Spatial patterns of overstory trees in late-successional conifer forests

Andrew J. Larson and Derek Churchill

Abstract: We analyzed spatial patterns of overstory trees in late-successional Abies amabilis (Dougl. ex Loud.) Dougl. ex J. Forbes forests and late-successional Pseudotsuga menziesii (Mirb.) Franco forests to establish reference spatial patterns for restoration thinning treatments, and to determine whether thinning treatments with minimum intertree spacing rules result in spatial patterns characteristic of late-successional forests. On average, 32.7% of overstory trees in Abies plots and 26.3% of overstory trees in Pseudotsuga plots occurred as members of multitree clusters (groups of trees in which trees are spaced within a specified minimum distance of each other) at a distance of 3.0 and 4.0 m, respectively. Multitree clusters occurred throughout the three Abies plots; the distribution of multitree clusters within the two Pseudotsuga plots was variable. Spatial patterns of overstory trees in late-successional forests were significantly different from those created by simulated restoration thinning treatments. Restoration thinning treatments that release both individual trees and multitree clusters promote characteristic late-successional tree spatial patterns at the within-patch scale (<0.04 ha). This formulation of restoration thinning highlights conservation of existing small-scale (<0.04 ha) spatial heterogeneity within the treatment area, elaborating on current practices that emphasize introduction of spatial heterogeneity at scales of 0.04 ha to 1.0 ha.

Introduction

Restoring late-successional conditions in previously harvested or otherwise anthropogenically modified forests is an increasingly common forest management objective (e.g., USDA and USDI 1994; City of Seattle 2000). Forest density management with thinning is the primary silvicultural intervention used to increase the rate of forest structural development (Carey 2003), and to promote development of characteristic late-successional forest structure and composi-
tion, 10 February 2008) recommends creating patches at the 0.1 to 0.5 ha scale with a 2:1 ratio of light to heavier thinning. These recommendations are based on spatial patterns of forest structure in late-successional forests capable of supporting populations of northern spotted owls (Carey et al. 1999a) and results from the Forest Ecosystem Study (Carey et al. 1999b). This method is known as variable density thinning (VDT) (Carey 2003) and is a specific case of “free” thinning (Tappeiner et al. 2007). In free thinning, the size and species of trees designated for removal and retention vary across the treatment area and are determined by the relative priority for retention and by the frequency of occurrence of different tree species and size classes (Tappeiner et al. 2007). Other recommendations for restoration thinning treatments in mesic Pacific Coast conifer forests include leaving unthinned “skips” and creating open “gaps” or heavily thinned patches at scales ranging from 0.04 to 0.3 ha (Carey and Harrington 2001; Roberts et al. 2007) up to 1.0 ha (Wilson and Puettmann 2007). Skips and gaps together usually occupy 10% to 25% of the treatment area (e.g., Roberts et al. 2007) and are embedded in the remaining 75% to 90% of the treatment area. This remaining area is thinned to one or sometimes two target densities using traditional spacing-based method (Roberts et al. 2007; Wilson and Puettmann 2007).

The recommended scale (0.04 to 1.0 ha) for introducing spatial heterogeneity with restoration or VDT thinning (Carey and Harrington 2001; Carey 2003; Roberts et al. 2007; Wilson and Puettmann 2007) appears to approximate patch-scale spatial patterns found in mesic late-successional conifer forests in Washington (Chen et al. 2004; Larson and Franklin 2006) and Oregon (Bradshaw and Spies 1992). However, guidance for restoration thinning treatments with respect to tree spatial patterns at the within-patch scale (i.e., less than ~0.04 ha, or a radius of about 11 m) is lacking.

Characterization and analysis of tree spatial patterns are carried out with stem-map data (Moore 1993): tree locations are surveyed in the field and then represented as points on a plane, with the spatial point pattern subjected to statistical or descriptive analysis. One popular method for analyzing tree spatial patterns is the family of distance-based spatial point pattern statistics (Loosmore and Ford 2006); Ripley’s K statistic is an example of this type of analysis. However, translating results from analyses with spatial point pattern statistics into management recommendations is extremely difficult and, in many cases, operationally infeasible.

Silvicultural prescriptions are often written and implemented in terms of specific forest structural elements such as individual trees or patches (e.g., “thin to a residual density of 150 trees/ha” or “leave one, 0.1 ha unthinned skirt per hectare”). Thus, a method of characterizing spatial patterns in terms of discrete groups of trees, rather than frequency distributions of intertree spacing or departure from a null spatial model, should be useful in the design of restoration thinning prescriptions.

In this study we examine the spatial patterns of overstory trees in several mesic late-successional conifer forests of the Pacific Northwest. Residual trees left following restoration thinning treatments in these forests are intended to become the initial cohort of overstory trees in the target late-successional (restored) stand structure. Thus, information about spatial patterns of overstory trees in late-successional forests will help managers ensure that restoration thinning prescriptions achieve their intended result. Our study proceeds in two stages. First, we characterize patterns of overstory tree spacing in five late-successional forests using the clustering algorithm of Plotkin et al. (2002). Second, we determine whether the spatial pattern of residual trees created by spacing-based restoration thinning treatments differs significantly from the spatial pattern of overstory trees in late-successional forests. Specifically, we test the null hypothesis that spatial patterns of overstory trees in five different mesic late-successional conifer forests are not significantly different from those created by simulated restoration thinning prescriptions that include a minimum intertree spacing rule. For sites characterized by the presence of the long-lived early-seral-dominant Pseudotsuga menziesii (Mirb.) Franco we repeated these analyses using only overstory Pseudotsuga stems to examine the spatial patterns of an overstory species that does not typically self-replace in late-successional forests.

**Methods**

**Study area**

The study sites are situated within Tsuga heterophylla Zone and Abies amabilis Zone forests in the western Washington Cascade Range. None of the study forests have experienced silvicultural manipulations. The Tsuga heterophylla Zone is the most extensive forest vegetation type in western Washington and Oregon, occurring on mesic, temperate sites below about 1000 m (Franklin and Dyrness 1988). Total precipitation ranges from about 1500 to 3000 mm, falling primarily as winter rains with transient snowfall. Mean annual temperatures are about 8 to 11 °C. Tsuga heterophylla Zone forests are equivalently termed Pseudotsuga forests, reflecting the early-seral dominance and long-lasting presence of P. menziesii in these forests (Franklin et al. 2002). The Abies amabilis Zone, where Abies amabilis (Dougl. ex Loud.) Dougl. ex J. Forbes occurs as the principal late-successional species, occupies middle- and upper-slope sites (about 1000 to 1500 m) in the western Cascade Range (Franklin and Dyrness 1988). Environmental conditions within the Abies amabilis Zone are characterized by cool temperatures (mean annual temperature of about 5 to 6 °C) and heavy precipitation (2000 to 2500 mm annually), with much precipitation falling as winter snow and accumulating to depths of 1000 to 3000 mm (Franklin and Dyrness 1988). We refer to the Abies amabilis Zone and Tsuga heterophylla Zone as Abies forests and Pseudotsuga forests, respectively.

We used previously published data sets to generate maps of overstory tree locations in two late-successional Pseudotsuga forests and three late-successional Abies forests (Table 1). Overstory trees were defined as those trees ≥25 m tall in the Abies plots (Larson and Franklin 2006). We defined overstory trees in the Canopy Crane plot as trees ≥40 m tall based on inspection of tree height distribution. A complete inventory of tree heights was not available for the Yellowjacket Creek plot. However, maximum tree height (~65 m) and diameter (190 cm) in the Yellowjacket Creek plot (Winter et al. 2002a) were similar to max-
The normalized mean cluster size \( \hat{c} \), which is useful for comparing results across patterns of different \( n \), is calculated as:

\[
\hat{c} = \tau/n
\]

The cluster size distribution at various scales is particularly useful, as it provides a quantitative, yet intuitive characterization of spatial heterogeneity.

### Statistical analysis

The \( G \) and \( K \) spatial point pattern statistics (Diggle 2003) were used to test the null hypothesis of no difference between the spatial patterns of overstory trees (all species pooled) in natural late-successional *Abies* forests and *Pseudotsuga* forests and the spatial patterns of trees created by spacing-based restoration thinning in young forests. Statistical analysis of spatial point patterns is based on comparing an empirical test statistic calculated from interpoint distances of the observed pattern to a null distribution of test statistics derived from a set of \( s \) Monte Carlo (MC) simulated spatial point patterns, where point-to-point distances are considered up to some maximum distance \( t_{\text{max}} \) (Diggle 2003). Traditionally, inference is made using a method known as the simulation envelope approach and a null model of complete spatial randomness (CSR; e.g., Kenkel 1988). Unfortunately, the simulation envelope method leads to sharply inflated type-I error rates (Loosmore and Ford 2006), rendering it inappropriate as a method of inference about pattern and scale. Loosmore and Ford (2006) developed a goodness-of-fit test for the \( G \) and \( K \) statistics that provides the expected type-I error performance; their method for inference is used in this present analysis. Briefly, the values of the spatial statistic of interest (\( G \) or \( K \)) over the range of scales examined are reduced to a single summary test statistic, \( u_i \) (eq. 3 in Loosmore and Ford (2006)). Test statistics (\( u \)) are calculated for the observed pattern (\( u_1 \)) and each of the MC simulated patterns (\( u_i; i = 2, \ldots, s \)). A statistical test can then be performed by ranking \( u_i \) against the test statistics for the \( s \) MC simulated patterns.

The nature of our hypothesis required that a null model other than CSR be used, because spacing-based thinning treatments by definition do not create CSR tree patterns. Postrestoration thinning tree spatial patterns in young forests were modeled with a hard-core inhibition spatial point process (simple sequential inhibition, Diggle 2003): locations of points (i.e., trees) are constrained such that no points occur within a specified distance \( t_{\text{min}} \) of each other. This method mimics operational guidelines and contract language for minimum spacing requirements in spacing-based restoration thinning prescriptions (Hunter 2001); e.g., “remove all trees

### Cluster analysis

The clustering algorithm is very straightforward. Trees are members of the same cluster if they are within distance \( t \) of each other. At any value of \( t \) the data set is partitioned into a set of unique clusters. In the case of \( t = 0 \) the number of clusters will equal the number of trees in the pattern. All trees are members of the same single cluster when \( t \) exceeds the maximum nearest neighbor distance in the pattern.

Clusters coalesce and grow in a pairwise fashion: not all trees within the cluster need be within \( t \) of each other; however, all trees in the cluster must link to at least one neighbor within \( t \). For example, if tree I and J are within \( t \) of each other, they are in the same cluster. If tree K is greater than \( t \) from either tree I or J, it forms a separate cluster. However, if a fourth tree is introduced, H, which is within \( t \) of tree J and tree K, the cluster grows to a size of four and now contains trees H, I, J, and K. Refer to Fig. 1 in Plotkin et al. (2002) for a graphical example. There are no constraints on the spatial configuration of the cluster: clusters may take any form as long as a chain of pairwise linkages \( \leq t \) is maintained among the cluster members.

Variation in cluster characteristics and demographics vary with respect to \( t \) provides the basis for spatial pattern characterization at multiple scales. For a given \( t \), the data set will be partitioned into \( m \) distinct clusters, with the size of the individual clusters represented as \( c_1, c_2, \ldots, c_m \). The total number of points in the pattern is then denoted as

\[
n = \sum c_i
\]

Mean cluster size (Plotkin et al. 2002) is then:

\[
\tau = \frac{1}{n} \sum_{i=1}^{m} c_i^2
\]

<table>
<thead>
<tr>
<th>Site</th>
<th>Forest Zone</th>
<th>Age (years)</th>
<th>Elevation (m)</th>
<th>Plot dimensions or size</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sutton Lake</td>
<td><em>Abies amabilis</em></td>
<td>~300</td>
<td>1160</td>
<td>100 m × 100 m</td>
<td>Larson and Franklin 2006</td>
</tr>
<tr>
<td>Sister Rocks</td>
<td><em>Abies amabilis</em></td>
<td>~600</td>
<td>1200</td>
<td>100 m × 100 m</td>
<td>Larson and Franklin 2006</td>
</tr>
<tr>
<td>Mosquito Lake</td>
<td><em>Abies amabilis</em></td>
<td>~300</td>
<td>1110</td>
<td>100 m × 200 m</td>
<td>Larson and Franklin 2006</td>
</tr>
<tr>
<td>Canopy Crane</td>
<td><em>Tsuga heterophylla</em></td>
<td>~500</td>
<td>370</td>
<td>200 m × 200 m</td>
<td>Shaw et al. 2004</td>
</tr>
<tr>
<td>Yellowjacket Creek</td>
<td><em>Tsuga heterophylla</em></td>
<td>~500</td>
<td>700</td>
<td>3.3 ha irregular polygon</td>
<td>Winter et al. 2002b</td>
</tr>
</tbody>
</table>

*According to Franklin and Dyrness (1988).*
within 3.5 m of the target tree”’. The value of $t_{\text{thin}}$ was set to 3.0 m for Abies plots and 4.0 m for Pseudotsuga plots; these values are conservative representations (i.e., more closely spaced) of tree spacing created by typical restoration thinning treatments in both merchantable and nonmerchantable stands of these respective forest types (e.g., Curtis et al. 2000; Curtis 2006). Tree spacing was implemented using pith-to-pith distances in simulations, which is also conservative; tree spacing in actual thinning treatments is usually between the outer radii of tree boles. The number of points in a simulated pattern was set equal to the number of overstory trees in the plot being tested. A null distribution of $n = 1999$ Monte Carlo simulated patterns was used for each test. Edge correction was carried out using the reduced sample method (Loosmore and Ford 2006): points are excluded from the sample when a neighbor point does not occur within a search radius less than the distance to the nearest plot boundary. The 2 ha Mosquito Lake study plot (Table 1) was subdivided into two, 1 ha plots (Mosquito Lake west and Mosquito Lake east) to reduce computation time and memory requirements, which were prohibitively large. Statistical analysis was not conducted for the Yellowjacket Creek plot because the method used (Loosmore and Ford 2006) does not accommodate plots with irregular boundaries.

The value of $t_{\text{max}}$ is user specified based on the spatial scale of the null process to which the observed pattern is compared (see eq. 3 and associated discussion in Loosmore and Ford (2006)). Initially, tests were conducted with $t_{\text{max}} = t_{\text{thin}}$, the scale at which the process of interest — restoration thinning — occurs. Tests were repeated with $t_{\text{max}} = 13.0$ m, the best estimate available for the maximum expected scale of competitive interactions — the ecological process that causes natural self-thinning in Pseudotsuga (Franklin et al. 2002) and Abies (Oliver et al. 1985) forests, and for which restoration thinning is a surrogate — among trees in mesic Pacific Coast conifer forests (Canham et al. 2004). Setting $t_{\text{max}} = 13.0$ m allowed comparisons of tree spatial patterns over the range of scales at which competition and, presumably, natural self-thinning occur.

A second test was conducted in which only Pseudotsuga trees were considered in the Canopy Crane plot. Limiting the analysis to only Pseudotsuga stems provided a more conservative test of the null hypothesis: Pseudotsuga does not self-replace in the absence of major disturbance (Franklin et al. 2002). The shade-tolerant conifers Abies amabilis, Tsuga heterophylla (Raf.) Sarg., and Thuja plicata Donn ex. D. Don, and the moderately shade tolerant species Abies grandis (Dougl. ex D. Don) Lindl. and Abies procera Rehd. can occupy canopy positions in natural late-successional Pseudotsuga forests (Table 2). Closely spaced overstory trees are less likely to be detected when these species are excluded from the analysis.

All analysis was carried out in the statistical program and language R (R Core Development Team, http://cran.r-project.org). We used R source code supplied as an online supplement to Loosmore and Ford (2006) for hypothesis

### Table 2. Overstory tree species composition in the study plots.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sutton Lake</th>
<th>Sister Rocks</th>
<th>Mosquito Lake</th>
<th>Canopy Crane</th>
<th>Yellowjacket Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies amabilis</td>
<td>77.0</td>
<td>171.0</td>
<td>181.0</td>
<td>1.0</td>
<td>—</td>
</tr>
<tr>
<td>Abies grandis</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>3.0</td>
<td>—</td>
</tr>
<tr>
<td>Abies procera</td>
<td>6.0</td>
<td>—</td>
<td>—</td>
<td>0.3</td>
<td>—</td>
</tr>
<tr>
<td>Pseudotsuga menziesii</td>
<td>3.0</td>
<td>—</td>
<td>1.0</td>
<td>34.0</td>
<td>13.9</td>
</tr>
<tr>
<td>Thuja plicata</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>11.0</td>
<td>9.1</td>
</tr>
<tr>
<td>Tsuga heterophylla</td>
<td>78.0</td>
<td>21.0</td>
<td>8.0</td>
<td>32.3</td>
<td>63.6</td>
</tr>
<tr>
<td>Tsuga mertensiana</td>
<td>51.0</td>
<td>—</td>
<td>35.0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Total</td>
<td>215.0</td>
<td>192.0</td>
<td>225.0</td>
<td>81.5</td>
<td>86.7</td>
</tr>
</tbody>
</table>

**Note:** Overstory trees are defined as trees $\geq 25$ m tall for the Sutton Lake, Sister Rocks, and Mosquito Lake sites (Larson and Franklin 2006); trees $\geq 40$ m tall for the Canopy Crane site; and trees $\geq 45$ cm DBH for the Yellowjacket Creek site. See Methods for further explanation.
testing with the G and K point pattern statistics. We developed R source code to implement the cluster algorithm and provide it as a supplement to this present article.3

Results

Cluster analysis

The shape of the normalized mean cluster size curve was similar among the three Abies plots (Fig. 1): normalized mean cluster size was very small up to about t = 5 m. From 5 to 10 m, however, the mean cluster size rose sharply, approaching the maximum cluster size. This transition marks the critical distance \( t_{crit} \) known as the “percolation threshold” (Plotkin et al. 2002), which is the scale at which trees transition from being primarily arranged in many small clusters to one single large cluster. This transition occurred consistently at about 7 to 8 m in the Abies plots. In other words, the majority of overstory trees had multiple neighbors within about 8 m, such that the trees formed a single or few large cluster(s).

Normalized mean overstory tree (all species pooled) cluster size increased with distance in the Pseudotsuga plots, but the scale of pattern differed from that observed in the Abies plots. Overstory trees in the both the Canopy Crane and Yellowjacket Creek plots were arranged such that \( t_{crit} \) was relative larger than that in the Abies plots, about 13 m, and the transition from many small to a few large clusters occurred at larger distances and over a greater range, from about 8 to 15 m (Fig. 2). When only P. menziesii trees were considered in the Canopy Crane and Yellowjacket Creek plots, the transition from small to large clusters occurred at larger distances and over a greater range, from about 7 to 43 m (Fig. 2). Conspecific P. menziesii clusters coalesced and grew relatively slowly until \( t_{crit} \) was reached at about 24 m in the Canopy Crane plot and 33 m in the Yellowjacket Creek plot (Fig. 2). The larger \( t_{crit} \) in the Yellowjacket Creek plot likely reflects the relatively lower density of P. menziesii trees in the Yellowjacket Creek plot (13.9 trees/ha) compared with that in the Canopy Crane plot (34.0 trees/ha): on average, P. menziesii trees should be spaced further apart in the Yellowjacket Creek plot.

The distribution of trees among clusters of different sizes at a given distance (Tables 3 and 4) is perhaps of greatest relevance to informing the design of restoration thinning treatments. In the three Abies plots 64.9% to 71.9% of overstory trees occurred in single-tree clusters at a distance of \( t_{thin} \) (3.0 m). However, multitree clusters were present at scales as small as 1 m in the Mosquito Lake plot and 2 m in the Sutton Lake and Sister Rocks plots (Table 3). Overstory trees occurred in clusters of three to six or more trees at a distance of \( t_{thin} \) in the Abies plots (Table 3). Similarly, only 73.3% of overstory trees in the Canopy Crane plot and 74.1% of overstory trees in the Yellowjacket Creek plot occurred in single-tree clusters at \( t_{thin} \) (4.0 m), and clusters as large as four trees were observed at \( t_{thin} \) (Table 4). Pseudotsuga menziesii trees were less likely to belong to conspecific multitree clusters at \( t_{thin} \); however, 8.8% and 4.3% of P. menziesii trees belonged to a conspecific cluster of size = 2 (i.e., composed of two trees) (Table 4).

The prevalence of multitree clusters at scales \( \leq t_{thin} \) explains the results from the statistical tests. Spacing-based thinning treatments eliminate multitree clusters at scales \( \leq t_{thin} \).

Multitree clusters at \( t_{thin} \) exhibited variable spatial patterns in terms of distribution of clusters across the plot area in the intensively studied stands (Fig. 3). Multitree clusters at \( t_{thin} \) were distributed throughout the plot area in all three Abies plots (Figs. 3b–d). Considerable heterogeneity was apparent in the distribution of multitree clusters in the Canopy Crane plot: a patch of approximately 1 ha lacked multitree clusters (Fig. 3a). Multitree clusters were distributed throughout the Yellowjacket Creek plot (data not shown).

3 Supplementary data for this article are available on the journal Web site (http://cjfr.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3849. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.
**Statistical analysis**

The spatial pattern created by simulated spacing-based restoration thinning prescriptions was statistically different from the spatial pattern of overstory trees (all species pooled) in *Abies amabilis* Zone stands occurring in clusters of different sizes at various spatial scales. The null hypothesis was rejected ($P \leq 0.009$) when $t_{\text{thin}} = t_{\text{max}}$ with both the $G$ and $K$ spatial statistics (Table 5). The spatial patterns of trees created by simulated spacing-based restoration thinning treatments remained significantly different from the spatial pattern of overstory trees in all plots when tests were repeated with $t_{\text{max}} = 13.0$ m ($P \leq 0.014$).

The spatial pattern trees in the Canopy Crane plot remained statistically different from patterns created by simulated spacing-based restoration thinning prescriptions when only *P. menziesii* trees were considered (Table 5). The null hypothesis was rejected with both the $G$ and $K$ spatial statistics ($P \leq 0.001$) when $t_{\text{thin}} = t_{\text{max}}$, and again when $t_{\text{max}} = 13.0$ m ($P \leq 0.003$).

**Discussion**

**Development and detection of spatial structure within forest patches**

Plant population ecology theory predicts that self-thinning in plant populations due to competitive mortality may lead to the development of spatial uniformity (or, equivalently, spatial regularity) in the distribution of plants surviving the self-thinning process (Greig-Smith 1957; Pielou 1962). Spatial uniformity is rare in natural plant populations (Greig-Smith 1957; Adler 1996), although some empirical studies have found that self-thinning leads to the development of modest spatial regularity in the arrangement of the trees surviving competitive mortality (e.g., Kenkel 1988).

Natural stand development often includes a self-thinning phase in *Pseudotsuga* (Oliver and Larson 1996; Franklin et al. 2002) and *Abies* forests (Oliver et al. 1985). A tendency towards spatial regularity in the distribution of overstory trees has been observed in mesic conifer forests of the Pacific Coast region (Stewart 1986; He and Duncan 2000;
Van Pelt and Franklin 2000; Zenner 2004) as well as in other forest types (e.g., Kenkel 1988; Oliver and Larson 1996). In a previous study of the Canopy Crane plot, trees ≥76 cm DBH were more regularly spaced than expected at distances of 0 to 15 m based on a null model of spatial randomness (North et al. 2004).

These earlier findings seem to contrast with results from the statistical tests (Table 5) reported in this present study, which indicate that overstory tree spatial patterns in the study plots are not regular. What might explain this apparent discrepancy? It is critical to note that the prior studies and this present study did not use similar spatial null models. The previous studies demonstrated that the spatial pattern of overstory trees in their study plots departed from (rejection of) a null model of spatial randomness, i.e., the patterns observed in these studies were more spatially uniform than the random expectation. However, the authors did not confirm strict regular (i.e., hard-core inhibition) tree spatial patterns.

<table>
<thead>
<tr>
<th>Cluster size (trees/cluster)</th>
<th>Scale (m)</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>≥6</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Canopy Crane</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>81.5 (100.0)</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>77.0 (94.5)</td>
<td>2.3 (5.5)</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>70.0 (85.9)</td>
<td>5.0 (12.3)</td>
<td>0.5 (1.8)</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>59.8 (73.3)</td>
<td>7.0 (17.2)</td>
<td>2.3 (8.3)</td>
<td>0.3 (1.2)</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>50.8 (62.3)</td>
<td>9.5 (23.3)</td>
<td>2.5 (9.2)</td>
<td>0.8 (3.7)</td>
<td>0.3 (1.5)</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>37.8 (46.3)</td>
<td>10.8 (26.4)</td>
<td>3.8 (13.8)</td>
<td>1.8 (8.6)</td>
<td>0.5 (3.1)</td>
<td>0.3 (1.8)</td>
<td>—</td>
</tr>
<tr>
<td>7</td>
<td>29.0 (35.6)</td>
<td>9.5 (23.3)</td>
<td>4.5 (16.6)</td>
<td>1.0 (4.9)</td>
<td>1.3 (7.7)</td>
<td>1.5 (11.9)</td>
<td>—</td>
</tr>
<tr>
<td>8</td>
<td>20.0 (24.5)</td>
<td>8.3 (20.2)</td>
<td>3.5 (12.9)</td>
<td>1.5 (7.4)</td>
<td>0.8 (4.6)</td>
<td>2.3 (30.4)</td>
<td>—</td>
</tr>
<tr>
<td>9</td>
<td>13.3 (16.3)</td>
<td>5.8 (14.1)</td>
<td>2.8 (10.1)</td>
<td>0.8 (3.7)</td>
<td>1.5 (9.2)</td>
<td>2.5 (46.6)</td>
<td>—</td>
</tr>
<tr>
<td>10</td>
<td>8.5 (10.4)</td>
<td>3.8 (9.2)</td>
<td>2.5 (9.2)</td>
<td>0.8 (3.7)</td>
<td>1.5 (9.2)</td>
<td>3.3 (58.3)</td>
<td>—</td>
</tr>
<tr>
<td><strong>Yellowjacket Creek</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>86.7 (100.0)</td>
<td>—</td>
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<td>2.1 (30.4)</td>
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By using a null model of hard-core inhibition we were able to test, and reject (Table 5), the upper limit on the degree of spatial regularity potentially present in the tree patterns (at a scale of \( t_{\text{thin}} \)). However, the cluster analysis indicates that some spatial regularity is apparent in the spatial distribution of overstory trees (Tables 3 and 4). Between 65% and 72% of overstory trees in Abies forests occurred as single trees (cluster size = 1) at a scale of 3 m. Pseudotsuga forests exhibited a slightly greater degree of regularity: 73% to 74% of overstory trees occurred as single trees at 4 m. Our results from both forest types, in combination with those of past studies, provide a more precise characterization of the spatial structure of overstory trees. Overstory tree spatial patterns appear to be best characterized by the gradient between spatial randomness and hard-core inhibition. This type of pattern is known as soft-core inhibition (Diggle 2003). Future studies that parameterize soft-core inhibition spatial point process models, such as the Strauss inhibition process, may allow for even more precise characterization of pattern intensity and scale (see Kenkel (1993) for an ecological application of the Strauss process).

Our results and those of past studies in similar forests are strong evidence that competition and subsequent nonrandom mortality influence the spatial distribution of overstory trees (Kenkel 1988). However, the results from the cluster analysis indicate that the intensity of the past self-thinning was not so great as to create a strict uniform pattern, the type of pattern created by spacing-based thinning treatments. Approximately one-third and one-quarter of overstory trees in Abies and Pseudotsuga forests, respectively, occur in multitree clusters at \( t_{\text{thin}} \). We cannot determine the precise cause of this heterogeneity. Several factors, such as favorable microsites or edaphic conditions; initial tree spacing or density; localized disturbance that released tree clusters from other neighboring competitors; or even resource sharing via root grafting or common mycorrhizal networks (Simard et al. 1997), are potential causes of the observed heterogeneity. Our results support the idea that natural forest development
and the resultant tree spatial patterns integrate the relatively
deterministic process of competitive self-thinning, which
drives the development of spatial uniformity, and other stoch-
astic factors that provide for the retention of spatial heter-
ogeneity in the form of tree clusters at small spatial scales.

What causes some forests to have many multitrue clusters of
overstory trees at small scales, while others have rela-
tively few? While the Abies and Pseudotsuga forests we
studied exhibited similar general trends, there are some con-
spicious differences in the results. The percolation threshold
was reached at smaller scales in Abies forests (Fig. 1) than
in Pseudotsuga forests (Fig. 2). The difference in scale be-
 tween the Pseudotsuga and Abies plots is likely due to the
relatively larger stature of the trees in the overstory of the
Pseudotsuga plots (Van Pelt and North 1996; Winter et al.
2002a, 2002b; Shaw et al. 2004; Larson and Franklin
2006). Additionally, more overstory trees occurred as mem-
ers of multitrue clusters at \( t_{\text{thin}} \) in Abies forests than in
Pseudotsuga forests (Tables 3 and 4). One possible expla-
nation for this difference is that there may be relatively less
intense competition and less complete self-thinning —
leaving more small scale aggregation — in the Abies forests.
However, this explanation does not seem likely because de-
veloping Abies stands have characteristically high stem den-
sities and a protracted (100–300 years) self-thinning stage
(Long 1976; Packee et al. 1982; Oliver et al. 1985). A more
likely explanation for the higher degree of clustering in the
Abies forests is the high degree of crown-level morphologi-
cal plasticity of A. amabilis, which allows for asymmetrical
crown development and increased tree survival under highly
aggregated initial tree spatial patterns (Sorrensen-Cothern, et
al. 1993).

Because natural self-thinning influences spatial patterns at
small scales (Kenkel 1988), it follows that stands with
different initial densities should exhibit divergent patterns
of clustering at scales \( \leq t_{\text{thin}} \). On a relative frequency (i.e.,
percentage) basis, one would expect multitrue clusters at
small scales to be more common in stands that developed
at low initial densities than in stands that developed at
high initial density. However, our analysis indicates that
high initial stand density does not necessarily lead to the
elimination of multitrue clusters; the Yellowjacket Creek
Pseudotsuga plot had a high initial density and formed a
closed canopy by stand age 40 years (Winter et al. 2002a).
Yet, 14.3% of P. menziesii stems in the Yellowjacket Creek
stand had their nearest conspecific neighbor within 4.0 m at
stand age 500 years. It is also necessary to determine how
non-stand-replacing disturbances influence the spatial dis-
tribution of overstory trees. The Yellowjacket stand experi-
cenced multiple canopy-thinning disturbances during its
500 year life (Winter et al. 2002b). Partial fire disturbance
is known to influence the spatial structure of Pseudotsuga
forests (Goslin 1997); however, the influence of non-stand-
thinning fire on the formation and persistence of multitrue
clusters at small scales has not been studied. Future studies
that incorporate permanent-plot and stand-reconstruction
 techniques will be necessary for identifying specific mecha-
nisms of spatial pattern formation throughout natural forest
stand development.

### Restoration thinning treatments in Abies and
Pseudotsuga forests

Spacing-based thinning prescrip tions eliminate pairs and
groups of closely spaced overstory trees (i.e., the solid black
symbols in Fig. 3), components of natural forest structure
(Fig. 4) that are not quickly replaced via stand development
processes. Spacing between residual post-thinning overstory
trees will increase through time as members of the overstory
cohort die. New trees must successfully establish and recruit
into the overstory to redevelop closely spaced pairs and

<table>
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<th>Site</th>
<th>( n_{\text{points}} )</th>
<th>( t_{\text{thin}} ) (m)</th>
<th>( t_{\text{max}} ) (m)</th>
<th>( P_{G} )</th>
<th>( P_{K} )</th>
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<td>145 4.0 13.0</td>
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<td>&lt;0.001</td>
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</table>

Note: Results shown are for tests of the null hypothesis of no difference between tree spatial pat-
terns created by simulated spacing-based restoration thinning treatments (see Methods) and observed
spatial patterns of overstory trees in late-successional conifer forests. The small \( P \) values for tests con-
ducted with both the \( G \) and \( K \) statistics indicate that the null hypothesis can be rejected.

- Number of points in the pattern.
- Minimum spacing distance between points in the simulated thinning patterns.
- Maximum scale considered for the goodness-of-fit tests.
- \( P \) value of the goodness-of-fit test with the \( G \) statistic.
- \( P \) value of the goodness-of-fit test with the \( K \) statistic.
groups of overstory trees in stands treated with spacing-based restoration thinning treatments.

Coastal *P. menziesii* does not readily regenerate under closed-canopy conditions (Herman and Lavender 1990). Recovery of closely spaced *P. menziesii* trees thus requires a stand-replacing or partial stand disturbance, allowing the establishment of a new cohort (e.g., Larson and Franklin 2005) and successful recruitment into the overstory, a process that requires many decades or centuries of forest development (Churchill 2005; Zenner 2005).

*Abies amabilis* and the associated species *Tsuga heterophylla* and *Tsuga mertensiana* (Bong.) Carrière are shade tolerant and capable of regeneration in the absence of significant overstory disturbance (Lertzman 1992). Seedlings of shade-tolerant tree species may establish and then persist in a suppressed state with virtually no height growth for several decades (Antos et al. 2005). Recruitment into the canopy occurs in canopy gaps (Lertzman 1992; Parish and Antos 2004); seedlings respond to small-scale disturbance by increasing height (Van Pelt and Franklin 1999) and diameter (Winter et al. 2002a) growth. However, understory and midstory trees are spatially segregated from overstory trees in old-growth *Abies* forests (Larson and Franklin 2006), suggesting that recruitment from subordinate height classes into the overstory class is not likely to occur in locations near established overstory trees. Consequently, redevelopment of closely spaced pairs and groups of overstory trees in *Abies* forests will likely proceed via gap-phase regeneration, a process that also requires many decades or centuries.

Restoration thinning treatments in both commercial and precommercial stands will be more effective at creating the fine-scale spatial patterns characteristic of late-successional forest structure if they are modified to allow for the retention of closely spaced clusters of trees. Multitree clusters occurred throughout the study plots (Fig. 3), indicating that the fine-scale spatial patterns characteristic of late-successional overstory trees cannot be achieved by leaving one or less unthinned skip per hectare (e.g., Roberts et al. 2007); retention of closely spaced tree clusters within thinned areas will be necessary. On average, 32.7% of overstory trees in *Abies* plots and 26.3% of overstory trees in *Pseudotsuga* plots occurred as members of multitree clusters at scales of 3.0 and 4.0 m, respectively. The data presented in Tables 3 and 4 can be used as a rough guideline for how many clusters of different sizes to retain per hectare in *Abies* and *Pseudotsuga* forests, respectively, if site-specific data on spatial patterns of late-successional overstory trees are not available.

Restoration thinning treatments that release individual trees as well as multitree clusters promote characteristic late-successional tree spatial patterns at the within-patch scale. This formulation of restoration thinning explicitly incorporates conservation of existing small-scale spatial heterogeneity within the treatment area as a core element of the silvicultural design process. This approach extends current restoration thinning practices that emphasize introduction of patch-scale spatial heterogeneity with “skips”, “gaps”, and variable thinning densities throughout the stand. Restoration thinning prescriptions will be most effective at creating desired spatial patterns when they do not include minimum tree spacing guidelines, and when they contain clear, operationally meaningful descriptions of the desired spatial patterns.
Acknowledgements

Conversations with Alina Cansler, Jerry Franklin, Rolf Gersonde, Amy LaBarge, and James Lutz helped clarify our ideas about relationships between restoration thinning and forest spatial structure. We thank the Wind River Canopy Crane Research Facility and Linda Winter for sharing data. Jon Bakker, Alina Cansler, Andy Carey, James Freund, Van Kane, Bert Loosmore, Bob Van Pelt, Linda Winter, and two anonymous reviewers provided constructive comments that greatly improved this paper.

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