Spatial Relationship of Biomass and Species Distribution in an Old-Growth Pseudotsuga-Tsuga Forest

Jiquan Chen, Bo Song, Mark Rudnicki, Melinda Moeur, Ken Bible, Malcolm North, Dave C. Shaw, Jerry F. Franklin, and Dave M. Braun

ABSTRACT. Old-growth forests are known for their complex and variable structure and function. In a 12-ha plot (300 m × 400 m) of an old-growth Douglas-fir forest within the T. T. Munger Research Natural Area in southern Washington, we mapped and recorded live/dead condition, species, and diameter at breast height to address the following objectives: (1) to quantify the contribution of overstory species to various elements of aboveground biomass (AGB), density, and basal area, (2) to detect and delineate spatial patchiness of AGB using geostatistics, and (3) to explore spatial relationships between AGB patch patterns and forest structure and composition. Published biometric equations for the coniferous biome of the region were applied to compute AGB and its components of each individual stem. A program was developed to randomly locate 500 circular plots within the 12-ha plot that sampled the average biomass component of interest on a per hectare basis so that the discrete point patterns of trees were statistically transformed to continuous variables. The forest structure and composition of low, mediate, and high biomass patches were then analyzed. Biomass distribution of the six major species across the stand were clearly different and scale- dependent. The average patch size of the AGB based on semivariance analysis for Tsuga heterophylla, Abies amabilis, A. grandis, Pseudotsuga menziesii, Thuja plicata, and Taxus brevifolia were 57.3, 81.7, 37, 114.6, 38.7, and 51.8 m, respectively. High biomass patches were characterized by high proportions of T. heterophylla and T. plicata depending on spatial locations across the stand. Low AGB patches had high densities of A. amabilis and T. brevifolia. We presented several potential mechanisms for relating spatial distribution of species and biomass, including competition, invasion and extinction, disturbance, and stand dynamics. Clearly, future studies should be developed to examine the details of how each process alters the spatial patterns of tree species with sound experimental designs and long-term monitoring processes at multiple scales. For. Sci. 50(3):364–375.

Key Words: Spatial pattern analysis, canopies, old-growth, aboveground biomass (AGB), semivariogram, Douglas-fir, WRCCRF.
In the study of ecological theory, the concept of scale is critical in understanding the organization and function of ecosystems. Scale refers to the size or magnitude of a phenomenon being observed, and it can vary across multiple levels, from microscopic to global. The choice of scale can significantly influence the interpretation of ecological patterns and processes. This is because ecological systems are inherently scale-dependent, with interactions and processes occurring at various spatial and temporal scales.

For example, at the microscale, interactions such as photosynthesis, respiration, and nutrient cycling are highly localized. At the landscape scale, processes like population dynamics, species distribution, and ecosystem productivity are influenced by the arrangement of patches and corridors. At the macroscale, environmental gradients, climate zones, and biogeographic patterns shape the distribution of species and ecosystems.

Understanding the scales of ecological processes is crucial for conservation and management strategies. It helps in identifying key areas for protection, predicting the impacts of disturbances, and designing effective restoration and reforestation efforts. The scale at which an ecological process is observed can determine whether it is considered a local, regional, or global phenomenon, and this has implications for how it is managed and protected.

acknowledgments: Funding for this project was partially provided by the USDA Forest Service Pacific Northwest Experimental Station (PNW94-0541), the Earthwatch Institute and the Durfee Foundation’s Student Challenge Awards Program, the Western Regional Center for Global Environmental Change of the Department of Environment, and the Charles Bullard Fellowship of the Harvard University (to J. Chen). We thank the following individuals for their help in data collection: Meredith Allen, Joel Benjamin, Joseph Brown, Hannah Chapin, Tim Crosby, Maria Garret, Matthew Madden, Heather Michaud, Cesary Mudrowicz, Scott Ramsburg, Angelia Smith, Lucia Stoisor, Julia Svoboda, and Beata Ziolkowska. Dee Robbins contributed a significant amount of time and thought to support our Earthwatch expeditions in 1997 and 1998. We thank the Wind River Canopy Crane Research Facility, The Gifford Pinchot National Forest, and Elizabeth Freeman for installation of the four hectares surrounding the canopy crane. Hiroaki Ishii and Elizabeth Freeman also participated in early fieldwork. Sari Saunders, Eugenie Euskirchen, Kim Arbington, Mary Bresee, Jeffrey Parker, and two anonymous reviewers provided valuable suggestions to improve the manuscript.
(PSME) range from 250 to >450 years (Franklin and War- ning 1980). They are slowly dying out of the stand and are being replaced by Tsuga heterophylla Raf., Sarg. (TSHE), Thuja plicata Donn (THPL), Abies amabilis (Dougl.) Forbes (ABAM), and Abies grandis (Dougl.) Lindl (AGBR). Also disappearing from the stand is Abies procera Rehd. (ABPR). Another pioneer species, Pinus monticola Dougl. Ex D. Don. (PIMO), was once more prevalent, but is disappearing due to a combination of blister rust (Ronartium ribicola Fischer)—an introduced fungal pathogen from Eurasia—and a native bark beetle—Dendroctonus ponderosae Hopkins—(Franklin and DeBell 1988). Dominant shrubs include Acer circinatum Pursh, Gaultheria shallon Pursh, Berberis nervosa Pursh, and Vaccinium parvifolium Smith. Dominant herbs, though not as abundant as shrubs, include Achlys triphylla (Smith) DC., Vancouveria hexandra (Hook.) Morr. & Dec., Pteridium aquilinum (L.) Kuhn, Linnaea borealis L., and Xerophyllum tenax (Pursh) Nutt. In 1995, an 85-m tall construction crane known as Wind River Canopy Crane Research Facility (WRCCRF) was installed in the western edge of the RNA for conducting ecological investigations within forest canopies.

**Data Collection**

A 4-ha square plot was established by a professional survey consulting firm in 1994 before the installation of the canopy crane. The plot was divided into a 25-m grid and marked with 50-cm reinforcement bars and aluminum caps. The WRCCRF researchers tagged all trees ≥5 cm in diameter at breast height (dbh: 1.37 m above the ground) with a precoded aluminum tag, tallied live/dead condition, and measured the coordinates of each tree within the plot, utilizing a Criterion 4000 survey laser station and the grid points marking the plot corners (Freeman 1997). Tree base elevations were calculated based on inclination measurements using the Criterion, and the elevations of the grid points that were measured in 1996 were determined using a total survey station (Wild TC600 total survey station). Using a similar protocol in 1996, we added another 4-ha plot adjacent to the west boundary. An additional 100 × 400-m plot (4-ha) was added along the southern border of the combined 8-ha in the summers of 1996 and 1997 for a total of 12-ha (Figure 1). After mapping all trees, we measured any cumulative surveying error by remeasuring original grid points and found <15 cm of difference on average.

**Biomass Distribution and Geostatistical Analysis**

Unlike tree distributions across a stand, which are discrete point patterns, spatial distribution of volume and biomass could be considered as continuous variables. Their spatial patterns can be best described using methods such as spectral (Cressie 1993) or wavelet analysis (Bradshaw and Spies 1992, Chen et al. 1999). Three steps were taken to quantitatively characterize the spatial distributions of AGB, including biomass of stem wood and bark and live branches, and foliage biomass. We applied dbh-height models (Song 1998, Ishii et al. 2000) to calculate tree height by species based on field-measured dbh. Heights of PIMO and ABPR

![Figure 1](image-url)
were calculated based on models for PSME and AGBR, respectively, because of the absence of dbh-height models in the literature. In our first step, using predicted heights and measured dbh, we calculated basal area (BA, m$^2$) and applied empirical models of Grier and Logan (1977) and Gholz et al. (1979) to calculate foliage biomass (FB, Mg), live branch biomass (Mb), and total stem biomass (Mg) for each tree within the plot. No adjustment was made for wood decay in biomass calculations.

In the second step, a FORTRAN program was developed to simulate randomly located circular plots within the 12-ha plot that sampled the average biomass component of interest on a per hectare basis (e.g., Mg.ha$^{-1}$). In this way, the discrete point patterns of trees were statistically transformed to continuous variables. The program was developed to allow for a variable plot size and number of samples. Our preliminary analysis of comparisons of changes in biomass with plot size and number of samples indicated that a 30-m diameter sample plot, and 500 total sample plots, were sufficient to capture the spatial variability while not being significantly ($P = 0.05$) influenced by the local details. Using these input variables, both the average and number of samples for each of the 500 sample plots as well as plots’ coordinates were generated for biomass of each species, FB of all species, total AGB of all species, and BA of individual species as well as that of all the species.

In the third step, we performed semivariance analyses (Cressie 1993) to quantify the spatial autocorrelation of the continuous variables. A maximum lag distance of 150 m (i.e., half of the minimum plot dimension) in 5-m increments was applied in the semivariance analysis. Several variogram models, including exponential, linear, and spherical, were tested to fit changes in semivariance with distance. The spherical models for each variable were presented in this article to allow for consistent comparisons. The values of nugget, sill, range, and correlation coefficient of determination ($R^2$) of the spherical models (Cressie 1993) were calculated and recorded for further analysis in kriging.

One-meter resolution block kriging was performed to emphasize the local variation around the sampling plots. The kriged maps were divided into three zones of biomass: high (4th quartile), medium (2nd and 3rd quartile), and low (1st quartile). For visualizing the spatial patterns of biomass of individual species, five equal bands were used for clear graphical presentations in the illustration. The biomass zones were intersected with the stem-mapped data set to isolate trees falling in each zone. Species composition and density within each biomass zone were calculated using the intersected data to examine the coherent relationships between species distribution and production (e.g., AGB and BA) across the stand.

**Results**

**Forest Structure**

The *Pseudotsuga-Tsuga* old-growth forest had an average density of 437 trees.ha$^{-1}$ and an average basal area of 72 m$^2$.ha$^{-1}$ (Table 1). Diameter frequency distributions for TSHE, ABAM, TABR, and AGBR were skewed toward smaller diameter classes in contrast to PSME (and to some extent THPL), which displayed a more linear distribution (Table 1). Maximum dbh for the above six species ranged from 80 to 187 cm. TSHE and TABR accounted for a total of 77% of the stand density, with TSHE representing over half of the total and TABR another 22%. By BA, TSHE and PSME accounted for 88% of the stand, with TSHE accounting for 44% of the BA. Obvious spatial patterns of tree distribution were visible (Figure 1), with TABR along the ephemeral stream on the north side of the plot, THPL in the northeast quarter of the plot, PSME in the central part of the plot with less PSME in the southwest quadrant, TSHE across the whole plot, and ABAM, AGBR, and ABR aggregated in several clusters (Figure 1).

**Biomass Distribution and Species Composition**

Overall, about 86% of the AGB of the major tree species was distributed as stem wood (72%) and branches (14%).

### Table 1. Species composition and diameter distribution of an old-growth Douglas-fir forest in the T.T. Munger Research Natural Area, Washington. All live trees greater than 5.0 cm in diameter at breast height (dbh) were stem-mapped and recorded by species and dbh between 1994 and 1999. Stand density (D, trees.ha$^{-1}$) and basal area (BA, m$^2$.ha$^{-1}$) were calculated using all trees within a 12-ha plot ($n = 5,238$). Values in the parenthesis indicate species composition (%) of the stand based on D or BA.

<table>
<thead>
<tr>
<th>dbh class (cm)</th>
<th>&lt;20</th>
<th>20–40</th>
<th>40–60</th>
<th>60–80</th>
<th>80–100</th>
<th>100–120</th>
<th>120–140</th>
<th>&gt;140</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>PSME</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>0.66</td>
<td>2.92</td>
<td>8.08</td>
<td>11.08</td>
<td>5.58</td>
<td>2.75</td>
<td>31.08</td>
<td>7.1</td>
<td></td>
</tr>
<tr>
<td>BA</td>
<td>0.24</td>
<td>1.14</td>
<td>5.21</td>
<td>10.44</td>
<td>7.24</td>
<td>4.92</td>
<td>29.19</td>
<td>40.6</td>
<td></td>
</tr>
<tr>
<td>TSHE</td>
<td>121.17</td>
<td>50.58</td>
<td>26.33</td>
<td>25.92</td>
<td>15.17</td>
<td>2.42</td>
<td>0.33</td>
<td>241.92</td>
<td>55.3</td>
</tr>
<tr>
<td>BA</td>
<td>1.13</td>
<td>3.37</td>
<td>5.14</td>
<td>9.96</td>
<td>9.31</td>
<td>2.12</td>
<td>0.42</td>
<td>31.64</td>
<td>44.0</td>
</tr>
<tr>
<td>ABAM</td>
<td>41.17</td>
<td>4.08</td>
<td>2.08</td>
<td>0.50</td>
<td>0.08</td>
<td></td>
<td></td>
<td>47.92</td>
<td>11.0</td>
</tr>
<tr>
<td>BA</td>
<td>0.26</td>
<td>0.26</td>
<td>0.39</td>
<td>0.18</td>
<td>0.18</td>
<td></td>
<td></td>
<td>1.14</td>
<td>1.6</td>
</tr>
<tr>
<td>THPL</td>
<td>3.58</td>
<td>2.08</td>
<td>1.50</td>
<td>2.08</td>
<td>1.58</td>
<td>1.17</td>
<td>1.25</td>
<td>0.83</td>
<td>14.08</td>
</tr>
<tr>
<td>BA</td>
<td>0.04</td>
<td>0.15</td>
<td>0.32</td>
<td>0.86</td>
<td>1.04</td>
<td>1.09</td>
<td>1.61</td>
<td>1.75</td>
<td>6.85</td>
</tr>
<tr>
<td>TABR</td>
<td>82.50</td>
<td>13.50</td>
<td>1.00</td>
<td>0.08</td>
<td>0.08</td>
<td></td>
<td></td>
<td>96.4</td>
<td>22.1</td>
</tr>
<tr>
<td>BA</td>
<td>0.95</td>
<td>0.73</td>
<td>0.16</td>
<td>0.03</td>
<td>0.05</td>
<td></td>
<td></td>
<td>1.92</td>
<td>2.7</td>
</tr>
<tr>
<td>ABGR</td>
<td>0.67</td>
<td>1.75</td>
<td>0.33</td>
<td></td>
<td>0.17</td>
<td></td>
<td></td>
<td>4.08</td>
<td>0.9</td>
</tr>
<tr>
<td>BA</td>
<td>0.01</td>
<td>0.10</td>
<td>0.35</td>
<td>0.12</td>
<td>0.09</td>
<td></td>
<td></td>
<td>0.67</td>
<td>0.9</td>
</tr>
<tr>
<td>Other</td>
<td>0.25</td>
<td>0.08</td>
<td>0.33</td>
<td>0.25</td>
<td>0.25</td>
<td></td>
<td></td>
<td>1.17</td>
<td>0.3</td>
</tr>
<tr>
<td>BA</td>
<td>0.02</td>
<td>0.02</td>
<td>0.12</td>
<td>0.14</td>
<td>0.23</td>
<td></td>
<td></td>
<td>0.53</td>
<td>0.7</td>
</tr>
<tr>
<td>All</td>
<td>249.17</td>
<td>71.75</td>
<td>33.33</td>
<td>32.17</td>
<td>25.42</td>
<td>14.92</td>
<td>7.17</td>
<td>3.58</td>
<td>437.5 (100)</td>
</tr>
<tr>
<td>BA</td>
<td>2.70</td>
<td>4.64</td>
<td>6.50</td>
<td>12.41</td>
<td>15.87</td>
<td>13.88</td>
<td>9.27</td>
<td>6.67</td>
<td>71.93 (100)</td>
</tr>
</tbody>
</table>

Forest Science 50(3) 2004 367
Several compositional characteristics were related to the distribution of biomass zones in the plot. First, high biomass zones had higher proportions of PSME and THPL, but lower proportions of TSHE and ABAM in both AGB and density (Figure 6). Likewise, low biomass zones were characterized by higher proportions of TSHE and ABAM. TABR biomass was higher in low biomass zones but its density was close to the stand average, suggesting that there are larger TABR trees in the low biomass zones. The biomass and density composition of medium biomass zones of the plot were not always similar to stand average values. These zones had relatively low PSME, THPL, and TABR biomass and density, but higher TSHE and ABAM proportions.

The biomass levels across the stand were also related to the biomass and density of different dbh classes (Tables 3 and 4). The high biomass zones had more PSME trees in all dbh classes, TABR in smaller dbh classes, and THPL in dbh classes larger than 60 cm; and fewer numbers of TSHE and ABAM in all dbh classes (Table 3). Similarly, low biomass zones had higher density of TSHE in smaller dbh classes (<60 cm) but relatively low density of larger TSHE in dbh classes greater than 60 cm. These low biomass zones had more small dbh ABAM trees. Stand density of TABR trees was significantly higher in all dbh classes in the low biomass zones.

Finally, within the stand, biomass zones were formed depending on tree size distribution and species composition (Table 4). For the high biomass zones, there was higher biomass of PSME in all dbh classes and higher THPL biomass in larger dbh classes (>60 cm); but TSHE contributed consistently less in all dbh classes. Medium biomass zones were predominantly characterized by significantly higher proportions of TSHE between 60 and 100 cm in dbh. Based on all species pooled by diameter class, high biomass zones had more biomass from trees >80 cm and lower biomass component from trees < 80 cm. The low biomass zone had higher proportion of biomass contributed by trees <60 cm than did the medium biomass zone.

Discussion

The biomass distribution of individual species and all species support the idea that spatial patterns need to be explored at various scales (Figure 3 and 5). The patch
pattern of biomass of AGBR and THPL were repeated at scales between 37 and 38.5 m (Figure 2, c and e), suggesting a minimum plot size of 40 m needed for adequate estimations of their contribution to the total biomass. However, for ABAM and PSME, their average patch size was 82 and 114 m, respectively (Figure 2, b and d). Clearly, both structure and function of the forest ought to be explored at appropriate scales (Holling 1992) and across a range of scales (Levin 1992). With the above conclusion, we argue that results based on fixed plot size less than 100 m would be very questionable.

The spatial distribution of species and their spatial associations reflected the spatial pattern of biomass (Figure 5). After we converted the discrete stem data to continuous variables of biomass and basal area, geostatistical tools were applied to detect the patchiness of each variable across the stand. Applications of such an approach are not error-free. First, the number and size of sampling plot need to be carefully examined because the means generated based on the above averages will have profound effects on semivariance analysis. Second, semivariance analysis does not help us to reveal underline patterns at multiple scales (Bradshaw and Spies 1992, Cressie 1993). Nevertheless, the formation of biomass patches based on semivariance analysis in this study appeared complex, especially when generating a spatial biomass patterns based on patch pattern of individual species. Each species had a unique biomass patch pattern such as size, shape, and spatial distribution (Figures 2 and

Figure 2. Semivariances of basal area (a), aboveground biomass (b), and foliage biomass (c) for distance up to half of the minimum plot dimension (i.e., 150 m). Five hundred 30-m diameter simulated circular sampling plots were randomly placed within the 12-ha plot to convert the point pattern to a continuous variable on a per hectare basis. Spherical models were used to calculate the range, sill, nugget, and $R^2$ values.
3). From Figure 3, it is clear that the spatial patterns of different species were mostly repulsive, with occasional overlaps. While each patch pattern contributed a different proportion to the overall biomass mosaic, the nonperfect exclusivity of patch patterns of the six species were probably responsible for the reduction in the scale of interaction of all three biomass measurements: BA, AGB, and FB, which ranged between 32 and 46 m (Figure 4). For example, high biomass patch H1 was formed because of high PSME biomass and intermediate TSHE biomass (Figure 3, a and d), while another high biomass patch H2 (Figure 5b) was likely associated with the high proportion of THPL (Figure 3e) and the absence of TSHE (Figure 3a). In both cases, patch size was reduced because of nonperfect exclusivity of multiple patterns in space.

An interesting result of this study was the high variation in biomass distribution across the stand and the distinct species composition for high-to-low biomass zones. The ecological literature suggests that old-growth Douglas-fir forests have high biomass ranging from 800 to 1600 Mg.ha\(^{-1}\) depending on stand location in the larger landscape (e.g., Franklin et al. 1981). The stand biomass of our stand was reported as 830 Mg.ha\(^{-1}\) (see Parker et al., in press). In contrast, the stem map depicts a forest that was not homogeneous, with biomass ranging from 0 to 1600 Mg.ha\(^{-1}\) (Franklin and Waring 1980). TSHE and/or PSME and THPL dominated the high biomass zones, with little overlap between them because the two species showed a clearly repulsive relationship, and low-biomass zones were dominated by mixtures of shade-tolerant species such as TABR and ABAM (Figure 6). These findings were in agreement with other studies (Franklin and Waring 1980, Franklin et
al. 1981) that suggested high biomass stands in broader landscapes in the Pacific Northwest were results of high proportion of PSME and THPL. It appeared that biomass-species relationships for the Douglas-fir forests may hold at any scale ranging from the patch to the landscape. PSME and THPL are long-lived species but will gradually decline relative to TSHE and Abies in the forest over the next 500 years. Due to the close spatial relationships between species composition and biomass, we would expect not only that stand biomass will decrease, but also that a new biomass mosaic will emerge.

The spatial distribution of trees, canopy patch patterns, and the relationship among these distributions and patchiness of biomass in this old-growth forest was a product of multiple ecological processes over a span of at least 500 years (Franklin et al. 2002). As pioneer ecologist Ramon Margalef stated, “Structure, in general, becomes complex, more rich, as time passes; structure is linked to history” (Margalef 1963). To understand patterns presented in this study requires careful exploration of various processes, including their frequency, intensity, and duration in the past five centuries. Although the underlying mechanisms responsible for these patterns and associations cannot be identified in detail with our field data, it was apparent that multiple mechanisms control spatial pattern and dynamics of a forest.

Stand structure and composition in an old-growth forest are usually viewed as the current manifestation of ongoing successional processes. During the time between stand replacement disturbances, Pseudotsuga-Tsuga forest stand dynamics are often modeled as gap-phase replacement (Spies and Franklin 1989, Lertzmann et al. 1996). Stand dynamics theory in silviculture also suggests that old-growth forests undergo slow replacement of pioneer species until a stand-replacement disturbance occurs (Oliver and Larson 1990). In studying old-growth eastern hemlock (Tsuga canadensis (L.) Carr.) in the upper Midwest, Frelich et al. (1993) proposed four hypotheses to explain the current old-growth conditions: soil and topographic variation, disturbance history, competitive interactions among trees, and invasive patterns. We believe at least four additional factors should be considered: (1) size and reproductive characteristics of the tree species such as their maximum tree height and age, seed production cycle and establishment, growth, and mortality, (2) ecology of tree species such as species responses and habitat requirements for light, moisture, and disturbances, (3) stand dynamics such as species replacement during forest succession, and (4) the random nature of many processes in time and space.

The biology of tree species in a forest is the basic information needed to understand some aspects of spatial patterns because each species has a unique form (roots, stems, and crowns), size, longevity, seed production cycle, rooting structure, and phenology. These evolutionary attributes directly control some aspects of spatial pattern and indirectly affect processes responding to disturbances and competition (Peet and Christensen 1987, White et al. 1999, Parker et al. in press). Most forests other than plantations are composed of more than one tree species with each species having a unique spatial pattern at any successional stage. In a detailed examination of species distribution in a tropical rainforest in Malaysia, He et al. (1997) found that 80% of 745 species were clustered while others were randomly distributed. No regular distribution was found for any species. Depending on the situation and level of aggregation for each species, very complex (but unique) patches can form, which in turn may be partially responsible for high functional variability across a tropical forest (cf. He et al. 1997). Even in a low diversity stand of southern boreal forest where three species (Picea, Abies, and Betula) dominate the forest, Chen and Bradshaw (1999) found that very complex patches were formed with different portions and distributions of various-sized individuals. These studies suggested the need to examine the spatial arrangement of individual species, emphasizing the spatial relationships among species in three-dimensional space and time (i.e., across successional stages, Van Pelt and Nadkarni 2004) and their potential roles in determining ecosystem function such as species diversity and productivity.
Figure 6. Stand biomass and density of five major species (i.e., ABAM and AGBR combined because of low AGBR component) in low, medium, and high biomass zones of the 12-ha plot.
as productivity and, ultimately, spatial distribution of bio-
mass across the stand.

Patch patterns and their cohesive spatial relationships are
scale-dependent, spatially and temporally. While shade-
tolerant species tend to aggregate at smaller scales, larger
PSME trees exhibit an average patch size of 114 m (North
et al. 2004), suggesting that a plot containing at least 100 canopy patches (i.e., gaps) is necessary to fully sample the configuration of overall forest structure. Specific species composition is responsible for the level and mosaic of biomass patches observed in the present day forest. Clearly, further studies are needed to reveal the details of how each process alters the spatial patterns of tree species with a complete factorial experimental design, and long-term monitoring process at broader scales is needed. An alternative is to examine the current spatial patterns and relate their spatial information to the possible underlying mechanisms and processes.

**Literature Cited**


