at short distances from remnant trees were directional. That is, species appeared to be positively or negatively associated with the north or south sides of remnants. In order to test whether such associations were present, I defined two spatial areas: the north crown area and the south crown area. Mapped canopy crown projections were divided into those portions lying to the north and to the south of the remnant trunk center. These crown projections were actual, asymmetric projections (typically larger toward the south, downslope) rather than circular projections using the average crown radius for each tree. North and south crown areas were constructed as polygons in a GIS coverage using ARC/INFO (E.S.R.I. 1995). For selected post-fire species, I tested the null hypotheses that tree locations were 1) independent of north remnant crown areas and 2) independent of south remnant crown areas.

I made counts of trees within north crown areas and south crown areas for the following post-fire species and species-crown classes: *Castanopsis chrysophylla*, canopy *Pseudotsuga menziesii* (intermediate, codominant and dominant crown classes), suppressed *Pseudotsuga menziesii*, canopy *Tsuga heterophylla* and suppressed *Tsuga heterophylla*. I tested the null hypotheses of independence with Monte Carlo simulations in a manner similar to that described for Ripley's bivariate K(t) (Moeur 1993). For each simulation, north and south crown polygons were maintained in fixed locations, while post-fire trees were shifted together a random distance and direction across a toroidal region. After randomly shifting tree locations, I made counts within the north and south crown polygon, such that the area in which post-fire trees could become established was not overestimated. I used 40 Monte Carlo iterations and constructed a two-tailed 95% confidence envelope by discarding the one largest and the one

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smallest value. A variation on this Monte Carlo procedure is used by Leemans (1991) to test whether tree sapling locations are independent of canopy gaps.

For each of these species classes, I also constructed frequency histograms across an axis representing the distance from remnant tree in north and south directions. These histograms included all trees which fell within the average crown radius of each remnant tree.

### Results

### Univariate analysis: remnant trees

Remnants in the extended plot (150 \* 250 m) at Eagle were clustered at 8 - 37 m with strongest clumping at about 25 m (Figure 3.1a). A similar pattern occurred in the standard plot (100 \* 200 m) with significant clumps of intermediate (12 - 13 m) and large size (29 m) (Figure 3.1b).

Remnants in the extended plot (150 \* 275 m) at Wolf displayed increasing clumping from 8 - >50 m (Figure 3.2b). In the west plot (100 \* 75 m), remnants were significantly clumped at 9.5 - 11 m with uniform spacing (28 - >30 m) between clumps (Figure 3.2b). In the east plot, remnants were uniformly spaced at 6 - 11 m (Figure 3.2c).

### Univariate analysis: mature post-fire species and crown classes

#### Eagle Rock

All mature post-fire species, except *Cornus*, were clustered over most or all of the 30 m range examined (Figure 3.3). *Cornus* alone were spatially random. The *Tsuga* pattern was distinguished by a strong peak in clustering at 1.5 m followed by less intense and then increasing clustering over the rest of the range.



Figure 3.1. Within-group patterns of remnant trees at Eagle Rock a) extended plot (150 \* 250 m) and b) standard plot (100 \* 200 m). Univariate Ripley's K(t): observed values of the transformation, L(t), (---) are tested against the null hypothesis of spatial randomness represented by the 90% confidence envelope (----) from random simulations.
Wolf: remnant tree pattern



Figure 3.2. Within-group patterns of remnant trees at Wolf Rock a) extended plot (150 \* 275 m), b) west plot (100 \* 75 m) and c) east plot (100 \* 75 m). The east and west plots are subplots within the larger plot which were used for the spatial analysis of post-fire tree patterns. Univariate Ripley's K(t): observed values of the transformation, L(t), (---) are tested against the null hypothesis of spatial randomness represented by the 90% simulation envelope (----).



Figure 3.3. Summary of within-group patterns for mature post-fire trees at Eagle Rock by a) species and (b, c) crown class based upon values of Ripley's K(t). Patterns were tested against a 90% simulation envelope.



Figure 3.4. Within-group patterns of mature post-fire *Pseudotsuga* crown classes at Eagle Rock. Univariate Ripley's K(t): observed values of the transformation, L(t), (—) are tested against the null hypothesis of spatial randomness represented by the 90% simulation envelope (…).

No crown class within *Pseudotsuga* or *Tsuga* was uniformly distributed at any scale and all crown classes were significantly clumped at some scale (Figure 3.3, 3.4). Because of the wide variation in crown class population sizes and the resulting variation in the confidence interval size, it is impossible to make direct comparisons between patterns. Nevertheless, subjective comparisons suggest that the strength and spatial range of clustering increases from the larger crown classes to smaller crown classes for both *Pseudotsuga* and *Tsuga* Also, suppressed *Tsuga* is distinguished by a peak in clustering at 1.5 m, followed by a slight reduction and then gradually increasing clustering.

### Wolf Rock

Mature *Pseudotsuga menziesii*, *Tsuga heterophylla* and *Thuja plicata* were all clustered over most or all of the range examined in both west and east plots (Figure 3.5).

In both plots, all *Pseudotsuga* crown classes were clustered through most or all scales. In contrast to Eagle, no consistent trends across crown classes could be discerned.

All *Tsuga* crown classes were clustered in both plots except dominants in the west plot, which were randomly distributed. In the east plot, codominant clusters were regularly spaced at larger distances.

*Thuja* displayed similar patterns in both plots. Suppressed trees were intensely clustered over almost the entire range examined. Intermediates and codominants were clustered over a narrower range, and dominants were spatially random.

# Univariate analysis: combined pattern of remnant trees and mature Pseudotsuga at Eagle

When combined with remnant trees into single point sets, the crown class patterns of mature post-fire *Pseudotsuga menziesii* at Eagle changed dramatically (compare Figure 3.6 with Figure 3.4). The combined post-fire *Pseudotsuga* + remnant tree point

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continued



Figure 3.5. Summary of within-group patterns for mature post-fire trees at Wolf Rock by a) species and (b, c, d) crown class based upon values of Ripley's K(t). Patterns were tested against a 90% simulation envelope





Figure 3.6. Within-group patterns for post-fire *Pseudotsuga* crown classes combined with remnant trees into single point sets at Eagle Rock. Univariate Ripley's K(t): observed values of the transformation, L(t), (---) are tested against the null hypothesis of spatial randomness represented by the 90% simulation envelope (----).

sets showed a clear trend from clustering among suppressed trees + remnants to uniformity among dominants + remnants. Suppressed + remnant (strong clustering) and intermediates + remnant (moderate clustering) patterns were similar to those of the *Pseudotsuga* crown classes without remnants. However, codominants + remnants were random, and dominants + remnants were uniform.

# Bivariate analysis: mature post-fire species and crown classes relative to all remnant trees

### Eagle Rock

Mature *Pseudotsuga menziesii*, *Tsuga heterophylla* and *Thuja plicata* were all dispersed away from old-growth remnant trees (Figures 3.7-3.9; also see Figures 3.14, 3.15 for results summary). Surprisingly, the distance of dispersion was smaller for shade-intolerant *Pseudotsuga* (< 5.5 m, RK) than for the shade-tolerants, *Tsuga* (< 8.5 m, RK) and *Thuja* (< 10 m, RK). *Cornus nuttallii* were spatially independent of nearest remnants (NNA), but *Cornus* were weakly aggregated at intermediate distances around all remnants (RK) (Figure 3.10). *Castanopsis chrysophylla* were aggregated around remnant trees at small and intermediate distances (Figure 3.11).

The distances over which *Pseudotsuga* were dispersed away from remnant trees increased dramatically with increasing crown class from intermediates to dominants (Figures 3.12, 3.15). Intermediates were dispersed up to 9 m, codominants to 16.5 m, and dominants at several distances up to 29.5 m (RK). Suppressed *Pseudotsuga* were aggregated around remnants at intermediate distances (9 - 15 m).

While suppressed *Tsuga heterophylla* were dispersed away from remnant trees, intermediate, codominant and dominant crown classes were generally independent, except for intermediate *Tsuga* which were aggregated around remnants at very small distances (1 - 2 m, RK) (Figures 3.13, 3.15). Codominants also displayed a peak (albeit non-significant) in aggregation at 1.5 m.

Eagle: Pseudotsuga to remnant trees



Figure 3.7. Spatial interaction between mature post-fire *Pseudotsuga* and remnant oldgrowth trees at Eagle Rock. a) Map of post-fire *Pseudotsuga* ( $\circ$ ) and remnant trees ( $\bullet$ ) with tick marks at 25 m intervals. b) Bivariate nearest neighbor analysis: vertical lines mark the range over which the observed cumulative distribution of F(t) (-) differs significantly (p < .05) from the null distribution (....). c) Bivariate Ripley's K(t): observed values of the transformation, L(t), (-) are tested against the null hypothesis of spatial independence shown by the 90% simulation envelope (....).



Figure 3.8. Spatial interaction between mature post-fire *Tsuga* and remnant old-growth trees at Eagle Rock. a) Map of post-fire *Tsuga* ( $\circ$ ) and remnant trees ( $\bullet$ ) with tick marks at 25 m intervals. b) Bivariate nearest neighbor analysis: vertical lines mark the range over which the observed cumulative distribution of F(t) (-) differs significantly (p < .05) from the null distribution (....). c) Bivariate Ripley's K(t): observed values of the transformation, L(t), (-) are tested against the null hypothesis of spatial independence shown by the 90% simulation envelope (....).



Figure 3.9. Spatial interaction between mature post-fire *Thuja* and remnant old-growth trees at Eagle Rock. a) Map of post-fire *Thuja* ( $\circ$ ) and remnant trees ( $\bullet$ ) with tick marks at 25 m intervals. b) Bivariate nearest neighbor analysis: vertical lines mark the range over which the observed cumulative distribution of F(t) (--) differs significantly (p < .05) from the null distribution (----). c) Bivariate Ripley's K(t): observed values of the transformation, L(t), (--) are tested against the null hypothesis of spatial independence represented by the 90% simulation envelope (----).





Figure 3.10. Spatial interaction between mature post-fire *Cornus* and remnant old-growth trees at Eagle Rock. a) Map of post-fire *Cornus* ( $\circ$ ) and remnant trees ( $\bullet$ ) with tick marks at 25 m intervals. b) Bivariate nearest neighbor analysis: vertical lines mark the range over which the observed cumulative distribution of F(t) (--) differs significantly (p < .05) from the null distribution (---). c) Bivariate Ripley's K(t): observed values of the transformation, L(t), (--) are tested against the null hypothesis of spatial independence represented by the 90% simulation envelope (---).



Figure 3.11. Spatial interaction between mature post-fire *Castanopsis* and remnant oldgrowth trees at Eagle Rock. a) Map of post-fire *Castanopsis* ( $\circ$ ) and remnant trees ( $\bullet$ ) with tick marks at 25 m intervals. b) Bivariate nearest neighbor analysis: vertical lines mark the range over which the observed cumulative distribution of F(t) (-) differs significantly (p < .05) from the null distribution (....). c) Bivariate Ripley's K(t): observed values of the transformation, L(t), (-) are tested against the null hypothesis of spatial independence represented by the 90% simulation envelope (....).



# Eagle: Pseudotsuga to remnant trees by crown class

Figure 3.12. Spatial interactions between mature post-fire *Pseudotsuga* crown classes and remnant old-growth trees at Eagle Rock. Bivariate Ripley's K(t): observed values of the transformation, L(t), (—) are tested against the null hypothesis of spatial independence represented by the 90% simulation envelope (---).



Eagle: Tsuga to remnant trees by crown class

Figure 3.13. Spatial interactions between mature post-fire *Tsuga* crown classes and remnant old-growth trees at Eagle Rock. Bivariate Ripley's K(t): observed values of the transformation, L(t), (—) are tested against the null hypothesis of spatial independence represented by the 90% simulation envelope (----).



Figure 3.14. Summary of spatial interactions between remnant old-growth trees and mature post-fire trees at Eagle Rock by a) species and (b, c) crown class based upon values of Ripley's K(t). Patterns were tested against a 90% simulation envelope.



Figure 3.15. Summary of spatial interactions between remnant old-growth trees and mature post-fire trees at Eagle Rock by a) species and (b, c) crown class based upon refined nearest neighbor analysis.

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### Wolf Rock

Mature *Pseudotsuga menziesii* were strongly dispersed away from remnant trees, with dispersion extending to larger distances in the west plot (< 14 m, RK) than in the east plot (< 7.5 m, RK) (Figure 3.16). In both plots, NNA indicated dispersion extending to even larger distances (< 17 m and <13 m, respectively). *Tsuga heterophylla* in the west plot were aggregated around remnant trees (Figures 3.17). RK indicated weak aggregation over a broad range of distances, while NNA detected weak aggregation over only a short range. In the east plot, *Tsuga* locations were generally independent of remnant trees. *Thuja plicata* were dispersed away from remnant trees in both plots, with dispersion extending to larger distances in the east plot (< 8.5, 12 - 14 m, RK) than in the west plot (< 5 m, RK) (Figure 3.18). Dispersion of *Thuja* was also more intense in the east plot than in the west plot than in the west plot (compare NNA *p*-values in Figure 3.20).

*Pseudotsuga* intermediates, codominants and dominants were all dispersed away from remnants in both plots, while suppressed trees were generally independent of remnant trees (Figures 3.19, 3.20). In general, the intensity and scale of dispersion increased from the smaller intermediate class to the larger dominant class in both plots, but these trends were less distinct and consistent than those for *Pseudotsuga* at Eagle.

For *Tsuga* in the west plot, codominants were strongly aggregated around remnant trees over a broad range of distances (Figures 3.19, 3.20). Intermediates were also aggregated, while suppressed and dominant trees were weakly aggregated (RK) or independent (NNA). RK suggested a decrease in the distance of aggregation (tighter aggregation) for the larger codominant class relative to the smaller intermediate and suppressed classes. In the east plot, all *Tsuga* crown classes were generally independent of remnants (although RK detected weak dispersion in some cases).

*Thuja* patterns in the west plot were not consistent across crown classes or between methods (Figures 3.19, 3.20). Crown classes were either independent or weakly dispersed, with the exception of suppressed *Thuja* for which RK detected aggregation at



Figure 3.16. Spatial interaction between mature post-fire *Pseudotsuga* and remnant trees at Wolf Rock, west (a, c, e) and east (b, d, f). (a,b) Map of post-fire *Pseudotsuga* ( $\circ$ ) and remnant trees ( $\bullet$ ) with tick marks at 25 m intervals. *Thuja* remnants are starred, but analyses here did not distinguish remnant species. (c,d) Nearest neighbor analysis: vertical lines mark range over which observed distribution of F(t) (-) differs (p < .05) from null distribution (...). (e,f) Ripley's K(t): observed values of L(t) (-) are tested against null hypothesis of spatial independence shown by the 90% simulation envelope (...).



Wolf: *Tsuga* to remnant trees





Figure 3.18. Spatial interaction between post-fire *Thuja* and remnant old-growth trees at Wolf Rock, west (a, c, e) and east (b, d, f). (a,b) Map of post-fire *Thuja* ( $\circ$ ) and remnant trees ( $\bullet$ ) with tick marks at 25 m intervals. *Thuja* remnants are starred, but analyses here did not distinguish remnant species. (c,d) Nearest neighbor analysis: vertical lines mark range over which observed distribution of F(t) (-) differs (p < .05) from null distribution (...). (e,f) Ripley's K(t): observed values of L(t) (-) are tested against null hypothesis of spatial independence shown by the 90% simulation envelope (...).

Wolf Rock		Dis	stance (m)					
	a.	Species 0	5	10	15	20	25	30
Ripley's K(t) Bivariate pattern relative to remnant trees Independent Aggregated Dispersed	Pseud	otsuga W E Tsuga W E Thuja W E						
b. Pseud	otsuga by cro West plot co int s	dominant dominant etermediate	5	10	15	20	25	<b>30</b>
	East plot c in s	dominant odominant termediate suppressed						

continued

Wolf Rock				Distance (n	n)					
	c.	<i>Tsuga</i> by	<u>crown class</u> (	<b>)</b>	5	10	15	20	25	30
		West plot	dominant		· · · · · · · · · · · · · · · · · · ·					
			codominant		· ····.					
			intermediate							
Ripley's K(t)			suppressed							
Bivariate pattern re	elative									
to remnant trees		East nlot	dominant	· · · · · · · · · · · · · · · · · · ·						
Independent		East Prov	codominant							
Aggregated			intermediate							
Dispersed			suppressed							
-	d.	<i>Thuja</i> by	crown class	0 [	5	10	15	20	25	30
		West plot	dominant							
			codominant							
			intermediate							
			suppressed							4
		East plot	dominant							
		-	codominant				·····			
			intermediate				· · · · · · · · · · · · · · · · · · ·			
			suppressed					121		

Figure 3.19. Summary of spatial interactions between remnant old-growth trees and mature post-fire trees at Wolf Rock by a) species and (b, c, d) crown class based upon values of Ripley's K(t). Patterns were tested against a 90% simulation envelope



continued



Figure 3.20. Summary of spatial interactions between remnant old-growth trees and mature post-fire trees at Wolf Rock by a) species and (b, c, d) crown class based upon refined nearest neighbor analysis

intermediate and large distances. In the east plot, suppressed, intermediate and codominant *Thuja* were consistently dispersed away from remnants at small scales. Dominants were generally independent. In both plots, trends across classes were not evident.

# Bivariate analysis: mature post-fire species relative to different remnant species (east Wolf)

The spatial interaction between mature post-fire species and remnant trees differed with the species of remnant tree in the east Wolf plot (Figure 3.21, see also maps in Figures 3.16 - 3.18). While mature *Pseudotsuga* were spatially independent of remnant *Thuja*, they were dispersed away from remnant trees of their own species. Mature *Thuja* were dispersed away from both remnant species, but dispersion extended to greater distances away from remnant *Thuja* (< 18.5 m, NNA; < 13.5 m, RK) than from remnant *Pseudotsuga* (< 7.5 m, NNA; < 7.5, RK). For post-fire *Tsuga*, RK detected no pattern relative to remnant *Pseudotsuga*, but dispersion was detected relative to remnant *Thuja*. NNA detected short-range aggregation of *Tsuga* around remnant *Pseudotsuga*, but no pattern relative to remnant *Thuja*. While the absolute pattern of *Tsuga* relative to remnant species differed between methods, both methods indicated that the interaction between post-fire *Tsuga* and remnant *Pseudotsuga* was more positive (or less negative) than that with remnant *Thuja*.

### Bivariate analysis: interactions among post-fire species

Spatial independence between post-fire species was rare (Table 3.4). Almost all interactions displayed dispersion or aggregation, but interactions were typically weak. The most distinct pattern was that of strong short-distance dispersion between *Pseudotsuga* and the hardwood, *Castanopsis*, at Eagle (Figure 3.22a). The other conifers, *Tsuga* and *Thuja*, were also dispersed small distances from *Castanopsis*, while *Cornus*, another hardwood, were weakly aggregated. The most consistent pattern across both stands was

# Wolf Rock: East plot

Bivariate pattern relative	to remnant t	rees of	differer	nt species		ndepende	ent	Aggreg	gated	Disp	ersed	
a. Ripley's K(t)												
Post-f	ire species:	Pseud	otsuga			Tsuga				Thuja		
Di	stance (m)											
Remnant tree species 0	5	10	15	20 0	5	10	15	20 0	5	10	15	20
Pseudotsuga												
Thuja												
b. Nearest neighbor analy	/sis											
<u>Post-f</u>	re species:	Pseud	otsuga			Tsuga				Thuja		
Di	stance (m)											_
Remnant tree species $0$	5	10	15	20 0	5	10	15	20 0	5	10	15	20
Pseudotsuga											· · / · ·	
Thuja												

Figure 3.21. Summary of spatial interactions between mature post-fire trees by species and remnant old-growth trees by species at east Wolf Rock based upon a) values of Ripley's K(t) and b) refined nearest neighbor analysis. Ripley's K(t) patterns were tested against a 90% simulation envelope. Nearest neighbor patterns significant at p < .05.



Interactions between post-fire species

Figure 3.22. Spatial interactions among species within mature post-fire class: a) *Pseudotsuga* and *Castanopsis* at Eagle Rock and b) *Pseudotsuga* and *Tsuga* at west Wolf Rock. Bivariate Ripley's K(t): observed values of the transformation, L(t), (--) are tested against the null hypothesis of spatial independence shown by the 90% simulation envelope (---).

the weak, but typically broad-range, dispersion between *Pseudotsuga* and *Tsuga* (Figure 3.22b).

### Species patterns within remnant crowns (Eagle Rock)

Canopy *Pseudotsuga* were negatively associated with projected crown areas on both the north and south sides of remnant trees (Table 3.5). Suppressed *Pseudotsuga*, however, were independent of both north and south crown areas. Both canopy and suppressed *Tsuga* were negatively associated with projected crown area on the south side of remnants. Both were independently distributed relative to north crown areas. Table 3.4. Summary of spatial interactions among species within the mature post-fire class at a) Eagle Rock and b) Wolf Rock, east and west plots, derived from bivariate Ripley's K(t). + and - indicate aggregation or dispersion (90% simulation envelope) between two post-fire species at distances of t up to 30 m. A 0 indicates spatial independence.

#### a. Eagle Rock

species/	Tsuga	Thuja	Cornus	Castanopsis
Pseudotsuga	-	0	+	-
Tsuga		÷	÷	-
Thuja			0	-
Cornus				+

b. <u>Wolf Rock</u>	West plot		East plot	
post-fire species/ post-fire species	Tsuga	Thuja	Tsuga	Thuja
Pseudotsuga	-	+	-	+
Tsuga		-		+

Table 3.5. Relationship between post-fire species and the remnant tree projected crown areas at Eagle Rock. North and south crown areas are those portions of the crown projection to the north and south of the trunk center. The expected range is a two-tailed 95% confidence interval generated by random toroidal shifts of post-fire tree locations. "Canopy" individuals are those individuals in intermediate, codominant and dominant crown classes. A "+" pattern indicates significantly more individuals than expected, "-"

		NORT	Ή			
Species-crown class	Pattern	Observed	Expected	Pattern	Observed	Expected
Pseudotsuga - canopy Pseudotsuga - suppressed Tsuga - canopy	- 0	54 71 5	105 - 143 50 - 93 10 - 26 22 - 53	- 0 0	27 27 7	43 - 68 21 - 46 3 - 14 9 - 29
Castanopsis	+	43	7 - 28	ŏ	14	2 - 14



Figure 3.23. Histograms of mature post-fire a) *Tsuga*, b) *Castanopsis* and c) *Pseudotsuga* across distances north or south of remnant bole centers. Only individuals found within the average crown radius of each remnant tree are included. Canopy trees include intermediate, codominant and dominant crown classes. Mean, minimum and maxium values for average remnant crown radii are shown. Also shown are mean and maximum values for the actual asymmetric (rather than averaged) north and south remnant crown radii.

*Castanopsis* was the only species which was positively associated with south crown areas. *Castanopsis* were independent of north crown areas.

Frequency histograms of distance and direction from crown bole suggest that Tsuga individuals tend to be found near to the remnant bole on the north side (< 1.5 m), but are mostly absent within 3 m of the south side of boles (Figure 3.23). *Castanopsis* appears to display a pattern opposite that of *Tsuga* on both sides of remnant trees.

### Discussion

### General trends and pervasiveness of pattern effects

The partial fires at Eagle and Wolf did not leave a blank slate for successional processes, but left instead legacies from the previous community, exemplified by the prominent remnant trees. Patterns of colonizing species were spatially dependent upon the remnant tree pattern. The variety of spatial interactions with remnant trees (from aggregation to dispersion) suggested that post-fire species may be differentially facilitated or inhibited by remnant trees or remnant-associated residual features. These interactions suggest that the direction of vegetation change may be influenced by the residual pattern and that alternative pathways may be possible with differences in fire severity and remnant density. This study's secondary questions revealed that the spatial interaction between post-fire species and remnant trees was complex. Interactions with remnant trees differed with remnant species and with orientation (north/ south) relative to remnant trees, and post-fire crown class patterns were also dependent on the remnant tree pattern. Both stands were characterized by pervasive patchiness, with significant within-group clustering and significant interactions between post-fire species.

The patterns of species which colonized after the partial fires were clearly dependent upon the pattern of surviving remnant trees. Of all the cases examined, only *Tsuga heterophylla* in the east Wolf plot were distributed independently of remnant tree locations. In most cases, species were dispersed away from remnant trees, suggesting a local inhibitory effect of remnant trees or remnant-associated features. However, the presence of several species appeared to be facilitated relative to remnant locations. At Eagle, both hardwoods, *Castanopsis chrysophylla* and *Cornus nuttallii*, were aggregated around remnant trees, and, at west Wolf, shade-tolerant *Tsuga* were aggregated around remnant trees. Spatial interactions between post-fire trees and remnant trees were typically significant at small distances (< 10 m), but sometimes extended to larger distances (up to 25.5 m, west Wolf *Tsuga*). Only one species, *Cornus*, displayed no small-scale interaction with remnant trees, but was patterned relative to remnant trees at larger distances (10.5 - 17 m, RK). Patterns for each species often differed between the two sites characterized by different environmental conditions. Most notably, *Tsuga heterophylla* were aggregated or independent relative to remnants at the cooler and wetter Wolf site, but, contrary to expectations, were dispersed from remnants at the south-facing Eagle site.

For each species of mature trees, crown (relative height) class patterns were typically dependent on the remnant tree pattern, but few trends across crown classes were evident. In the one exception, suppressed *Pseudotsuga* were independent of or aggregated around remnant trees, but non-suppressed crown classes were dispersed from remnant trees, and the distance of dispersion increased markedly with increasing crown class size. This trend is not simply an artifact of crown class definitions; that is, a tree is not defined as suppressed simply because it is adjacent to a much larger remnant tree, but is defined as suppressed or dominant relative to other surrounding mature trees. The trend across *Pseudotsuga* size classes suggests a persistent inhibitory effect by remnant trees upon *Pseudotsuga*'s growth and mortality relative to other species in the mature cohort.

For each post-fire species, the spatial interaction with remnant trees differed between remnant tree species. At east Wolf, post-fire *Pseudotsuga* were dispersed away from remnants of their same species, but were spatially independent of remnant *Thuja*. Post-fire *Thuja* were dispersed from both remnant species, but dispersion extended to much greater distances away from remnant *Thuja*. These patterns are suggestive of reciprocal replacement hypotheses. They also indicate the potential for post-fire species patterns to differ with the species composition of the survivors. At Wolf, the differences in post-fire species patterns between the east and west plot can largely be explained by the distinct differences in remnant species composition between the two plots.

The interaction between post-fire species and remnant trees can be directional. At south-facing Eagle Rock, *Tsuga* were negatively associated with the south portions of projected remnant crowns, but were independent of north portions of crown projections. Although *Castanopsis* were also independent of north remnant crown areas, they were positively associated with south crown areas. These strong differences suggest the potential for niche differentiation beneath remnant crowns. They also indicate that the interaction between a colonizing species and remnant trees -- facilitation, inhibition or neutral -- may differ depending on its orientation relative to the remnant tree.

The within-group patterns of remnant trees were predominantly clustered. At the largest scale examined (the extended remnant plots), clustering occurred over a broad range of distances at both stands. In the smaller plots (used for the analysis of post-fire species -- east Wolf, west Wolf and the standard Eagle plot), remnants were also clustered, except at east Wolf, where a high density of remnant trees was evenly spaced within this smaller analytical window. However, even at east Wolf, a small increase in the plot's size (i.e. 25 m on each side, examine map in Figure 3.15b) yielded a clustered remnant pattern (results not shown).

The within-group patterns of almost all mature species were clustered over a large range of distances. Randomly distributed *Cornus* was the one exception. Within each post-fire species, almost all crown classes were clustered and none were uniform. Clustered patterns are typical of forest communities, often being attributed to limited seed dispersal, microsite heterogeneity, environmental gradients and disturbance-opened patches (Bonnicksen and Stone 1981, Hatton 1989, Stewart and Rose 1990, Briggs and Gibson 1992. Burns 1993, Duncan 1993). Nevertheless, the overwhelming dominance of clustered patterns was striking. Since all of the examined conifer species are long-distance seed dispersers, limited dispersal was not likely the source of clustering at the scale examined here. Patchy microsites were no doubt critical for regeneration, but cannot account for the prevalent clustering beyond smaller distances. At Eagle, large-scale environmental heterogeneity was clearly a factor in the clustering of *Thuja* and *Tsuga*, which were associated with wetter areas (results not shown). But associations with large-scale environmental patches were not evident for other species at Eagle, and no large-scale features were perceivable at Wolf. If limited dispersal, microsite heterogeneity and large-scale environmental heterogeneity cannot fully account for the clustering at Eagle and Wolf, the source may be in the disturbance-caused residual pattern.

The predominant clustering can, in part, be attributed to the spatial dependence of each species' pattern upon the clustered remnant tree pattern. If a group of trees is aggregated around a clustered group of trees, its own pattern will also be clustered. Furthermore, if a group of trees is dispersed away from a clustered group, its own pattern will also be clustered, being concentrated in areas with low densities of the initial clustered group. As a result, the spatial interactions between post-fire species and clustered remnant trees imprint upon these stands a pervasive clustering among post-fire species and size classes.

Within the post-fire cohort, almost all species-to-species interactions displayed significant dispersion or aggregation. Some of these interactions occurred at very small distances (< 5 m), most notably the repulsion between the resprouting hardwood, *Castanopsis* and each conifer species. Other interactions occurred at larger distances or across a broad range of scales. Broad scale interactions may reflect species differentiation across underlying environmental gradients and/or differences in species patterns relative to remnant trees. At Wolf, where no underlying environmental gradients are apparent, the broad-scale repulsion between post-fire *Pseudotsuga* and *Tsuga* can be attributed to

*Pseudotsuga*'s dispersion from remnant trees and *Tsuga*'s aggregation or independence relative to remnants. Thus, the spatial interaction between post-fire species and remnant trees may result in repulsion or aggregation between the post-fire species, themselves.

### Possible pattern-generating mechanisms

The interaction between the mature species and old-growth remnants can be better understood by giving attention to each of the post-fire species' patterns. Although processes cannot be deduced from patterns, each species' autecological and life history traits can suggest and limit the potential processes giving rise to the observed patterns.

### Pseudotsuga menziesii

At both sites, *Pseudotsuga* were dispersed away from remnant trees, and larger *Pseudotsuga* were found at much greater distances away from remnants than were smaller *Pseudotsuga*, suggesting a remnant effect upon *Pseudotsuga* growth (Figures 3.12, 3.15, 3.19, 3.20). It is unlikely that establishment was inhibited by remnant trees, since *Pseudotsuga* regeneration rates are typically highest beneath partial shade (Isaac 1943, Franklin 1963, Williamson 1973). However, *Pseudotsuga* growth is limited beneath partial shade (Isaac 1943). Being less shade-tolerant than either *Tsuga* or *Thuja* (Carter and Klinka 1992), *Pseudotsuga* is likely surpassed where shaded by remnants. The elevated remnant crowns, themselves, probably do not cast sufficient shade to induce suppression mortality, but mortality may ensue after the dense crowns of *Tsuga* overtop *Pseudotsuga*. The much smaller distance of dispersion at Eagle as compared to Wolf may reflect the shorter remnant tree shadows on the steep south-facing slope of Eagle or the lack of competing *Tsuga* around remnant trees at Eagle.

Within-group patterns of *Pseudotsuga* crown classes were all clustered. This consistent clustering was unexpected. Forest stands typically exhibit a trend from

clustering among small size classes toward uniformity among large size classes (Christensen 1977, Whipple 1980, Good and Whipple 1982, Franklin et al. 1985a, Stewart 1986a, Stewart and Rose 1990, Moeur 1993). The even spacing among large individuals has been attributed to density-dependent thinning and one-sided competition for light (Kenkel 1988). Therefore, it was surprising that neither codominant nor dominant *Pseudotsuga* were regularly spaced. The clustering of these larger crown classes is attributable to their interaction with remnant trees. When remnant trees and *Pseudotsuga* crown classes were combined into single point sets, the patterns of dominants+remnants (uniform) and codominants+remnants (random) differed dramatically from those of dominants or codominants alone (clustered) and remnants alone (clustered). As a result, the remnants+*Pseudotsuga* crown class series displayed the expected trend from clustering to uniformity with increasing size class. The uniformity of the dominants+remnants pattern implies that the even spacing between post-fire dominants develops in relation to remnant locations in addition to those of other dominants. In effect, remnant trees pre-empt the competitive space that would otherwise be occupied by *Pseudotsuga* dominants.

At Wolf, post-fire *Pseudotsuga* were dispersed with greater intensity and farther away from remnant trees in the west plot than in the east plot. This difference is explained by the relative absence of *Thuja* remnant trees in the west plot and their abundance in the east plot. While post-fire *Pseudotsuga* were dispersed from remnant *Pseudotsuga*, they were independent of remnant *Thuja* (Figure 3.21).

Why should post-fire *Pseudotsuga* be independent of remnant *Thuja*, but dispersed from remnants of their own species? *Thuja* remnants should cast less shade than *Pseudotsuga* remnants. *Thuja* crowns were shorter, narrower and often missing over fire-killed portions of the tree. Shade-intolerant *Pseudotsuga* may experience less growth reduction near *Thuja* remnants.

A complementary, but more speculative, explanation may lie in *Thuja*'s influence upon soils. Soil is less acidic beneath *Thuja* than beneath other conifers (Tarrant et al.
1951, Alban 1969, Turner and Franz 1985a, Turner et al. 1993), and, in the Oregon Coast Range, nitrification rates were higher beneath old-growth *Thuja* than beneath old-growth *Pseudotsuga* or *Tsuga* (Turner et al. 1993). Differences in soil quality beneath remnant *Thuja* could potentially alter the relationship between post-fire *Pseudotsuga* and *Tsuga*, its chief competitor. *Pseudotsuga* uptakes nitrogen more efficiently than *Tsuga* (Burgess 1991) and, in contrast to *Tsuga*, appears to preferentially uptake nitrogen as nitrate (Krajina et al. 1973). Indeed, Ripley's K(t) indicated that post-fire *Tsuga* were weakly dispersed from remnant *Thuja*, but were independent of remnant *Pseudotsuga*, a pattern opposite that of post-fire *Pseudotsuga*.

# Tsuga heterophylla

At Wolf, *Tsuga* were aggregated around remnants in the west plot and independent of remnants in the east plot, patterns consistent with *Tsuga*'s shade-tolerance (Figure 3.17). Age distributions indicated that *Tsuga* regenerated immediately after the fire along with less tolerant pioneers, and few, if any, *Tsuga* regenerated later beneath the mature canopy (Chapter 2). Relative to less tolerant species, *Tsuga*'s establishment and growth appears to have been facilitated or, at least, not inhibited by the remnant trees.

The difference between the east and west plot may result from differences in remnant density, the east plot containing twice as many remnants as the west. In the east plot, remnant density is so high that negligible area remains that is sufficiently distant from remnant trees for *Pseudotsuga* canopy status to become independent of remnant trees. (This estimation is based upon the distance of dispersion for nearest codominant and dominant *Pseudotsuga*). Within all of this area, *Tsuga* should be able to compete effectively with *Pseudotsuga*, leading to a distribution independent of remnants. In contrast, the lower remnant density of the west plot leaves 20-30 % of the area beyond the distance across which *Pseudotsuga* canopy status is negatively impacted by remnants. Within these areas of low remnant influence, *Pseudotsuga* may have overtopped *Tsuga* 

from the early stages of regeneration onward. Areas of lower *Tsuga* density at large distances from remnant trees resulted in an aggregated pattern around remnants. *Tsuga* crown class patterns in the west plot also suggest reduced competitive ability at large distances, with codominant *Tsuga* more "tightly" aggregated around remnant trees (more intensely and at smaller distances) than smaller classes (RK).

It is also possible that remnant shade facilitated the establishment of exposure-sensitive *Tsuga*, leading to lower establishment rates in areas of low remnant density in west Wolf.

In stark contrast to the patterns at Wolf, *Tsuga* were strongly dispersed from remnants at Eagle (Figure 3.8). This pattern raised two questions. Why was shade-tolerant *Tsuga* dispersed from remnants at Eagle? Why were post-fire *Tsuga* and post-fire *Pseudotsuga* repulsed from each other at Eagle, when both displayed the same interaction (dispersed) with remnant trees? On the drier, south-facing slope of Eagle, I hypothesized that post-fire species patterns reflected differences in drought and exposure tolerance. Remnant trees should affect these patterns by altering water availability and blocking or reflecting radiation. The patterns within projected remnant crown areas were consistent with these processes, helping explain both the overall *Tsuga* pattern and the repulsion between post-fire *Pseudotsuga* and *Tsuga*.

At Eagle, water availability is likely reduced around remnant trees via precipitation interception and evapotranspiration. *Pseudotsuga* trees reduce throughfall and produce negligible stemflow (Rothacher 1963, Hutchinson and Roberts 1981, Crampton 1982, Bouten et al. 1992) Transpiration from large remnant crowns should further reduce soil water. On the north side of remnants, these negative impacts should be offset by shading from the large remnant boles and, to a lesser extent, crown shade. On the south side of remnants, negative impacts should be exacerbated by a lack of shade and, possibly, radiation reflected from the remnant bole. The projected crown area models the area of intercepted precipitation. Root distributions for mature *Pseudotsuga* are typically proportional to, but greater than, crown areas. However, root distributions are problematic to model, typically being asymmetric, but not corresponding to slope direction or crown asymmetry (Steinbrenner and Gessel 1956, Berndt and Gibbons 1958, McMinn 1963, Eis 1974, Kuiper and Coutts 1992).

The negative association of both suppressed and canopy Tsuga with south remnant crown areas is consistent with Tsuga's intolerance of drought and exposure (Table 3.5). Water availability is presumably less beneath remnant crowns and the areas south of remnant boles remain unshaded. Of those Tsuga that did establish within south crown areas, about 50% were located in the moist seep or riparian slope, even though less than 20% of the remnant trees occurred in these areas. Tsuga commonly experiences high mortality in the hot, dry summers of the Northwest -- up to 100% in south-facing clear cuts. Tsuga seedlings are particularly vulnerable to high surface temperatures, and Tsuga's slow root growth cannot keep pace with rapidly drying soil at exposed sites (Larsen 1940, Haig et al. 1941, Isaac 1943). The striking lack of Tsuga within 2.5 m of remnant south faces suggests that reflected radiation and high surface temperatures inhibited Tsuga establishment (Figure 3.23). In contrast, on the north sides of remnants, bole shade may create safe sites for Tsuga by ameliorating the dry conditions. Although Tsuga were independent of north remnant crown areas, the peak in Tsuga abundance to the immediate north of remnant trees (< 2 m) suggests a short-range facilitory effect, with microclimate amelioration decreasing sharply thereafter (Figure 3.23). This peak is reflected in the aggregation of intermediate Tsuga at 1-2 m detected by Ripley's K(t) and the striking, but non-significant, peak for codominant Tsuga at this same scale.

In contrast with *Tsuga*, suppressed *Pseudotsuga* were independent of projected crown areas on both sides of remnant trees, while canopy *Pseudotsuga* were fewer than expected on both sides. These results are consistent with successful establishment, but unsuccessful growth in proximity to remnants. Possessing physiological mechanisms which permit tolerance of water stress and having faster root growth, *Pseudotsuga* is better adapted than *Tsuga* for survival in droughty, exposed conditions (Livingston and Black

1987, Livingston and Black 1988). Nevertheless, *Pseudotsuga* growth is reduced by remnant shade, leading to the lack of canopy *Pseudotsuga*.

At Eagle, the within-group *Tsuga* pattern peaked with strong clustering at 1.5 m, plateaued and then climbed with increasing clustering at large scales. At Wolf, *Tsuga* displayed similar peaks in clustering at distances of 1 - 2 m. This strong small-scale clustering is consistent with Gray's (1995) conclusion that, relative to its associates, *Tsuga* establishment is particularly sensitive to microsite heterogeneity. At Eagle, linear clusters were clearly evident and may mirror moisture-rich decayed wood or log-shaded patches.

#### Thuja plicata

*Thuja plicata* at west Wolf displayed weak, brief dispersion away from remnant trees, while those at east Wolf were strongly dispersed from remnants (Figure 3.18). It is unlikely that the dispersion of *Thuja* resulted from differential growth and mortality near remnants. *Thuja* is the most shade-tolerant and least gap-responsive of the major species at Wolf (Carter and Klinka 1992, Daniels 1994). In the east plot, the consistent dispersion across crown classes (from suppressed to codominant) and the absence of any trend with increasing size suggests a negative effect upon initial establishment as opposed to an effect upon growth.

*Thuja* 's dispersion from remnant trees may be explained by initial fire effects upon seedbed distribution and *Thuja*'s seedbed requirements. *Thuja* is an enigmatic species. Although it is very shade-tolerant, regeneration beneath canopies is extremely poor (Schmidt 1955, Gregory 1957, Keenan 1993). While a preference for mineral soil and/or decayed wood is shared by several species, *Thuja*'s preference for mineral soil appears to be particularly strong and may limit regeneration (Haig et al. 1941, Parker 1986, Minore 1990, Daniels 1994). At Wolf, the remnant pattern likely reflects the initial post-fire pattern of seedbeds. Prior to the 1892 fire, litter accumulation was likely greater around remnants. The previous 1829 fire first established a younger cohort around the remnants, and older, large-crowned *Pseudotsuga* produce substantially more litter than younger trees (Tarrant et al. 1951). Furthermore, the 1892 fire intensity appears to have been less in areas of high remnant density (Chapter 2). After this fire, *Thuja* regeneration may have been limited by litter accumulation near remnants that was not removed by lower fire intensities. Away from remnant trees, mineral soil seedbeds allowed higher regeneration rates.

Differences in *Thuja* pattern between remnant species and between west and east plots were consistent with this hypothesis. Post-fire *Thuja* were dispersed farther away from remnants of their own species than from remnant *Pseudotsuga* (Figure 3.21). It is tempting to suggest that young *Thuja* were dispersed from remnant *Thuja* by allelopathy or interference for the same resources, but the literature does not suggest such an explanation. Rather, the critical difference between remnant species may have been a difference in the post-fire pattern of litter substrate. *Thuja* produces litterfall at a much greater rate than *Pseudotsuga*, such that remnant *Thuja* likely had greater pre-fire litter accumulation (Tarrant et al. 1951). *Thuja* is also less fire-resistant than *Pseudotsuga*, its shallow root system being vulnerable to surface fire (Minore 1983, Agee 1991). Where remnant *Thuja* survived, fire intensity was presumably less. The interaction of these factors likely left larger islands of intact forest floor around remnant *Thuja*, resulting in greater distances of dispersion for post-fire *Thuja*.

The 1892 fire burned most completely in the west plot, leaving a few isolated remnant trees and only one remnant *Thuja*. Greater litter removal around remnants may account for the weaker dispersion in this plot. In contrast, the east plot contained both a higher density of remnant trees and a large proportion of remnant *Thuja*. Lower fire intensity in the east plot likely left remnant litter accumulations intact, including the larger accumulations around remnant *Thuja*, resulting in the stronger dispersion of post-fire *Thuja* from remnant trees.

At Eagle, post-fire *Thuja* were strongly dispersed away from remnant trees (Figure 3.9). The dispersion from remnants may be coincidental. After accounting for topographic

associations, *Thuja* was positively associated with young patches which regenerated after the 1870 fire, but survived the 1892 fire (Chapter 2). Contrary to initial expectations, very few remnant trees were located in the areas where young trees survived the 1892 fire, and the highest density of remnants were located within the areas which burned completely in 1892. As a result of its association with the 1870 fire patches, *Thuja* displayed a pattern of dispersion from remnants. (It should be noted that *Pseudotsuga* and *Tsuga* were abundant in both fire patches, such that their dispersion from remnant trees was not confounded by an association with a particular fire patch). These results suggest that *Thuja* regenerated successfully after the 1870 fire, but poorly after the 1892 fire. If the 1892 fire was less intense than the earlier 1870 and 1848 fires, the litter layer may have been incompletely consumed, leaving fewer mineral soil patches. Alternatively, stochastic factors, such as a seed crop failure or a population increase of *Thuja*-preferring herbivores (deer and elk), may have limited regeneration (McCune and Allen 1985).

## Cornus nuttallii

*Cornus*, a deciduous broadleaf abundant only at Eagle, was unique in both its within-group pattern and its interaction with remnant trees. At Eagle, all other species showed strong, small-scale dispersion or aggregation relative to remnants. In contrast, *Cornus* were weakly aggregated around remnants at intermediate scales (Figure 3.10). *Cornus* was also the only species with a random within-group pattern (Figure 3.3). These patterns suggest that, at small scales, *Cornus* distribution was influenced by randomly distributed processes within the post-fire cohort. However, *Cornus*' aggregation around remnants at intermediate scales suggests that its presence may be enhanced by indirect remnant effects upon overall stand structure.

At Eagle, *Cornus*' presence may be dependent on the relatively open canopy and incomplete regeneration of this south-facing slope. *Cornus*, capable of resprouting after disturbance, is usually associated with early stages of stand development. But *Cornus* can

persist at lower densities into later stages, often being associated with canopy gaps (Halpern and Spies 1995). *Cornus*' random within-group pattern may reflect a random distribution of canopy openings and regeneration gaps. As stand development continues, canopy filling may preclude *Cornus*. At present, many *Cornus* show poor vigor. *Cornus* appears to be less abundant in areas where the post-fire canopy has developed furthest. While *Cornus* may decline in importance, it is unlikely to disappear. Areas of poor regeneration and growth -- the dry ridge, south remnant crown areas and high density remnant patches -- may provide refuges. Snapped and uprooted remnant trees have created rare, but very large, openings which may also facilitate *Cornus* maintenance. Eventually, the post-fire canopy's development will give rise to large gaps. Until that time, remnant effects upon stand structure -- patches of slow development and large treefall gaps -- may facilitate *Cornus* persistence.

#### Castanopsis chrysophylla

The most striking pattern in either stand was that of *Castanopsis*, an evergreen broadleaf abundant at Eagle (Figure 3.11). *Castanopsis* were strongly aggregated around remnant trees at both small and intermediate scales. I explored three explanations of *Castanopsis*' aggregation. 1) *Castanopsis* stems predated the most recent fire (1892), escaping where intensities were low. 2) *Castanopsis* were stem-killed by the fire but resprouted near remnant trees where intensities may have been low. *Castanopsis* is a prolific resprouter after moderate ground fires, but complete kill can occur where burns are most intense (Halpern 1989, Kauffman and Martin 1990, McKee 1990). 3) On this southfacing slope, rain interception and water uptake by remnant trees have created droughty areas where *Castanopsis* is competitively superior.

The ages of cored *Castanopsis* indicated that no stems predated the 1892 fire (Chapter 2). Consistent with immediate resprouting, there was little or no lag time between the 1892 fire and *Castanopsis* regeneration. However, the hypothesis of differential mortality and resprouting with variable fire intensity was not corroborated. Reconstruction of the 1892 fire indicated that it was most severe (relative to young, newly established trees) in the areas of highest remnant density (Chapter 2). It is possible that remnant locations reflect an earlier fire pattern. The earlier fire may have caused differential resprouting and the most recent fire simply maintained this pattern. Nevertheless, given that no fire in this stand could have been of great intensity, a strong link between *Castanopsis* pattern and differential fire mortality is questionable. After a post-harvest broadcast burn, Halpern (1989) observed resprouting *Castanopsis* distribution to be more closely linked to its initial distribution than to disturbance intensity. If this was the case at Eagle, each fire simply reinforced the existing pattern. An alternative, or complementary, explanation of pattern development, both before and after the fire, might then be *Castanopsis*' drought tolerance and low water availability near remnant trees.

*Castanopsis* was the only species positively associated with south portions of projected remnant crown areas, patches presumably drier than the stand as a whole (Table 3.5). Sclerophyllous *Castanopsis* has thickened, relatively narrow leaves lined with hairs underneath. Typically a minor understory species when present, *Castanopsis*' importance increases on nutritionally poor and droughty sites (Keeler-Wolf 1988, McKee 1990). In contrast to exposure sensitive *Tsuga*, *Castanopsis* were found immediately adjacent to south remnant faces where reflected radiation should be greatest (Figure 3.23). *Castanopsis* were least abundant immediately to the north of remnant faces where *Tsuga* abundance peaked and where bole shade would be most effective. Remnant trees appear to facilitate niche differentiation between *Castanopsis* and *Tsuga* via their differences in drought and exposure tolerance.

Remnant trees may also facilitate differentiation between *Castanopsis* and *Pseudotsuga*. *Castanopsis* is intermediate in shade tolerance between *Pseudotsuga* and *Tsuga* (McKee 1990). While *Pseudotsuga* may tolerate droughty conditions, it cannot match *Castanopsis*' vigor where indirect or direct light has been reduced, such that canopy

*Pseudotsuga* were negatively associated with remnant crown areas. *Castanopsis* also gained a head start by resprouting. *Pseudotsuga* seedling photosynthesis can be severely limited by evergreen hardwood sprout clumps (Harrington et al. 1994). Such interference may explain the strong short-scale (< 4 m) repulsion between *Pseudotsuga* and *Castanopsis* (Figure 3.22a). The only species that was not repulsed from *Castanopsis* was *Cornus*, another resprouting hardwood (Table 3.4).

An additional factor in the distribution of *Castanopsis* may be the caching of its nutlike seed by small mammals (McKee 1990). Remnant trees which survived pre-1892 fires may have been centers of small mammal activity, leading to adjacent seed caches and *Castanopsis* clusters.

*Castanopsis* pattern appears to stem primarily from an interaction between its drought tolerance and its capacity to resprout. *Castanopsis* competitive status may interact with the fire pattern. At distances away from remnants, less vigorous *Castanopsis* may be more susceptible to complete fire kill. Among the species at Eagle, *Castanopsis* may be the most dependent upon a regime of multiple, partial fires. On south-facing slopes, remnant trees give rise to droughty microsites where *Castanopsis* is competitively superior. Each fire reinforces the outcome of previous *Castanopsis* establishment and competitive interactions. Without fire, *Castanopsis* would decline in importance. At the H.J. Andrews Experimental Forest in Oregon, maximum ages of *Castanopsis* ranged from 130 to 150 years (McKee 1990). More complete conifer shade will reduce *Castanopsis* vigor, but fires grant a new lease on life. For *Castanopsis*, partial, multiple fires provide favorable microsites, prevent exclusion and permit consolidation.

# Partial fires: successional pathways, cascading patterns and species diversity

#### The potential for multiple successional pathways

Concurring with the models of Nobel and Slatyer (1980), my results indicate the potential for multiple pathways at each disturbance, with disturbance characteristics and species life history traits critical for predicting the successional pathway. Fires of intermediate frequency may be necessary for the persistence of short-lived, but resprouting, species such as Castanopsis and Cornus, and longer fire return intervals might lead to their decline. Fire severity determines the abundance of remnant trees and other residual elements (e.g. litter accumulations). Where species are differentially inhibited or facilitated relative to remnant locations, species proportions and successional direction may differ with remnant density. At Eagle, Castanopsis appears to be facilitated in remnant tree patches, such that its presence may be linked to the abundance of remnant tree patches left by moderate severity fires. On non-south-facing slopes such as Wolf, the proportions of Pseudotsuga and Tsuga -- two species with opposing interactions with remnant trees -may depend on remnant tree density. Since Pseudotsuga is inhibited by remnant trees, more severe fires, reducing remnant density, should favor Pseudotsuga in the post-fire cohort. Less severe fires should favor the facilitated species, Tsuga. Corroborating these predictions, Pseudotsuga was less abundant in the east Wolf plot (14%), where remnant tree density was twice as great, than in the west Wolf plot (23 %). Conversely, Tsuga was more abundant in the east Wolf plot (59 %) than in the west Wolf plot (50 %). Zenner's (1995) survey of 14 stands impacted by partial fires likewise found that post-fire Pseudotsuga volume decreased with increasing remnant tree density.

Fire severity may also influence successional pathways by altering the species composition of remnant trees. Among the potential remnant tree species at Wolf, *Thuja* is much less resistant to fire than *Pseudotsuga*, such that an increase in fire severity might leave *Pseudotsuga* remnant trees, but eliminate *Thuja* remnant trees. Such a fire would

also create more mineral soil, enhancing post-fire establishment of *Thuja* and dramatically altering *Thuja*'s population structure. Given that the interaction of post-fire *Pseudotsuga* and *Tsuga* with remnants differed with remnant species, changes in remnant composition could also alter their abundance in the post-fire cohort.

Environmental conditions may interact with fire severity to determine successional pathways. Greater remnant densities may favor *Tsuga* at the cooler and wetter Wolf site. However, given the apparent inhibition of *Tsuga* by remnant trees at the Eagle site, *Tsuga* may decline with greater densities on south-facing slopes.

These scenarios suggest that the facilitation or inhibition of colonizing species by remnant trees and residual elements makes possible alternative successional pathways. Fire severity and frequency, interacting with environmental conditions, may be critical determinants of the successional pathway.

#### Cascading patterns and spatial heterogeneity

Partial disturbances enhance vertical and horizontal (spatial) heterogeneity. Vertical stratification is a defining result of a partial-mortality fire: surviving plants become emergents above a regenerating cohort. The results here indicate that the species and size class patterns of the regenerating cohort are dependent upon the residual pattern. The resulting patterns are characterized by spatial heterogeneity or "pattern diversity" (sensu. Rebertus et al. 1989): rather than being evenly mixed across the stand, groups are intensely clustered (at both small and larger scales) and significant associations (repulsion or attraction) occur between species. In these stands, patchy fire has initiated a sequence of cascading patterns: patchy fire has left a clustered pattern of remnant trees; the dependence of colonization patterns upon the patchy remnant pattern has led to patch formation among post-fire species.

The clustered pattern of the remnant trees, the first feature of this heterogeneity, is the signature of fire. In the absence of fire, stand patterns are expected to trend from clustering toward uniformity with stand development and non-random mortality (Laessle 1965, Christensen 1977, Ghent and Franson 1986, Kenkel 1988, Rebertus et al. 1989, Duncan 1991, Moeur 1991). In unburned stands in the Cascade Mountains, old-growth dominants, similar in age and size to the remnant trees in this study, were uniformly distributed (Stewart 1986a). Variable and uneven in intensity, fire interrupts this tendency toward uniformity, leaving patches of mortality and clustered survivors (Rebertus et al. 1989).

In addition to the heterogeneous pattern of survivors, the community's spatial heterogeneity is enhanced by the clustered patterns of colonizing species and significant associations, both positive and negative, between colonizing species. As discussed earlier, the clustering of post-fire species can, in part, be attributed to their spatial dependence upon the remnant pattern, and the associations between species may, in part, be due to differences in their spatial interaction with the remnant pattern. In certain cases, aggregation or dispersion may have resulted from remnant tree effects upon resource availability or microclimate. In other cases, such as that of *Thuja* at Wolf, a species' distribution may reflect initial fire effects upon substrate patterns, patterns which may be coincident with the remnant tree pattern. In either case, the post-fire species patterns are a product of the disturbance event and residual patterns. The initial heterogeneity of the disturbance, imprinted in the survivors' pattern, is perpetuated in the heterogeneous patterns of the regenerating cohort.

One of the few experimental studies of spatial pattern also concluded that fires of intermediate frequency and severity promote spatial heterogeneity (Rebertus et al. 1989). In the Florida sandhills, *Quercus laevis* became less clustered with time in unburned reference plots. In contrast, post-fire *Q. laevis* in burned plots were more intensely and discretely clustered than pre-fire *Q. laevis*. Furthermore, repulsion between *Q. laevis* and the other dominant species, *Pinus palustris*, increased after the fire (Rebertus et al. 1989).

## An alternative conception of patch dynamics

Models of patch dynamics have typically focused upon patch formation in openings -- ranging from single-tree canopy gaps to large fire-created openings -- where space and resources have become available within a relatively undisturbed, closed matrix (White and Pickett 1985, Belsky and Canham 1994). In the present study, an alternative model is suggested by the formation of patches relative to remnant trees which occupy space and resources within an otherwise open matrix. In an analogous case, isolated savanna trees occupy space within the matrix of an open grassland. As with the remnant trees, patch formation occurs with the inhibition (grasses) or facilitation (shrubs, other trees) of different species around the savanna tree (Belsky and Canham 1994).

The area of vegetation response, i.e. the patch, associated with an isolated tree or a gap may extend beyond and be less discrete than the edges of a gap or tree crown (Belsky and Canham 1994). In the present study, the distances over which species were aggregated or dispersed from remnant locations almost always extended beyond remnant crown edges ( $\approx 4.5$  m), and, at most, extended up to 25.5 m away from remnant trees. Although patterns became statistically insignificant at specific distances, the graphs of Ripley's K(t) reveal that the dependence of patterns upon remnant locations changed gradually with distance and did not end abruptly. Furthermore, the distance of vegetation response around remnant trees varied by species. Point pattern analysis may be a particularly appropriate method for describing patch responses: patch boundaries are not drawn a priori, and entire populations of plant locations are taken into account. Nevertheless, while patch boundaries may not be discrete, the dependence of species patterns upon remnant locations over limited distances does suggest the formation of remnant-dominated patches within an otherwise open matrix.

Previous studies of pattern in fire-impacted forests have focused upon the commonly observed clustered pattern of even-age groups and have attributed this clustering to the regeneration of cohorts within fire-opened patches (Cooper 1961, Bonnicksen and Stone 1981, Stewart 1986b). Less attention has been given to the interaction between colonizers and survivors and the potential for patch formation relative to survivors. However, Duncan (1993) describes positive, negative and neutral spatial interactions between regenerating species and survivors of a moderate intensity flood in New Zealand. Duncan (1993) concludes that the differing interactions with survivors resulted in establishment opportunities for all four colonizing species, enhancing species coexistence.

#### Species diversity and stratification

Consistent with Duncan's (1993) conclusions, the present study suggests that, in addition to enhancing spatial heterogeneity, partial fires of intermediate frequency may also enhance species diversity. In the Pacific Northwest, most species are present throughout succession, changing in abundance but rarely replacing each other (Franklin and Hemstrom 1981, Franklin and DeBell 1988, Halpern and Spies 1995). Halpern and Spies (1995) found no significant differences in richness between young, mature and old-growth stands (mean ages 60, 115, 395 years) in the Oregon Cascades, but species heterogeneity, a measure of proportionality, was higher in young and old forests than in mature forests. Increased heterogeneity resulted from the more consistent presence of shorter-lived hardwoods in the young stands and the greater abundance of shade tolerants in the older stands. Similar features may enhance diversity in stands with a history of multiple, partial fires. Fires of intermediate frequency promote the persistence of short-lived, but resprouting hardwoods. Castanopsis may be facilitated in remnant tree patches on southfacing sites. Hardwood persistence may also be enhanced by the creation of large gaps by dead remnant trees. Late seral species, such as Tsuga, may increase in importance where remnant tree shade inhibits the growth of intolerant competitors or ameliorates exposure. Fallen, dead remnants may provide a continuous supply of decaying wood essential for subcanopy establishment of Tsuga. The extremely fire-sensitive old-growth associate, Taxus brevifolia, may persist in unburned patches. The Eagle and Wolf stands suggest

that, in a regime of multiple, partial fires, species diversity may be enhanced by the persistence of early seral hardwoods and the greater proportion of late seral species at earlier stages.

The means by which species coexist may distinguish succession within a regime of multiple, partial fires from that initiated by infrequent, catastrophic fires. Succession has been described as a gradient in time along which species dominance is stratified (Pickett 1976). At the Eagle and Wolf stands, however, early and late successional species coexisted, species dominance being stratified by different interactions with residual elements. The time interval between fires in a regime of partial fires is typically much shorter than that between catastrophic fires (Morrison and Swanson 1990). In the Pacific Northwest, changes in species dominance take place extremely slowly, given the longevity of the early seral dominant, *Pseudotsuga* (Franklin and DeBell 1988). Within the shortened intervals between multiple, partial fires, time-driven changes in species dominance are likely less than those which can occur across residual-defined patches and spatial gradients. Thus, between catastrophic fires, the primary gradient for species stratification may be temporal, but between partial fires, spatial.

After a partial-mortality fire, patterns of the colonizing species are spatially dependent upon the pattern of surviving remnant trees. The variety of spatial interactions, including aggregation and dispersion, between post-fire species and remnant locations suggests that remnant trees or associated residual features may differentially facilitate or inhibit colonizing species. Stands may be characterized by a cascading sequence of patterns resulting in spatial heterogeneity: patchy fire leaves a clustered remnant pattern, and spatial dependence upon the remnant pattern leads to pervasive clustering among colonizing species. Both early and late seral species may coexist within the community, potentially enhancing species diversity. Within a regime of intermediate frequency, partial fires, the primary gradient along which species are stratified may be spatial rather than temporal. Disturbance characteristics, by varying the amount and species composition of

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survivors, are critical to determining the post-fire successional pathway. Disturbance edits, but does not eliminate the past (Franklin and Halpern 1987). Present communities are interwoven with and dependent upon those of the past.

#### Summary

Reconstructions of fire history at Eagle and Wolf Rock indicated that the lower, mature canopy consisted of multiple cohorts initiated by multiple fires in the nineteenth century. At Eagle Rock, strong evidence existed for fires in 1848, 1870 and 1892. An 1892 fire at Wolf Rock left strong evidence; an earlier fire at about 1829 and an immediate reburn in 1896 appeared likely, but evidence was weaker. Fire severity patterns were complex. Severity patterns were reconstructed from the locations of mature trees which had established after one of the earlier nineteenth century fires (1829, 1848 or 1870) and survived the most recent fire (1892) as very young trees. Survival ("low severity") patches varied in shape and size, from isolated individuals to large patches (.24 ha) with complex shapes. Remnant tree locations did not necessarily correspond to young tree survival patches in the most recent fire and, at Eagle, the highest density of remnant trees occurred where there were relatively few surviving young trees. No area in either stand remained unburned during the nineteenth century. Particular species in the mature lower canopy were often associated with patches initiated by specific fire events, leading to differing proportions of species between fire patches. Cohorts were layered and interspersed among each other rather than juxtaposed as discrete patches, making the conception of the forest as a "mosaic" problematic for these stands.

Establishment dates of lower canopy *Pseudotsuga* and *Tsuga* indicated that the regeneration of both was initiated by the fire events and neither displayed continuous recruitment. *Pseudotsuga* regenerated more quickly than *Tsuga* at both sites, but *Tsuga* regeneration continued for longer time periods. *Castanopsis* regeneration predated *Pseudotsuga* and was tightly clustered immediately after the 1892 fire at Eagle, consistent with its ability to resprout after fire. Although the sequence of species establishments was similar at both sites, the median establishment time for both *Pseudotsuga* and *Tsuga* was

longer at Eagle than at Wolf, and the *Pseudotsuga* age distribution, in particular, was compressed at Wolf. Regeneration delays may have resulted from exposure on the southfacing slope at Eagle, and the scarcity of *Tsuga* may reflect its intolerance of exposure. In contrast, the abundance of *Tsuga* at the less exposed Wolf site may have resulted in a denser canopy which limited further regeneration of shade-intolerant *Pseudotsuga*, thus compressing the age distribution of *Pseudotsuga*. Size-to-age relationships for *Pseudotsuga* and *Tsuga* were particularly poor (relative to those relationships reported in the literature) at both Eagle and Wolf, suggesting that the complexity of interactions in these multi-cohort stands may break down the relationship between age and size.

The spatial patterns of post-fire species were clearly dependent upon the remnant tree pattern. In most cases, species were dispersed away from remnant trees and this dispersion was significant at small distances (< 10 m). However, *Castanopsis* (at small through large distances) and *Cornus* (at large distances only) were aggregated around remnant trees at Eagle. *Tsuga* displayed distinctly different patterns between the two sites, being independent of (east plot) or aggregated around (west plot) remnant trees at Wolf, but dispersed away from remnant trees at Eagle.

For each post-fire species, crown class patterns were often dependent upon the remnant tree pattern, but trends in pattern across crown classes were typically not evident. However, *Pseudotsuga* displayed a clear trend; larger crown classes of post-fire trees were dispersed away from remnant trees at much greater distances than smaller crown classes, suggesting a persistent remnant tree effect upon growth and mortality.

The spatial relationship between each post-fire species and remnant trees differed among remnant tree species at Wolf. Post-fire *Pseudotsuga* were dispersed away from remnant trees of the same species, but independent of *Thuja* remnant trees. Post-fire *Thuja* was dispersed from both remnant species, but the distance of dispersion extended to much greater distances away from *Thuja* remnant trees than from *Pseudotsuga* remnants. Differences in interactions with remnant trees of different species suggested that proportions of species colonizing after a partial fire could potentially differ with differing species composition of the survivors.

On the south-facing slope at Eagle, interactions between remnant trees and post-fire species were often directional. Both post-fire *Tsuga* and *Castanopsis* were independent of the north portions of remnant tree crown projections, but *Tsuga* was negatively associated and *Castanopsis* positively associated with south portions of remnant crown projections. The strong difference among species within south remnant crown areas suggested the potential for niche differentiation beneath remnant crowns.

The within-group patterns of remnant trees were predominantly clustered. Post-fire species and crown classes overwhelmingly exhibited clustered patterns. While many processes may contribute to clustering, the predominance of clustered patterns among postfire species was striking. To a large extent, this clustering may reflect the spatial dependence of each post-fire species' pattern upon the clustered remnant tree pattern. Almost all species-to-species interactions within the post-fire cohort displayed significant repulsion or aggregation. As with the clustered within-group patterns, these significant species-to-species interactions may, in part, be due to the differing interactions among each post-fire species and the remnant trees. For instance, at west Wolf, post-fire Pseudotsuga was dispersed away from remnant trees, while Tsuga was aggregated around the remnant trees. These opposing interactions with remnant trees may result in the repulsion between the two species and the clustered within-group pattern of each. The patchy pattern of a partial fire leaves behind the signature of a clustered remnant tree pattern. This begins a cascade of complex patterning. The pattern of each post-fire species is spatially dependent upon the remnant tree pattern, and this dependence may lead to significant within-group patterns and between-species interactions within the post-fire cohort.

The aggregation around remnant trees of early seral *Castanopsis* at Eagle and of late seral *Tsuga* at Wolf suggest that partial fires may enhance species diversity. Partial fires may enhance species coexistence by promoting the persistence of early seral species or the

earlier invasion of late seral species. Succession has been described as a gradient in time along which species dominance is stratified. At Eagle and Wolf, however, dominance of early and late seral species was stratified spatially by differing interactions with remnant trees. In the intervals between catastrophic fires, the primary gradient for species stratification may be temporal, but between partial fires this gradient may be spatial, occurring across residual-defined patches.

# Management implications

# Pattern of retained live trees

In discussions of live-tree retention, a central issue has been the pattern in which retained trees should be left. Generally, two alternatives have been considered: scattered live trees distributed in a random to uniform pattern or clusters of live trees contained within uncut patches. As with any management practice, the choice between these options depends largely upon the management objective. Growth models suggest that clumped live trees will have less impact on the regenerating cohort's growth (stand-level basal area/ unit area) than an equivalent number of scattered live trees (Birch and Johnson 1992, Hansen et al. 1995). Wampler's (1993) retrospective study of two-story stands also indicates that aggregated overstory trees have less effect on height growth than scattered overstory trees. However, the litterfall pattern of epiphytic lichen in the Eagle Rock stand suggests that dispersion processes, such as those of old-growth dependent lichens may be enhanced by a scattered pattern of retained trees (Sillett 1996).

The standards and guidelines of the Northwest Forest Plan emphasize the role of retained trees in providing suitable microclimates and habitat for old-growth dependent species (F.E.M.A.T. 1993). The plan emphasizes retention in large patches, deeming such patches to be more suitable habitat for most species, but recommends retention of some single trees, since other species may benefit from single trees. Specifically, it is

recommended that 70% of the retained area (total retained area is to be 15% of the cutting unit) be retained in patches of .2 - >1 ha ("patches should generally be larger than 2.5 acres [1 ha]") and the remainder dispersed as single trees or clumps < .2 ha (F.E.M.A.T. 1993).

If the objective of a green-tree retention cut is to mimic a partial fire, then the patterns described for the Eagle and Wolf Rock stands can suggest an appropriate residual pattern. The spatial analysis of the extended plots (150 \* 250 or 275 m) indicated that remnant trees were clumped. At Eagle Rock, clustering peaked (indicating average clump radius) at about 25 m and did not extend beyond 37 m, indicating an average clump area of about .2 ha. At Wolf Rock, clustering appeared to peak between 45 - 50 m, indicating average clump sizes of .6 - .8 ha, but the scale of analysis did not extend beyond 50 m.

While spatial statistics indicate that the remnant trees are clumped, reconstruction of fire patterns made clear that remnant trees survived not only in patches, but also as isolated individuals. Furthermore, clusters of remnant trees were overlaid upon areas which burned during the recent partial fires. Regeneration from the nineteenth century fires occurred throughout each stand, indicating that no portion of either stand was left unburned.

The Eagle and Wolf Rock stands suggest that leaving retained trees either entirely in a scattered pattern or entirely in uncut patches does not appropriately mimic partial fires. Rather, a mix of single trees and clusters, with trees left predominantly in clusters, may more closely mimic natural fire. The Northwest Forest Plan appropriately recommends such a mix (F.E.M.A.T. 1993). However, uncut patches may not resemble natural remnant tree clusters in that such clusters may typically have been underburned (and, as a result, likely thinned). Completely mimicking natural fire may be difficult within retained patches, such that the benefits of mimicry may be offset by the costs of management intrusion within these patches.

# Implications for post-harvest development

The increasing distance of dispersion of mature *Pseudotsuga* away from remnant trees with larger crown classes suggests a distance-dependent effect upon *Pseudotsuga* growth and mortality. Dominant *Pseudotsuga* were found in fewer numbers than expected with independence up to distances of 12.5 - 14.5 m away from remnant trees. This suggests a negative impact on height growth at least to this distance, and these distances are consistent with the effective radius of remnant tree influence upon volume suggested by Acker (1995) from growth models. It should be noted, however, that the Ripley's K(t) bivariate analysis at Eagle Rock also indicates a second, larger scale of dispersion at 18.5 - 27 m.

The pattern of the combined remnant tree + dominant Pseudotsuga point set at Eagle Rock also implied that remnant trees have important distance-dependent effects upon Pseudotsuga growth and mortality. The within-group patterns of both remnant trees and dominant Pseudotsuga were clustered. The clustered within-group pattern of dominant Pseudotsuga was unexpected in that thinning processes typically produce uniform spacing within large size classes. However, when remnant trees and dominant Pseudotsuga were combined into a single point set, a pattern of uniform spacing was evident. This change in pattern suggests that spacing between Pseudotsuga dominants in a regenerating cohort will develop with reference to the positions of retained trees, in addition to those of other dominants. Remnant trees occupy space that would otherwise be occupied by regenerating dominants. It is possible that the primary effect of retained trees upon stand growth may not be a reduction in the growth of dominants, but in the number of dominants in the regenerating cohort (Zenner pers. comm.). Dominants may develop at distances from retained trees where growth impacts are negligible. But, where retained trees occupy competitive space, the development of post-fire dominants is precluded. While the distance of dispersion for dominants will differ in managed stands with different characteristics, a

minimum distance should be expected within which dominant *Pseudotsuga* are unlikely to develop.

The present study suggests that remnant trees alter the competitive interactions between species in the regenerating cohort creating distance-dependent species patterns relative to remnant tree positions. The study also indicates that remnant-associated species patterns differ with different environmental conditions. In cool, mesic environments such as Wolf, Tsuga growth and survival may be superior to that of Pseudotsuga in areas adjacent to retained trees. Where live-tree retention is the chosen management practice, planting Tsuga within short distances from retained trees may maximize stand productivity in addition to enhancing species richness. Alternatively, if Pseudotsuga wood production is the primary goal, retaining fewer or no live trees may be appropriate in environments where Tsuga would be an important competitor (Wampler 1993). On moderately dry sites such as Eagle, Pseudotsuga will likely experience less competition from Tsuga, but may still be suppressed adjacent to retained trees. Within short distances of retained trees, controlling hardwoods such as Castanopsis may not be cost-effective, and resprouting Castanopsis could enhance the stand's species richness. Alternatively, Tsuga could be planted in the apparent safe sites to the immediate north of retained trees. At short distances to the south of remnant trees, hardwoods could be permitted, or a conifer tolerant of drought and shade (e.g. Libocedrus decurrens) could be planted.

No other studies have examined intra-stand species patterns in two-story stands, but several have discussed residual tree effects on stand-level species composition. Simulation models indicate that increasing retention levels will lead to increasing *Tsuga / Thuja* dominance in the regeneration, even where only *Pseudotsuga* has been planted (Hansen et al. 1995). In two-story stands in Washington, *Tsuga* height growth was negatively impacted by remnant trees, but individuals were typically taller than adjacent *Pseudotsuga* (Wampler 1993). Zenner's (1995) retrospective study of two-story stands in the Oregon Cascades yielded results which, at first, are not entirely consistent with predictions of increasing *Tsuga* dominance with increasing retention levels. Stand-level *Pseudotsuga* volume was negatively correlated with remnant tree density, but *Tsuga* volume had no association with remnant tree density. Furthermore, regressions of individual tree growth relative to remnant density indicated that *Tsuga* growth was more strongly limited by remnant trees than that of *Pseudotsuga* (Zenner 1995). The absence of a positive association between *Tsuga* volume and remnant tree density and the greater growth impacts of remnant trees upon individual *Tsuga* (than upon *Pseudotsuga*) might be explained by the overrepresentation of south-facing sites among Zenner's (1995) data: 11 of 14 sites had south-facing aspects (90 - 270°). The present study suggests that *Tsuga* presence may be facilitated near remnant trees on moist sites, but that the effects upon *Tsuga* may be neutral or inhibitory on south-facing sites.

One underlying theme of ecosystem management is to promote more natural levels of complexity in managed stands and landscapes (Swanson and Franklin 1992). The Eagle and Wolf stands display patterns which set a very high standard for complexity after a partial disturbance. Complexity is not limited to the vertical stratification created by the fire, but is propagated in horizontal heterogeneity in the pattern of the remnant trees and the species and size class patterns of the mature age class. In both stands, the mature age class was initiated by multiple fires, such that complexity was enhanced by the temporal and spatial overlapping of cohorts within the mature age class. In managed stands, live-tree retention will create immediate and obvious vertical stratification in regenerating stands. Nevertheless, it should be recognized that green-tree retention is a small, albeit important, step toward the level of complexity created by multiple partial wildfires. It may be appropriate to experiment with additional management practices to enhance complexity. Additional practices (without regard to economic feasibility) might include: complex patterning of retained trees, mixed species plantings, temporally staggered plantings, continued retention of some initially retained trees at the second harvest in addition to newly

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retained trees, thinnings of the young stand which vary in intensity across the stand, and patch cuts within the young stand.

# Questions for further research

The results from the present study raise a number of additional questions which could be addressed within these stands. 1) Individual and area-based growth models for Pseudotsuga and Tsuga in the context of remnant tree competition could be developed from these stands. 2) Hypotheses regarding the pattern-driving processes could be tested. For instance, soil moisture content at different distances from remnant trees could be measured at Eagle to determine whether remnant trees are indeed creating droughty microsites. Soil pH, nitrogen concentrations and nitrification rates at Wolf Rock could be measured to determine whether Thuja and Pseudotsuga remnant trees differ in their effects upon soil quality. 3) Other possible fire or remnant-dependent patterns could be explored: understory shrubs and herbs, lichen, mycorrhizae and pathogens (e.g. the mistletoe infection at Wolf Rock). 4) Interactions between the remnant pattern and other disturbances could be explored. For instance, blowdown of remnant trees imposes another layer of disturbance. Are single remnant trees or clustered remnant trees more susceptible to blowdown? Also, at Wolf Rock, a recent snowdown event has caused high mortality among the mature cohort. Wampler (1993) found that remnant trees affect the height-todiameter ratio of regenerating individuals. If this is the case, is there a relationship between the remnant tree pattern and the susceptibility of mature individuals to snowdown or blowdown mortality?

The present study is limited by the difficulty of making generalizations from two case studies. In order to test the generality of the findings here, spatial patterns should be described from a larger sample of stands including a range of environmental conditions. In particular, the spatial patterns of *Pseudotsuga* and *Tsuga* relative to remnant trees should be explored. Is *Tsuga* generally random or aggregated around remnant trees on northern

aspects while dispersed from remnants on southern aspects? Is Pseudotsuga dispersed farther from remnant trees on north aspects than on south aspects? Another key pattern is that of the remnant trees. Are remnant trees generally clustered and what is the typical size of remnant clusters? Mapping stands is a time-consuming process, and a sufficient area must be mapped to permit the appropriate spatial method and scale of analysis. In order to address the generality of the present observations, it may be necessary to map smaller areas than those mapped here. Plots 50 \* 50 m may be the minimum size required. Ripley's K(t) edge correction method permits analysis of distances up to 1/2 the smallest edge, and 25 m is an appropriate maximum distance for the bivariate analysis. The size of Zenner's (1995) residual tree plots may be too small, but the refined nearest neighbor analyses used here should be attempted with these completely mapped plots. Patterns in two-story stands might also be described with less rigorous point pattern methods which require sampling rather than complete mapping (e.g. Pielou 1959). The issue of remnant tree pattern and cluster size might be effectively addressed using aerial photographs from which remnant trees could be individually identified and mapped. The patterns documented in the Eagle and Wolf stands are provocative, but their usefulness would be enhanced if similar patterns could be documented in a greater number of stands.

#### Bibliography

- Acker, S. A. 1995. Structure, composition, and dynamics of two-age forest stands on the Willamette National Forest: a retrospective study concerning green-tree retention. Dept. of Forest Science, Oregon State University, Corvallis, OR, USA.
- Agee, J. K. 1991. Fire history of Douglas-fir forests in the Pacific Northwest. Pages 25-33 in L. F. Ruggiero, K. B. Aubry, A. B. Carey and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S.D.A. Forest Service Pacific Northwest Research Station, Portland, OR, USA.
- Agee, J. K. and M. H. Huff. 1987. Fuel succession in a western hemlock/ Douglas-fir forest. Canadian Journal of Forest Research 17:697-704.
- Alban, D. H. 1969. The Influence of western hemlock and western redcedar on soil properties. Soil Science Society of America Proceedings **33**:453-457.
- Andersen, M. 1992. Spatial analysis of two-species interactions. Oecologia 91:134-140.
- Belsky, A. J. and C. D. Canham. 1994. Forest gaps and isolated savanna trees. Bioscience 44:77-84.
- Berndt, H. W. and R. D. Gibbons. 1958. Root distribution of some native trees and understory plants growing on three sites within ponderosa pine watersheds in Colorado. U.S.D.A. Forest Service Rocky Mountain Forest and Range Experiment Station Station Paper 37.
- Besag, J. and P. J. Diggle. 1977. Simple Monte Carlo tests for spatial pattern. Applied Statistics **26**:327-333
- Birch, K. R. and K. N. Johnson. 1992. Stand-level wood-production costs of leaving live, mature trees at regeneration harvest in coastal Douglas-fir stands. Western Journal of Applied Forestry 7:65-68.
- Bonnicksen, T. M. and E. C. Stone. 1981. The giant sequoia-mixed conifer forest community characterized through pattern analysis as a mosaic of aggregations. Forest Ecology and Management **3**:307-328.
- Boots, B. N. and A. Getis. 1988. Point pattern analysis. Sage Publications, Newbury Park, CA, USA.
- Bouten, W., T. T. Heimovaara and A. Tiktak. 1992. Spatial patterns of throughfall and soil-water dynamics in a Douglas-fir stand. Water Resources Research 28:3227-3233.

Briggs, J. M. and D. J. Gibson. 1992. Effect of fire on tree spatial patterns in a tallgrass prairie landscape. Bulletin of the Torrey Botanical Club **119**:300-307.

Brown, P. M. and T. W. Swetnam. 1994. A cross-dated fire history from coast redwood near Redwood National Park, California. Canadian Journal of Forest Research 24:21-31.

Burgess, D. 1991. Western hemlock and Douglas-fir seedling development with exponential rates of nutrient addition. Forest Science **37**:54-67.

- Burns, B. R. 1993. Fire-induced dynamics of *Araucaria araucana- Nothofagus antarctica* forest in the southern Andes. Journal of Biogeography **20**:669-685.
- Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and ropical forests. Canadian Journal of Forest Research 20:620-631.
- Carter, R. E. and K. Klinka. 1992. Variation in shade tolerance of Douglas-fir, western hemlock, and western red cedar in coastal British Columbia. Forest Ecology and Management 55:87-105.
- Christensen, N. L. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. American Midland Naturalist 97:176-188.
- Clark, P. J. and F. J. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in plant populations. Ecology **35**:445-453.
- Cline, S. P., A. B. Berg and H. M. Wright. 1980. Snag characteristics and dynamics in Douglas-fir forests, Western Oregon. Journal of Wildlife Management 44:773-786.
- Collins, S. L. and S. C. Klahr. 1991. Tree dispersion in oak-dominated forests along an environmental gradient. Oecologia **86**:471-477.
- Cooper, C. F. 1961. Pattern in ponderosa pine forests. Ecology 42:493-499.
- Crampton, C. B. 1982. Podzolization of soils under individual tree canopies in southwestern British Columbia, Canada. Geoderma 28:57-61.
- Daniels, L. D. 1994. Structure and regeneration of old-growth *Thuja plicata* stands near Vancouver, British Columbia. Thesis. The University of British Columbia, Vancouver, BC, Canada.
- DeBell, D. S. and R. O. Curtis. 1993. Silviculture and new forestry in the Pacific Northwest. Journal of Forestry **December**:25-30.
- Diggle, P. J. 1983. Statistical analysis of spatial point patterns. Academic Press, London, UK.
- Duncan, R. P. 1991. Competition and the coexistence of species in a mixed podocarp stand. Journal of Ecology **79**:1073-1084.
- Duncan, R. P. 1993. Flood disturbance and the coexistence of species in a lowland podocarp forest, south Westland, New Zealand. Journal of Ecology **81**:403-416.
- Duncan, R. P. and G. H. Stewart. 1991. The temporal and spatial analysis of tree age distribution. Canadian Journal of Forest Research 21:1703-1710.
- Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology **54**:57-69.
- Egler, F. E. 1954. Vegetation science concepts. 1. Initial floristic composition -- a factor in old-field vegetation development. Vegetatio 4:412-417.

- Eis, S. 1974. Root system morphology of western hemlock, western red cedar and Douglas-fir. Canadian Journal of Forest Research 4:28-38.
- E.S.R.I. (Environmental Systems Research Institute, Inc.). 1995. ARC/INFO, version 7.0. Redlands, CA, USA.
- F.E.M.A.T. (Forest Ecosystem Management Assessment Team). 1993. Forest ecosystem management: an ecological, economic, and social assessment. U. S. D. A. Forest Service Pacific Northwest Research Station, Portland, OR, USA.
- Franklin, J., J. Michaelsen and A. H. Strahler. 1985a. Spatial analysis of density dependent pattern in coniferous forest stands. Vegetatio 64:29-36.
- Franklin, J. F. 1963. Natural regeneration of Douglas-fir and associated species using modified clear-cutting systems in the Oregon Cascades. U.S.D.A. Forest Service Research Paper PNW-3.
- Franklin, J. F. 1989. Toward a new forestry. American Forests 95:37-44.
- Franklin, J. F. and D. S. DeBell. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga -Tsuga* forest. Canadian Journal of Forest Research **18**:633-639.
- Franklin, J. F. and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. U.S.D.A. Forest Service Pacific Northwest Research Station General Technical Report PNW-8.
- Franklin, J. F. and C. B. Halpern. 1987. Influence of biological legacies on succession. Pages 54-55. Symposium on land classifications based on vegetation: applications for resource management, Moscow, ID, USA.
- Franklin, J. F. and M. A. Hemstrom. 1981. Aspects of succession in the coniferous forest of the Pacific Northwest. Pages 213-229 in D. C. West, H. H. Shugart and D. B. Botkin, editors. Forest succession: concepts and application. Springer-Verlag, New York, NY, USA.
- Franklin, J. F., J. A. MacMahon, F. J. Swanson and J. R. Sedell. 1985b. Ecosystem responses to the eruption of Mount St. Helens. National Geographic Research 1:197-216.
- Garza, S. 1995. Fire history and fire regimes of East Humbug and Scorpion Creeks and their relation to the range of *Pinus lambertiana* Dougl. Thesis. Oregon State University, Corvallis, OR, USA.
- Ghent, A. W. and S. E. Franson. 1986. Changes in mortality and size-class spatial distribution patterns in pre-closure and post-closure conifer plantations. Forest Science 32:559-575.
- Good, B. J. and S. A. Whipple. 1982. Tree spatial patterns: South Carolina bottomland and swamp forests. Bulletin of the Torrey Botanical Club **109**:529-536.
- Goslin, M. N. 1993. Proposed sampling design of lower canopy tree ages and heights for modelling growth in stands with emergent remnant trees. Unpublished manuscript

- Gray, A. N. 1995. Tree seedling establishment on heterogenous microsites in Douglas-fir forest canopy gaps. Dissertation. Oregon State University, Corvallis, OR, USA.
- Green, D. G. 1989. Simulated effects of fire, dispersal and spatial pattern on competition within forest mosaics. Vegetatio 82:139-153.
- Gregory, R. A. 1957. Some silvicultural characteristics of western redcedar in southeast Alaska. Ecology **38**:646-649.
- Haig, I. T., K. P. Davis and R. H. Weidman. 1941. Natural regeneration in the western white pine type. U.S.D.A. Technical Bulletin No. 767.
- Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology **69**:1703-1715.
- Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology **70**:704-720.
- Halpern, C. B. and J. F. Franklin. 1990. Physiognomic development of *Pseudotsuga* forests in relation to initial structure and disturbance intensity. Journal of Vegetation Science **1**:475-482.
- Halpern, C. B. and T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5:913-934.
- Hamill, D. N. and S. J. Wright. 1986. Testing the dispersion of juveniles relative to adults: a new analytic method. Ecology 67:952-957.
- Hansen, A. J., S. L. Garman, J. F. Weigand, D. L. Urban, W. C. McComb and M. G. Raphael. 1995. Alternative silvicultural regimes in the Pacific Northwest: simulations of ecological and economic effects. Ecological Applications 5:535-554.
- Harrington, T. B., R. J. Pabst and J. C. T. III. 1994. Seasonal physiology of Douglasfir saplings: response to microclimate in stands of tanoak or Pacific madrone. Forest Science 40:59-82.
- Hatton, T. J. 1989. Spatial analysis of a subalpine heath woodland. Australian Journal of Ecology 14:65-75.
- Hemstrom, M. A. and J. F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quaternary Research 18:32-51.
- Hemstrom, M. A., S. E. Logan and W. Pavlat. 1987. Plant Association and Management Guide, Willamette National Forest. U.S.D.A. Forest Service Pacific Northwest Region, Willamette National Forest R6-Ecol 257-B-86.
- Henry, J. D. and J. M. A. Swan. 1974. Reconstructing forest history from live and dead plant material -- an approach to the study of forest succession in southwest New Hampshire. Ecology **55**:772-783.
- Hoyer, G. E. 1993. The influence of Douglas-fir overstory on understory tree height growth in coastal forests of Washington. Washington Department of Natural Resources FLMRC Contribution 348.

- Hudson, J. C. and P. M. Fowler. 1966. The concept of pattern in geography. Department of Geography, University of Iowa Discussion paper: Series 1
- Huff, M. H. 1995. Forest age structure and development following wildfires in the western Olympic mountains, Washington. Ecological Applications 5:471-483
- Hutchinson, I. and M. C. Roberts. 1981. Vertical variation in stemflow generation. Journal of Applied Ecology 18:521-527.
- Isaac, L. A. 1940. Vegetative succession following logging in the Douglas-fir region with special reference to fire. Journal of Forestry **38**:716-721.
- Isaac, L. A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Pack Foundation, Washington, D. C., USA.
- Isaac, L. A. and G. S. Meagher. 1936. Natural reproduction on the Tilamook Burn two years after the fire. U.S.D.A. Forest Service Pacific Northwest Research Station, Portland, OR, USA.
- Kauffman, J. B. and R. E. Martin. 1990. Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra Nevada mixed conifer ecosystems. Forest Science **36**:748-764.
- Keeler-Wolf, T. 1988. The role of *Chrysolepsis chrysophylla* (Fagaceae) in the *Pseudotsuga* hardwood forest of the Klamath Mountains of California. Madrono **35**:285-308.
- Keenan, R. J. 1993. Structure and function of western red cedar and western hemlock forests on northern Vancouver Island. Dissertation. The University of British Columbia, Vancouver, B. C., Canada.
- Kenkel, N. C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology **69**:1017-1024.
- Krajina, V. J., S. Modoc-Jones and G. Mellor. 1973. Ammonium and nitrate in the nitrogen economy of some conifers growing in Douglas-fir communities of the Pacific North-West of America. Soil Biology and Biochemistry 5:143-147.
- Kuiper, L. C. and M. P. Coutts. 1992. Spatial disposition and extension of the structural root system of Douglas-fir. Forest Ecology and Management 47:111-125.
- Laessle, A. M. 1965. Spacing and competition in natural stands of sand pine. Ecology 46:65-72.
- Larsen, J. A. 1940. Site factor variations and responses in temporary forest types in northern Idaho. Ecological Monographs 10:2-54.
- Leemans, R. 1991. Canopy gaps and establishment patterns of spruce (*Picea abies* (L.) Karst.) in two old-growth coniferous forests in central Sweden. Vegetatio **93**:157-165.
- Leps, J. 1990. Can underlying mechanisms be deduced from observed patterns? Pages 1-11 *in* F. Krahulec, A. D. Q. Agnew, S. Agnew and J. H. Willems, editors. Spatial processes in plant communities. SPB Academic Publishing, The Hague, Netherlands.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

- Livingston, N. J. and T. A. Black. 1987. Water stress and survival of three species of conifer seedlings planted on a high elevation south-facing clear-cut. Canadian Journal of Forest Research 17:1115-1123.
- Livingston, N. J. and T. A. Black. 1988. The growth and water use of three species of conifer seedlings planted on a high-elevation south-facing clearcut. Canadian Journal of Forest Research 18:1234-1242.
- Lotwick, H. W. and B. W. Silverman. 1982. Methods for analysing spatial processes of several types of points. Journal of the Royal Statistical Society, Series B 44:406-413.
- Martin, R. E., D. D. Robinson and W. H. Schaeffer. 1976. Fire in the Pacific Northwest -- Perspectives and Problems. Tall Timbers Fire Ecology Conference 15:1-23.
- McCune, B. and T. F. H. Allen. 1985. Will similar forests develop on similar sites? Canadian Journal of Botany 63:367-376.
- McKee, A. 1990. *Castanopsis chryophylla* (Dougl.) A. DC.: giant chinkapin. Pages 234-239 *in* R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America: Volume 2, hardwoods. U.S.D.A. Forest Service, Washington, D.C., USA.
- McMinn, R. G. 1963. Characteristics of Douglas-fir root systems. Canadian Journal of Botany 41:105-122.
- Means, J. E. 1982. Developmental history of dry coniferous forests in the central western Cascade range of Oregon. Pages 142-158 *in* J. E. Means, editor. Forest succession and stand development research in the Northwest. Forest Research Laboratory, Oregon State University, Corvallis, OR, USA.
- Means, J. E. 1989. Estimating the date of a single bole scar by counting tree rings in increment cores. Canadian Journal of Forest Research **19**:1491-1496.
- Minore, D. 1979. Comparative autecological characteristics of Northwestern tree species -- a literature review. U.S.D.A. Forest Service Pacific Northwest Research Station Station General Technical Report PNW-87.
- Minore, D. 1983. Western redcedar -- a literature review. U. S. D. A. Forest Service Pacific Northwest Research Station General Technical Report PNW-150.
- Minore, D. 1990. Thuja plicata. Pages 590-600 in R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America, Vol. 1. conifers. U. S. D. A. Forest Service, Washington, D. C., USA.
- Moeur, M. 1991. Spatial variation in conifers regenerating beneath old-growth forest canopies. Dissertation. University of Washington, Seattle, WA, USA.
- Moeur, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. Forest Science **39**:756-775.

- Morrison, P. H. and F. J. Swanson. 1990. Fire history and pattern in a Cascade range landscape. U.S.D.A. Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-254.
- Munger, T. T. 1940. The cycle from Douglas-fir to hemlock. Ecology 21:451-459.
- Oliver, C. D. and E. P. Stephens. 1977. Reconstruction of a mixed-species forest in central New England. Ecology 58:562-572.
- Pabst, R. J., M. Goslin, S. Splean and G. Spycher. 1993. Using a geographic information system (GIS) to generate stem and log maps from field survey data. Unpublished manuscript
- Pacala, S. W. and D. H. Deutschman. 1995. Details that matter: the spatial distribution of individual trees mantains forest ecosystem function. Oikos 74:357-365.
- Padien, D. J. and K. Lajtha. 1992. Plant spatial pattern and nutrient distribution in pinyon-juniper woodlands along an elevational gradient in northern New Mexico. International Journal of Plant Science 153:425-433.
- Parker, T. 1986. Ecology of western redcedar groves. Dissertation. University of Idaho, Moscow, ID, USA.
- Peterson, C. J. and E. R. Squiers. 1995. An unexpected change in spatial patterns across 10 years in an aspen-white-pine forest. Journal of Ecology 83:847-855.
- Pickett, S. T. A. 1976. Succession: an evolutionary interpretation. American Naturalist **110**:107-119.
- Pielou, E. C. 1959. The use of point-to-plant distances in the study of the pattern of plant populations. Journal of Ecology **48**:575-584.
- Rebertus, A. J., G. B. Williamson and E. B. Moser. 1989. Fire-induced changes in *Quercus Laevis* spatial pattern in Florida sandhills. Journal of Ecology **77**:638-650.
- Remmert, H. 1991. The mosaic-cycle concept of ecosystems -- an overview. Pages 1-19 in H. Remmert, editor. The mosaic-cycle concept of ecosystems. Springer-Verlag, Berlin, Germany.
- Ripley, B. D. 1977. Modelling spatial patterns (with discussion). Journal of the Royal Statistical Society, Series B **39**:172-212.
- Ripley, B. D. 1979. Tests of 'randomness' for spatial point patterns. Journal of the Royal Statistical Society, Series B 41:368-374.
- Rose, C. R. 1993. Relationship of green-tree retention following timber harvest to forest growth and species composition in the western Cascade Mountains. Thesis. Oregon State University, Corvallis, OR, USA.
- Rothacher, J. 1963. Net precipitation under Douglas-fir forest. Forest Science 9:423-429.

SAS Institute Inc. 1987. SAS/STAT language guide, version 6. Cary, NC, USA.

- Schmidt, R. L. 1955. Some aspects of western red cedar regeneration in the coastal forests of British Columbia. British Columbia Forest Service Research Note 29.
- Schoonmaker, P. and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade mountains of Oregon. Forest Science 34:960-979.
- Sillett, S. C. 1996. Canopy epiphyte studies in the central Oregon Cascades: implications for the management of Douglas-fir forests. Dissertation. Oregon State University, Corvallis, OR, USA.
- Spies, T. A. and J. F. Franklin. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology **70**:543-545.
- Spies, T. A. and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91-109 in L. F. Ruggerio, K. B. Aubry, A. B. Carey and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S.D.A. Forest Service Pacific Northwest Research Station, Portland, OR, USA.
- Spies, T. A., J. F. Franklin and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research 20:649-658.
- Stamp, N. E. and J. R. Lucas. 1990. Spatial patterns and dispersal distances of explosively dispersing plants in Florida sandhill vegetation. Journal of Ecology 78:589-600.
- Steinbrenner, E. C. and S. P. Gessel. 1956. Windthrow along cutlines in relation to physiography on the McDonald Tree Farm. Weyerhaeuser Timber Company Forestry Research Note 15.
- Sterner, R. W., C. A. Ribic and G. E. Schatz. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. Journal of Ecology 74:621-633.
- Stewart, G. H. 1986a. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. Canadian Journal of Forest Research **16**:558-568.
- Stewart, G. H. 1986b. Population dynamics of a montane conifer forest, western Cascade range, Oregon, USA. Ecology 67:534-544.
- Stewart, G. H. and A. B. Rose. 1990. The significance of life history strategies in the developmental history of mixed beech (*Nothofagus*) forests, New Zealand. Vegetatio 87:101-114.
- Swanson, F. J. and J. F. Franklin. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. Ecological Applications 2:262-274.
- Szwagrzyk, J. 1990. Natural regeneration of forest related to the spatial structure of trees: a study of two forest communities in Western Carpathians, southern Poland. Vegetatio **89**:11-22.
- Szwagrzyk, J. 1992. Small-scale spatial patterns of trees in a mixed *Pinus sylvestris-Fagus sylvatica* forest. Forest Ecology and Management **51**:301-315.

- Tarrant, R. F., L. A. Isaac and J. Robert F. Chandler. 1951. Observations on litter fall and foliage nutrient contents of some Pacific Northwest tree species. Journal of Forestry 49:914-915.
- Teensma, P. D. A. 1987. Fire history and fire regimes of the central western Cascades of Oregon. Dissertation. University of Oregon, Eugene, OR, USA.
- Thomas, T. B., J. F. Lehmkuhl, M. G. Raphael and D. S. DeBell. 1993. Sites for retrospective studies: opportunities for research in western Washington and Oregon. U.S.D.A. Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-312.
- Turner, D. P. and E. H. Franz. 1985a. The influence of western hemlock and western redcedar on microbial numbers, nitrogen mineralization, and nitrification. Plant and Soil 88:259-267.
- Turner, D. P. and E. H. Franz. 1985b. Size class structure and tree dispersion patterns in old-growth cedar-hemlock forests of the northern Rocky Mountains (USA). Oecologia **68**:52-56.
- Turner, D. P., P. Sollins, M. Leuking and N. Rudd. 1993. Availability and uptake of inorganic nitrogen in a mixed old-growth coniferous forest. Plant and Soil 148:163-174.
- Upton, G. and B. Fingleton, editors. 1985. Spatial data analysis by example. Vol. 1. point pattern and quantitative data. Wiley series in probability and mathematical statistics. Applied probability and statistics section. John Wiley and Sons, Inc., New York, NY, USA.
- Walker, L. R. and F. S. C. III. 1987. Interactions among processes controlling successional change. Oikos 50:131-135.
- Wampler, M. 1993. Growth of Douglas-fir under partial overstory retention. Thesis. University of Washington, Seattle, WA, USA.
- Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology **35**:1-22.
- West, P. W. 1984. Inter-tree competition and small-scale pattern in monoculture of *Eucalyptus obliqua* L'Herit. Australian Journal of Ecology 9:405-411.
- Whipple, S. A. 1980. Population dispersion patterns of trees in a southern Louisiana hardwood forest. Bulletin of the Torrey Botanical Club **107**:71-76.
- White, P. S. and S. T. A. Pickett. 1985. Natural Disturbance and Patch Dynamics: An Introduction. Pages 1-13 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., San Diego, CA, USA.
- Williamson, R. L. 1973. Results of shelterwood harvesting of Douglas-fir in the Cascades of western Oregon. U.S.D.A. Forest Service Pacific Northwest Research Station Research Paper PNW-161.

- Wilson, M. V. 1991. Age structure patterns in *Abies amabilis* stands of the Cascade Mountains. American Midland Naturalist **125**:331-339.
- Zenner, E. K. 1995. Effects of residual trees on growth of young to mature Douglas-fir and western hemlock in the western central Oregon Cascades. Thesis. Oregon State University, Corvallis, OR, USA.
APPENDIX



Map 1. Eagle Rock Reference Stand, HJA RS 40

All area burned in 1892 except



Map 2. Wolf Rock Reference Stand, HJA RS 39

All area burned in 1892 except