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DO RESIDUAL TREES INCREASE STRUCTURAL COMPLEXITY IN PACIFIC NORTHWEST CONIFEROUS FORESTS?

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Abstract. Green-tree retention has been promoted as an alternative management tool to create structurally complex forests that would resemble late-successional forests faster than single-aged stands planted after clearcuts. To evaluate if and how overstory residual trees were associated with a higher structural complexity, nine pairs of naturally regenerated stands, initiated between 55 and 110 yr ago with and without residual trees, were investigated. The new Structural Complexity Index (SCI) was used to relate the observed structure to residual trees and other structural components such as tree density, tree size variation, species composition, and environmental variables such as aspect, slope, and elevation. The SCI-ht, which is based on tree height variation, was negatively associated with residual trees, indicating that residual trees reduced vertical structural complexity. The SCI-dbh, which is based on the tree diameter variation, was positively associated with residual trees up to a density of 40 residual trees/ha, indicating that at low densities residual trees increased horizontal structural complexity. Generally, stands with intermediate densities of the young cohort and a mixture of about equal proportions of *Pseudotsuga menziesii* and shade-tolerant tree species such as *Tsuga heterophylla,* had the highest structural complexity. The most structurally complex stands were generally on east aspects. In addition to green-tree retention, species mixture and differences among aspects need to be considered when managing stands for structural complexity.

Key words: Douglas-fir; forest structure; green-tree retention; Oregon Cascades; retrospective study; structural complexity.

INTRODUCTION

Structural complexity has been recognized by ecologists as the hallmark of natural forests of all ages in the Pacific Northwest of North America (Hansen et al. 1995). Structural complexity has traditionally been equated with the distribution of individuals among diameter classes, their arrangement into different canopy layers, and variation in species composition (Smith 1986). Variation of tree sizes has been recognized as one of the more distinctive features of the Pacific Northwest's old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) forests, contributing to diversity in microhabitats, both vertically and horizontally (Spies and Franklin 1991). The variability of tree sizes is thus generally regarded as a key element of structural complexity (e.g., Buongiorno et al. 1994). Structurally complex stands result from natural disturbances that occur over a broad range of scales, sizes, shapes, and intensities, which often leave large residual trees, create snags and logs, and facilitate subsequent regeneration that can enhance the vertical complexity of the forest (Spies 1990). Young natural forests that show a high variability in tree sizes and canopy layers are frequently contrasted with intensively managed, monospecific even-aged plantations that lack both diversity of size and species (Spies et al. 1988). The conversion of mature and old forests to young plantations, and disturbances imposed by timber management (e.g., clearcutting) create conditions that deviate to varying degrees from those created by natural disturbances (McComb et al. 1993) and are believed to result in more homogeneous stand structures than natural disturbances (Hansen et al. 1995). It is believed that the lack of structural complexity may degrade the habitat quality for many species associated with mature and old forests (McComb et al. 1993).

Enhancing structural complexity in managed second-growth forests has become an important focal point of ''ecosystem management'' (e.g., Grumbine 1994) and ''structure-based management'' (Oregon Department of Forestry, ''structure-based management'' [1996; available online]).[2] Silvicultural systems are being designed that aim to mimic closely the frequencies, shapes, sizes, intensities, and patterns of natural disturbances in Pacific Northwest forests, to enhance structural complexity (McComb et al. 1993). To create, restore, and maintain structural complexity, green-tree retention, longer rotations, a thinning regime that is variable in time and intensity, and uneven-aged management, have been proposed as possible alternatives to clearcuts (FEMAT 1993*a, b,* McComb et al. 1993,

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[2] URL: ⟨http://www.odf.state.or.us/pubaff/horiz/hzbsm196.htm⟩

Hansen et al. 1995, Tappeiner et al. 1997). Green-tree retention is hypothesized to produce larger trees, a greater variability in tree sizes, and multistoried canopies (FEMAT 1993*a*, *b*). Studies on green-tree retention so far have primarily focused on the relation between levels of green-tree retention and growth reductions of the young cohort (e.g., Birch and Johnson 1992, Hansen et al. 1995, Rose and Muir 1997, Acker et al. 1998, Zenner et al. 1998), but the relation of green-tree retention levels to structural complexity has not been tested in field studies.

Managers, charged with creating old-forest conditions in short times, need objective criteria to evaluate the success of management strategies. The quantification of structural complexity is, however, not an easy task. Structural complexity has often been approximated by easy-to-measure, one-dimensional stand parameters such as the mean diameter at breast height (dbh), the standard deviation of the dbh's, tree density per unit area, or the density per unit area of Douglas-fir with dbh >100 cm (e.g., Spies and Franklin 1991, Hansen et al. 1995). To quantify the structural complexity of a stand, however, comparing these variables may give contradictory results as to which stand is the most structurally complex, depending on the criterion used for evaluation. Although one-dimensional stand parameters may provide some insights into mean structural condition of a stand, they do not incorporate the horizontal or vertical spatial arrangements of the trees, and thus ignore important characteristics of forest structure.

Recently, researchers have begun to investigate two-dimensional horizontal patterns using stem-mapped data with nearest neighbor analysis and Ripley's K function as a better descriptor of structural complexity (e.g., Moeur 1993, Pretzsch 1995, Kuuluvainen et al. 1996, Goslin 1997). Pretzsch (1995) has given an example of forest stands with the same tree densities, basal areas, and size distributions, but different spatial arrangements that may be the result of different silvicultural treatments, underlining the importance of spatial considerations in forest management. He argued that the spatial arrangement of trees, not just a one-dimensional summary of the tree size distribution, was necessary to better describe forest structure. It is, however, the combination of spatial arrangement and tree sizes, usually described as the ''patchiness'' (sensu Kotliar and Wiens 1992) that is at the center of forest structure. For example, suppose that the spatial arrangement of trees is held constant and tree sizes from a known tree size population are randomly assigned to the positions of the trees. Differences in the forest structure would then depend on tree size differences among neighboring trees, and not at all on the spatial arrangement of the trees, illustrating why structural complexity is a three-dimensional concept. To combine the spatial tree arrangement and size differences among neighboring trees, Zenner (1998) proposed a structural complexity index (SCI) that uses known or simulated point patterns to connect neighboring trees in x-y-z-space to form a rough surface area that may be used to quantify and compare the three-dimensional structural complexity of forest stands.

The goal of this study was to investigate, retrospectively, how the structure of young-to-mature stands is related to the density of large residual trees that survived the natural disturbance that initiated the young-to-mature tree cohort. Structure was first described by one-dimensional summary statistics (e.g., tree size distribution, proportion of Douglas-fir in the young cohort) that have been used in other studies as surrogates for structural complexity. Then, the spatial structure was examined with the use of the Clark-Evans index for spatial aggregation (Clark and Evans 1954). Finally, the structural complexity index (SCI) was applied to the stem-mapped stands to more fully explore the three-dimensional structure associated with residual trees and to test the hypothesis that residual trees enhanced the structural complexity of forests. More specifically, the mechanisms that may be responsible for the observed structural complexity in two- and multiple-storied stands were addressed in this study, and a framework for structural development in green-tree retention stands provided.

METHODS

Nine pairs of plots were established in the lower elevations (520–855 m) of the *Tsuga heterophylla* (western hemlock) zone (Franklin and Dyrness 1973), in the Willamette National Forest in Oregon's western central Cascade Range. Dominant species in the these stands included *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock). *Thuja plicata* Donn. (western red cedar), *Libocedrus decurrens* Torr. (incense cedar), *Cornus nuttallii* Audubon (Pacific dogwood), *Acer macrophyllum* Pursh. (bigleaf maple), and *Castanopsis chrysophylla* (Dougl.) A.DC. (golden chinkapin) were often present in the understory.

Paired plots were established to compare the structure of naturally developed stands with residual trees, to adjacent naturally developed stands without residual trees. Sites were included in the study when two 61.8 m diameter plots could be located on one topographic feature, to assure similarity in aspect, slope, elevation, and topographic position. Stands with recent excessive mortality in the understory or understocked stands were excluded from the study.

Trees were measured in a 12.6-m (500-m^2) circular plot, corrected for slope, nested in a 30.9-m (3000-m^2) plot, corrected for slope, one with and one without residual trees. Tree species, diameter at breast height (dbh), and canopy class relative to the general understory for all live trees ≥ 5 cm in dbh, were recorded. Slope-corrected distances and azimuths to the plot center were also recorded and later converted to Cartesian

TABLE 1. Forest site and stand characteristics.

							Density (trees/ha)					Basal area (m^2/ha)	
Stand	Age (yr)†	Elevation (m)	Aspect	Slope (%)	SCI-ht	SCI-dbh	Residual trees	Young cohort	PSME‡	TSHE§	Hardwoods	All trees	Young cohort
BR08-R	108	823	E	75	5.38	7.41	80	1480	160	1260	0	82.4	42.8
BR08-N	111	823	E	80	6.61	7.94	0	1920	340	1580	0	61.0	61.0
BR17-R	65	853	S	73	6.14	9.51	20	900	880	0	20	70.9	46.7
BR17-N	58	853	S	77	6.63	8.66	0	1040	840	0	160	63.3	63.3
DE06-R	81	640	S	30	3.48	7.01	20	680	640	0	20	77.6	64.0
DE06-N	67	640	S	40	3.76	6.15	0	860	840	20	0	68.6	68.6
LO01-R	61	731	S	62	5.98	7.99	80	940	400	540	0	107.0	39.9
LO01-N	61	731	S	55	5.48	6.70	0	1240	920	60	240	56.4	56.4
LO05-R	83	701	E	28	3.12	6.65	60	460	160	240	60	96.6	38.1
LO05-N	85	701	E	17	9.68	11.31	0	840	420	420	0	65.1	65.1
LO07-R	92	518	S	10	6.39	10.90	60	660	260	400	0	148.0	47.4
LO07-N	87	518	S	17	5.81	7.47	0	800	360	380	0	82.0	82.0
LO08-R	83	792	S	60	5.99	9.38	20	860	420	440	0	80.2	52.0
LO08-N	85	792	E	57	3.44	6.57	0	680	680	0	0	74.5	74.5
MC04-R	88	671	S	33	5.05	9.10	20	620	560	60	0	81.6	58.6
MC04-N	94	671	S	25	3.73	6.88	0	740	640	60	40	86.5	86.5
SH13-R	74	640	S	30	7.23	10.14	40	1200	500	660	40	106.0	47.2
SH13-N	77	640	S	30	6.18	7.89	0	860	520	260	40	60.2	60.2

† Age of the young cohort.
‡ PSME = *Pseudotsuga menziesii.*
§ TSHE = *Tsuga heterophylla.*

coordinates. Tree heights and crown lengths were measured on all residual trees and at least two randomly selected undamaged understory trees for each species in each canopy class. For age estimation, increment cores were extracted from all residual trees and a subsample of understory trees. Age of the understory was defined as the mean breast-height age of dominant and codominant trees. Aspect was transformed into two discrete aspect classes (east, south). Site characteristics of these stands were reported in Zenner et al. (1998). Relevant site and stand characteristics important for this study are listed in Table 1.

The most commonly used statistical test for the analysis of mapped-point patterns is the Clark-Evans test (Andersen 1992), which performs well under cases of clumping, when total density is known and corrections are made for irregularly shaped plot boundaries (Donnelly 1978, Stohlgren 1993). Nearest neighbor analysis in form of the index of aggregation (Clark and Evans 1954), as modified by Donnelly (1978) for lack of a boundary strip, was used in this study to characterize the horizontal tree distribution pattern. The aggregation index relates the observed mean distance of all trees to their respective nearest neighbors, to the mean distance expected under a random or Poisson spatial distribution. The expected distance (CE_{exp}) to the nearest neighbor is related to the actual number of trees in the test area by:

$$CE_{exp} = \frac{1}{2\sqrt{N/A}} + \left(0.051 + \frac{0.041}{\sqrt{N}}\right)\frac{L}{N} \qquad (1)$$

with a standard error calculated as

$$CE_{se} = \frac{\sqrt{0.07A + 0.037L\sqrt{A/L}}}{N} \qquad (2)$$

where N = the number of trees in the test area, A = the area of the test plot in square meters, and L is the perimeter length of the plot. The z test was used to test for significant deviation from a random pattern as

$$z = \frac{CE_{obs} - CE_{exp}}{CE_{se}} \qquad (3)$$

where CE_{obs} is the observed mean distance between the trees. If $|z|$ was <1.96, trees were considered randomly spaced, z values below -1.96 indicate a clustered pattern, and z values above 1.96 a uniform pattern.

Calculation of the Structural Complexity Index was based on a three-dimensional model of the structure of these nine pairs of stands, where three neighboring pairs of trees formed triangles. Trees are represented as three-dimensional irregularly spaced data points (x, y = spatial coordinates, z = tree sizes such as tree heights or dbh's). Three, horizontally adjacent points in this x, y, z space can be connected to form a triangular surface. When extended across a stand of trees, this spatial tessellation concept, known as a triangulated irregular network (TIN), forms a network of non-overlapping triangles (Fraser and van den Driessche 1971), which forms a continuous faceted surface (Fig. 1). This approach allows the comparison of stands based on the distribution of size differences of neighboring trees (Zenner 1998).

The Delaunay triangulation routine (Matlab 1997) was used to create a network of non-overlapping triangles, where the triangulation is independent of the

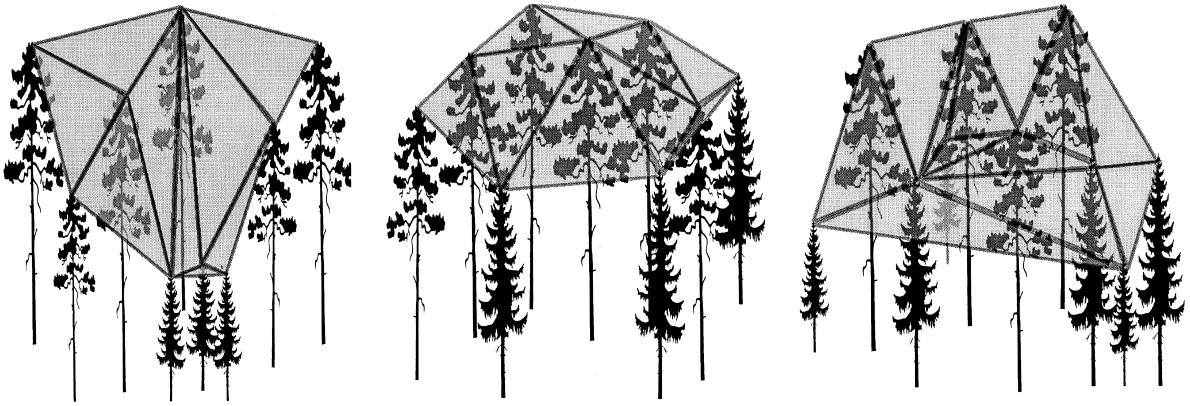

FIG. 1. Visual representation of a triangular irregular network, showing the triangulated surface area connected at the tops of three neighboring trees.

order in which the points are processed. Delaunay triangles are as equiangular as possible such that all sample points are connected to their two nearest neighbors to form triangles. Possible edge effects were corrected by omitting triangles suspected to contain trees whose actual nearest neighbors may have been outside the plot boundary. This was done by finding the midpoint between the two trees that were closest to the plot center of each triangle. When the distance from this midpoint to the third (farthest) tree was greater than the distance from this midpoint to the edge of the plot, the triangle was omitted. Thus, the horizontal ground area covered by triangles depended on the actual spatial distribution of the trees, and varied among plots.

The SCI (Zenner 1998), which is based on differences in tree heights or diameters, and distances of neighboring trees, was created to directly compare the structural variability among stands. This SCI is defined as the sum of the surface areas of the TINs for a stand (SCI*) divided by the horizontal ground area covered by all triangles:

$$\mathrm{SCI} = \frac{\mathrm{SCI}^*}{A_T} \tag{4}$$

where A_T is the sum of the horizontally projected areas of all triangles and

$$\mathrm{SCI}^* = \sum_{i=1}^{N} \frac{1}{2} |a \times b| \tag{5}$$

where $i = 1, \ldots, N$ is the number of triangles in the test plot, $|a \times b|$ is the absolute value of the vector product of the vector AB with coordinates $a = (x_b - x_a, y_b - y_a, z_b - z_a)$ and the vector AC with coordinates $b = (x_c - x_a, y_c - y_a, z_c - z_a)$. The SCI is related to structural complexity in that the greater the sum of the tilted triangles, the larger the SCI, and the more complex the structure. Two indices of the SCI were calculated, the SCI-ht based on the heights of all trees, and the SCI-dbh based on the diameters at breast height of all trees as the z variable.

Multiple linear regression analysis was used to test which site descriptors were associated with one-, two-, and three-dimensional structural characteristics. All measured variables were tested; only those with significant coefficients were retained and are presented in Table 2. Where indicated, natural logarithmic transformations were applied to dependent and independent variables, to linearize regression models. Predicted values were plotted against observed values to ensure that residuals were centered around zero, and no systematic trends remained unexplained. To model how the density of green trees may influence the SCI, the density of residual trees and the young cohort were fixed at a range of values and predicted values of *Pseudotsuga* in the young cohort. The standard deviations of the tree heights and dbh from the regression models were used to model the SCI for each combination of residual tree and young cohort density and for east and south aspects.

RESULTS

One-dimensional summary statistics

Means and standard deviations of tree heights and dbh's.—Means and standard deviations of tree heights and dbh's showed clear differences both within paired plots and among pairs, with greater differences among pairs than within pairs (Fig. 2 A, B). Mean tree heights and their standard deviations ranged from 15.9 to 32.9 m and from 7.2 to 15.6 m, respectively. Mean dbh's and their standard deviations ranged from 18.2 to 35.8 cm and from 9.2 to 34.9 cm, respectively. The mean of the tree heights (Table 2) was associated with the density of the young cohort, the proportion of *Pseudotsuga* in the young cohort, and, negatively, with the density of residual trees. The standard deviation of tree heights, $\mathrm{std}_{\mathrm{ht}}$ (Table 2), was associated with the density of the young cohort and the proportion of *Pseudotsuga* in the young cohort, but was not directly related to the density of residual trees ($P = 0.503$). The density of the young cohort had a quadratic association with the

TABLE 2. Multiple linear regressions (full model) for the one- and two-dimensional structural characteristics and the SCIs.

Response	Model	R^2 (%)	P
One-dimensional			
ln(PSME-%)	3.851 − 0.009 res − 0.001 tpha + 0.002 elev − 0.503 I(east)	85	<0.001
Mean tree height	593.327 − 0.827 ln(res) − 157.026 ln(tpha) + 10.667 ln(tpha^2) + 0.083 PSME%	87	<0.001
Mean tree dbh	150.447 − 0.037 res − 15.334 ln(tpha) − 0.316 PSME% + 0.003 PSME%^{2} − 0.015 elev	96	<0.001
std$_{ht}$	−438.673 + 137.181 ln(tpha) − 10.358 ln(tpha^2) − 0.062 PSME%	49	0.022
ln(std$_{dbh}$)	3.344 + 0.024 res − 0.0003 res^2 − 0.0004 tpha − 0.0051 PSME% − 0.166 I(east)	82	<0.001
Two-dimensional			
Clark-Evans index	1.660 − 0.023 tpha + 0.0002 tpha^2	60	0.002
Three-dimensional			
SCI-ht	−28.189 + 3.661 ln(tpha) + 0.416 std$_{ht}$ + 0.160 PSME% − 0.001 PSME%^{2} + 1.670 I(east)	80	<0.001
SCI-dbh	−29.093 + 3.810 ln(tpha) + 0.279 std$_{dbh}$ + 0.205 PSME% − 0.001 PSME%^{2} + 2.130 I(east)	77	0.002

Notes: Model variables are defined as follows: res = residual trees/ha, tpha = young cohort density/ha, PSME% = proportion of *Pseudotsuga* in the young cohort, std$_{ht}$ = standard deviation for tree heights, std$_{dbh}$ = standard deviation for tree diameters at breast height, I(east) = indicator variable (1 for east aspects, 0 otherwise), SCI-ht = Structural Complexity Index based on tree heights, SCI-dbh = Structural Complexity Index based on tree diameters (dbh), and elev = elevation.

mean tree height and the std$_{ht}$, such that when the density was at intermediate levels, mean tree height was lowest and the std$_{ht}$ was highest. The mean of the tree diameters (Table 2) was negatively associated with the density of the residual trees and the young cohort, and elevation. The proportion of *Pseudotsuga* in the young cohort had a curvilinear association with the mean tree dbh, with a minimum at 63% *Pseudotsuga* in the young cohort. The standard deviation of tree diameters, std$_{dbh}$ (Table 2), was associated with the density of the residual trees, the density of the young cohort, and the proportion of *Pseudotsuga* in the young cohort and aspect. Residual tree density had a quadratic association with std$_{dbh}$, such that the std$_{dbh}$ was highest at intermediate levels of the residual tree density. South aspects had a higher std$_{dbh}$ than east aspects.

Proportion of Pseudotsuga *in the young cohort.*— Residual trees, the density of the young cohort, and east aspects were negatively associated, and the slope of the stand was positively associated, with the proportion of *Pseudotsuga* in the young cohort (Table 2). South aspects had higher proportions of *Pseudotsuga* in the young cohort than east aspects.

Two-dimensional spatial structure

Stands in this study exhibited a variable spatial structure (Table 3): some stands showed a clustering (lowest Clark-Evans index $R = 0.78$), some a random pattern, and some a uniform pattern (highest Clark-Evans index $R = 1.24$). Overall, the Clark-Evans index showed a quadratic association with the density of the young cohort (Table 2), indicating a tendency for more clustering at low and high densities of the young cohort.

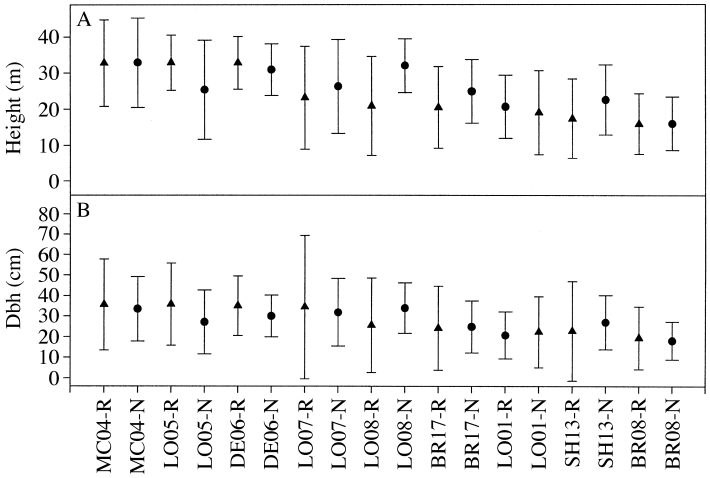

FIG. 2. Mean and standard deviation of tree height and tree diameters. The extension "-N" refers to stands with no residual trees (circles), "-R" refers to stands with residual trees (triangles).

TABLE 3. Dispersion characteristics.

	All trees		*Pseudotsuga*		*Tsuga*	
Stand	Distance (m)	C-E *z* score†	Distance (m)	C-E *z* score	Distance (m)	C-E *z* score
BR08-R	1.27 (0.64)	−0.65	5.14 (2.81)	2.21‡	1.49 (0.89)	0.27
BR08-N	1.23 (0.64)	0.64	3.03 (1.87)	0.08	1.35 (0.66)	0.45
BR17-R	1.62 (0.94)	−0.87	1.68 (0.97)	−0.64		
BR17-N	1.40 (0.87)	−1.88	1.69 (1.01)	−0.90		
DE06-R	2.10 (0.98)	0.42	2.19 (1.13)	0.52		
DE06-N	1.86 (0.80)	0.30	1.94 (0.71)	0.67		
LO01-R	1.72 (1.30)	0.52	2.90 (1.52)	1.57	1.90 (1.40)	−1.75
LO01-N	1.16 (1.02)	−3.12†	1.27 (1.25)	−3.37†		
LO05-R	2.90 (1.06)	2.12‡	4.78 (2.33)	1.62	4.53 (2.13)	1.24
LO05-N	1.89 (1.05)	0.37	3.02 (1.26)	1.14	2.91 (1.94)	0.79
LO07-R	2.12 (1.42)	0.70	3.75 (1.88)	1.59	2.56 (1.87)	−0.55
LO07-N	1.88 (1.33)	−0.02	3.49 (1.70)	1.63	2.03 (1.15)	−2.29†
LO08-R	1.92 (1.17)	0.88	3.31 (1.29)	2.41‡	1.68 (1.31)	−3.11†
LO08-N	2.38 (0.96)	1.70	2.38 (0.96)	1.70		
MC04-R	2.62 (1.04)	2.45‡	3.06 (1.11)	3.35‡		
MC04-N	2.20 (1.62)	1.35	2.65 (1.67)	2.60‡		
SH13-R	1.62 (0.64)	1.20	2.66 (1.40)	1.38	2.19 (1.10)	0.50
SH13-N	1.70 (0.90)	−0.75	2.03 (0.92)	−1.35	2.97 (2.24)	−1.02

Note: Distance = the mean distance (with 1 SE in parentheses) between trees; C-E *z* scores = Clark and Evans *z* scores.
† Significantly clumped at $P < 0.05$.
‡ Significantly uniform at $P < 0.05$.

The Clark-Evans index was not associated with residual trees ($P > 0.20$).

Three-dimensional structure: tree-height and tree-diameter based SCIs

SCI-ht.—The SCI-ht was positively associated with the std$_{\text{ht}}$ and the density of the young cohort. East aspects had a higher SCI-ht than south aspects. The proportion of *Pseudotsuga* in the young cohort also had a quadratic association with the SCI-ht, such that the SCI-ht was highest at intermediate levels of of *Pseudotsuga* in the young cohort.

SCI-dbh.—The SCI-dbh was positively associated with the std$_{\text{dbh}}$, the density of the young cohort, the proportion of *Pseudotsuga* in the young cohort, and aspect, where east aspects had higher SCI-dbh values than south aspects. SCI-dbh also had a quadratic association with the proportion of *Pseudotsuga* in the young cohort.

Modeling the influence of residual trees on the SCIs

Predictions for the proportion of Pseudotsuga *in the young cohort, std$_{ht}$ and std$_{dbh}$.*—Using fixed values for residual tree and young cohort densities, and predicted tree species composition from the regressions, enabled the standard deviations for different stand conditions to be modeled. Regression models predict that the proportion of *Pseudotsuga* (Fig. 3A, B) would generally decline with increasing residual tree and young cohort densities, and would be higher on south aspects than on east aspects. The std$_{\text{ht}}$ (Fig. 3C, D) is predicted to be at a maximum at intermediate densities of the young cohort (∼750 trees/ha, 95% CI is 360–900 trees/ha) for a given residual tree density. The std$_{\text{ht}}$ would generally increase with a higher residual tree density beyond the range of residual trees in this study, being generally higher on east than on south aspects. The std$_{\text{dbh}}$ (Fig. 3E, F) is predicted to be at a maximum at 44 residual trees/ha (95% CI is 36–52 trees/ha), and would increase with increasing densities of the young cohort, with only small differences between east and south aspects.

Predictions for the SCI-ht and SCI-dbh.—Using the predicted tree species composition and tree size standard deviations as input variables in the regression equations for the SCIs allows the modeling of the structural complexity for a range of residual tree and young cohort densities. Generally, east aspects would have a higher structural complexity than south aspects. Regardless of the aspect, the SCI-ht (Fig. 3G, H), would show the greatest structural heterogeneity when no residual trees are present. The SCI-ht would be highest at intermediate densities of the young cohort and be at a maximum with 66% (95% CI is 56–76%) *Pseudotsuga* in the young cohort. Whereas values for the SCI-ht would generally decline with increasing residual tree densities, the SCI-dbh (Fig. 3I, J) would generally increase with a higher residual tree density up to ∼40 residual trees/ha on both aspects, beyond which the SCI-dbh would decline. As with the SCI-ht, the SCI-dbh would be highest at intermediate densitites of the young cohort, being at a maximum with 73% (95% CI is 64–83%) *Pseudotsuga* in the young cohort.

DISCUSSION

Stand development in the context of complex interactions of residual tree survival, initiation of the young cohort, and environmental conditions represented by aspect, slope, and elevation, has led to unique stand

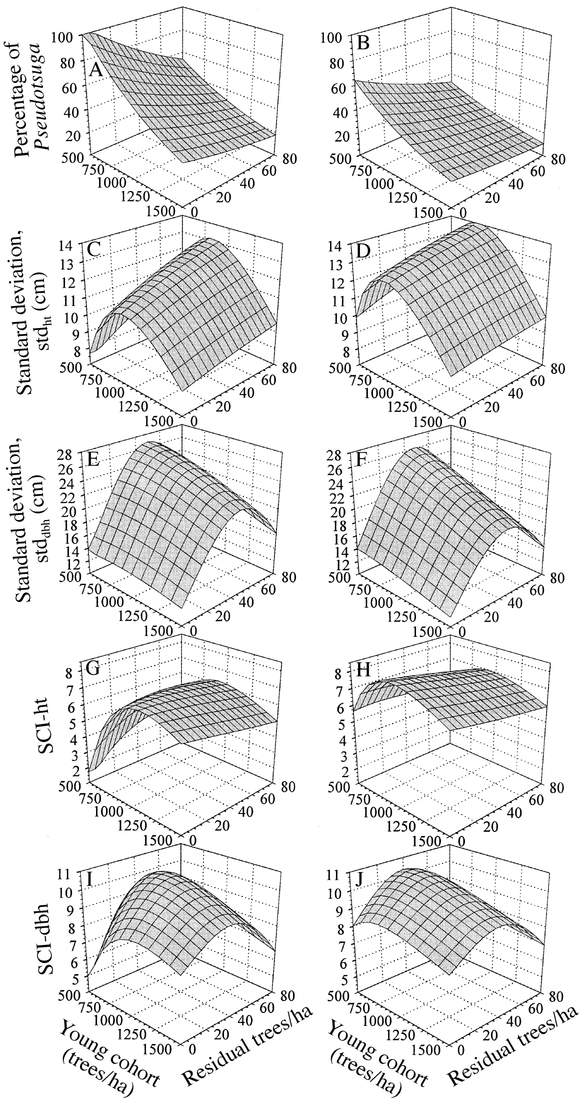

FIG. 3. Response of the (A, B) proportion of *Pseudotsuga* in the young cohort, (C, D) standard deviation of tree heights, (E, F) standard deviation of tree diameters, (G, H) SCI-ht, and (I, J) SCI-dbh to a range of residual tree and young cohort densities for south (figures on left) and east (figures on right) aspects.

structures in each of the stands in this study. Stands differed by (1) how many residual trees survived the disturbance that initiated the young cohort, (2) the density of the young cohort, (3) the tree species proportions of the young cohort, and (4) the tree size distributions.

In this study, structural complexity showed a complex association with residual tree density. The impact of residual trees on structural complexity depended on the criterion used to evaluate it. Structural complexity was influenced by environmental variables such as aspect and elevation, which were strongly related to the species composition of the young cohort, but not by the spatial pattern. The three-dimensional SCIs integrated the effects of residual trees on the structural variables through associations with the density of the young cohort, the size distributions of the trees, and the composition of the young cohort. Generally, the greater the size variability in tree heights and diameters, the greater the SCI and the structural complexity of the stands in this study. Increased residual tree densities were associated with an increase in the std_{dbh} and hence the SCI-dbh, indicating a greater horizontal structural complexity. This was, however, not the case for the SCI-ht. Although residual trees were indirectly associated with a slight increase in the std_{ht}, the overall association with the SCI-ht was negative, leading to a more even, less complex canopy, and a reduced structural complexity. Mechanisms responsible for these apparently contradicting results lie in the association between residual trees and the understory composition, and in the differential weighting of residual trees and the dominant trees of the young cohort in the algorithm of both SCIs.

Composition of the young cohort.—The increase in the std_{dbh} and the SCI-dbh was directly and indirectly related to presence of residual trees. First, residual trees add to the std_{dbh} by their own size, having generally larger dbh's than the trees of the young cohort. Second, and more importantly, with increasing residual tree densities there was a shift in the composition of the young cohort from *Pseudotsuga* to a more even composition of the understory of *Pseudotsuga* and *Tsuga*. At low residual tree densities the young cohort consisted almost entirely of large *Pseudotsuga* of more or less uniform size arranged in a single-layered canopy. At high residual tree densities, *Tsuga* dominated the young cohort and also formed a single-layered canopy. Both std_{dbh} and SCI-dbh were at a maximum at intermediate densities of residual trees and the young cohort, when the young cohort consisted of ∼two-thirds *Pseudotsuga* and one-third shade-tolerant species. With fewer dominant *Pseudotsuga* in the young cohort (Zenner et al. 1998), residual trees took the place of dominant young cohort *Pseudotsuga* trees, and along with an increasing abundance of suppressed, shade-tolerant *Tsuga*, *Thuja*, *Acer*, and *Cornus*, formed a multi-tiered canopy and thus increased structural complexity. This can generally be observed in stands with a mixed species composition, where stand development is usually characterized by a progressive differentiation of species into distinct size strata, in which the least shade-tolerant species occupy the larger size classes, and species of increasing shade tolerance occupy successively smaller size-classes (Smith 1986), thus forming a multi-layered canopy with high structural complexity.

Stands with high residual tree densities were associated with high densities in the young cohort, which were mostly small, shade-tolerant *Tsuga* showing little size differentiation and, through elimination of most dominant and codominant *Pseudotsuga*, reached a two-tiered structure less complex than a multi-tiered canopy. This can be particularly well observed in the association between the density of the young cohort and the $\mathrm{std}_{\mathrm{ht}}$ and the SCI-ht (Fig. 3 C and G), where both the $\mathrm{std}_{\mathrm{ht}}$ and the SCI-ht are at a maximum value at intermediate densities of the young cohort with a more balanced understory composition of shade-tolerant and shade-intolerant tree species. These findings are consistent with Hansen et al. (1995), who showed that tree species composition was strongly related to the level of green-tree retention. Species mixture has been recognized as a key component for structural complexity in late-successional and old-growth stands (e.g., Franklin et al. 1981), and vertical and horizontal heterogeneity have been attributed to the proportion of shade-tolerant species (Spies and Franklin 1988). Structural complexity is thus typically the result of heterogeneous overstories with various-sized canopy gaps, and is often the result of interspersion of various-sized and aged trees among superdominants and dominants (Hedman and van Lear 1995).

Aspect differences.—It has also become evident, however, that structural complexity is not only the outcome of the presence of residual trees; it has to be considered within the context of environmental variables. Species composition may reflect the disturbance that initiated the young cohort. Whether *Pseudotsuga* or *Tsuga* dominate the regeneration may depend on seed source availability and also, as was observed in this study, the aspect of a site. Different structural complexities were found at a given residual tree density, depending on the aspect, due to different species compositions and size distributions among aspects. Aspect, with its associated light and moisture regime, may create conditions that are more or less favorable for different species in the young cohort. These conditions may then be modified by the presence of seed sources and the impact of residual trees on the established young cohort. In this study, the proportion of *Pseudotsuga* in the understory was still very high on south aspects even at high densities of residual trees, either because *Tsuga* did not become established or was outcompeted by *Pseudotsuga.* The proportion of *Pseudotsuga* can also be low on some east aspects even in the absence of residual trees, perhaps because *Pseudotsuga* did not become established due to a lack of a seed source, or was outcompeted by the more shade-tolerant *Tsuga.* Although the species composition is specific to the stands in this study and cannot be generalized to aspects in the whole region, abundances, proportions, and competitiveness of *Pseudotsuga* in the young cohort may vary substantially among aspects. Goslin (1997) came to a similar conclusion after finding that suppressed *Pseudotsuga* were able to survive on a south aspect where *Tsuga* was absent, but a stand on a north aspect was dominated by *Tsuga,* and *Pseudotsuga* was almost entirely absent. Greater frequencies of *Pseudotsuga* (Williamson and Twombly 1983) and higher basal area growth on south aspects (Stage 1976, Youngberg and Ellington 1982) have also been reported previously.

Spatial patterns.—In this study the Clark-Evans index of spatial aggregation indicated that the spatial patterns among the stands were highly variable, with most stands showing a random pattern, others a uniform pattern, and yet others a clustered pattern, reflecting different stages of differentiation among these stands (Zenner et al. 1998). Whereas *Pseudotsuga* generally showed a tendency toward random and uniform spatial distributions, *Tsuga* showed a tendency toward clustered spatial distributions (Table 2). Clustered patterns were related to high densities of the young cohort and reflected ongoing self-thinning. Spatial differences between *Pseudotsuga* and *Tsuga* also reflect their canopy status as a more dominant and suppressed tree species in these stands, respectively. This is consistent with the tendency for trees to go from clustered to random to regular spacing, as trees get larger and older (Stohlgren 1993). For example, Williamson (1975) found a random spatial distribution of dominant trees in old-growth beech–maple forests, and Franklin et al. (1985) found regular spatial distributions in large pine trees in northeastern California.

While two-dimensional statistics of forest structure, such as the Clark-Evans statistic or Ripley's K function, can describe the spatial pattern of a forest, they typically ignore the tree sizes or have to be computed for each size class separately (Kuuluvainen et al. 1996). Results from spatial point pattern analyses have been linked to ecological processes (e.g., gap processes, self-thinning; e.g., Kenkel 1988, Kuuluvainen et al. 1996), but the importance of spatial patterns with regard to structural heterogeneity is still unclear. For example, is the structural complexity different for clustered, random, or regular patterns (see Zenner 1998)? Is the scale at which these patterns are observed related to the scale at which structural complexity may be high? The nonsignificance of the Clark-Evans index in the regression of the SCIs indicates that the spatial pattern was not related to the observed structural complexity at the scale used in this study. It may thus be more important to investigate whether trees of similar sizes tend to be clustered, random, or regularly distributed across several scales. To do this, however, scales larger than the one used in this study are necessary.

Differences between both SCIs.—Relationships between residual trees and the SCIs suggest that there may be an optimal density and perhaps spatial distribution of residual trees that maximizes structural complexity by optimizing the stds, density, and the proportion of *Pseudotsuga* in the young cohort. The greatest variation in tree dbh's, and the highest SCI-dbh, generally point to the retention of intermediate ($\sim$40 trees/ha) levels of green trees. These levels are at the upper end of the reported range of typical densities of 18 to 29 *Pseudotsuga* $>$100 cm dbh per hectare (95% CI = 2–51 trees/ha) in old-growth forests (Spies and

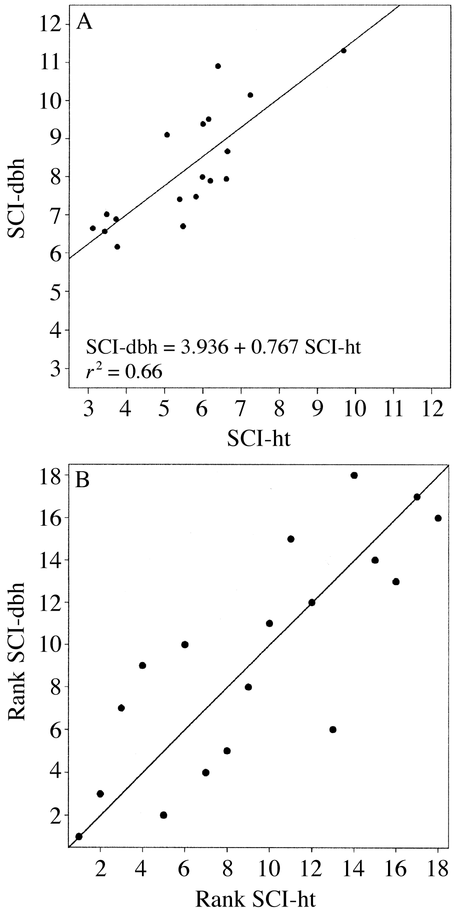

FIG. 4. Relationship between (A) SCI-ht and SCI-dbh and (B) between ranking of the stands according to SCI-ht and SCI-dbh.

Franklin 1991). Although the std_{ht} had an indirect positive association with residual trees, the SCI-ht had an indirect negative association with residual trees, and was at a maximum in the absence of residual trees.

Greater SCI-ht values generally also mean greater SCI-dbh values (Fig. 4A). However, ranking structural complexity of stands by the SCI-ht resulted in a somewhat different order than ranking structural complexity by the SCI-dbh (Fig. 4B). The different ranking orders and conclusions based on SCI-dbh and SCI-ht are the result of a differential weighting of residual trees between the SCI-dbh and the SCI-ht. The SCI-dbh gives more weight to large trees than does the SCI-ht, since the z coordinates are dbh's (in cm) for the SCI-dbh, and height (in m) for the SCI-ht. For example, whereas a residual tree of 200-cm dbh can create twice the z differences to its neighbors than a tree with a dbh of 100 cm, their heights are very similar, thus limiting size differences among neighboring trees to smaller values when the SCI-ht is used. The differential weighting of the components of an index must be kept in mind when using the SCI and other indices.

Due to the different weighting of large trees, the difference between the SCI-ht and the SCI-dbh may relate to and highlight the mechanisms that may be responsible for the observed structural complexites in these stands, and may provide a framework for the structural development in future green-tree retention stands. The differences in the associations between both SCIs and residual trees is related to having additional residual trees coming at the expense of losing more dominant and codominant understory trees in the vicinity of residual trees into lower crown classes. This is reflected in the SCI-ht, where residual trees are treated as if they were a dominant tree of the young cohort (due to their similar heights). Here, residual trees reduce structural complexity by excluding proportionately more dominant trees in the young cohort (Zenner et al. 1998), than they themselves add to it. Consequently, although residual trees sharply increase the very localized structure, their negative influence on the growth of *Pseudotsuga* in the young cohort (Zenner et al. 1998) reaches further than their immediate neighborhood. The effect of residual trees is thus a more even canopy around residual trees, possibly composed of similar-sized *Tsuga*. Residual trees themselves can offset a reduced structural complexity in the young cohort when based on the SCI-dbh, and may increase the structural complexity up to ~40 residual trees/ha, when *Pseudotsuga* is beginning to be outcompeted by *Tsuga* and a two-tiered canopy is being formed.

MANAGEMENT IMPLICATIONS

Structural complexity is a function of the number of retained trees, the density and species mixture in the understory, and environmental factors such as aspect. The results of this study may have important ramifications for green-tree retention systems. Beyond the retention of green trees, lengthened rotations, and variable thinning regimes (McComb et al. 1993, Hansen et al. 1995, Tappeiner et al. 1997), successful strategies to enhance structural complexity and habitat diversity need to take species mixtures into account, because they add to the variation in tree sizes. Rather than regarding the presence of *Tsuga, Thuja,* and hardwoods as a potential threat to *Pseudotsuga,* management strategies that seek to integrate timber production as well as habitat restoration need to consider shade-tolerant species as the backbone of, and the means to, enhanced structural complexity. Overall, the data suggest that there may be an optimal degree of canopy retention to maximize structural complexity. Intermediate levels of retention of ~40 trees/ha seem to promote the development of a shade-tolerant understory, without eliminating *Pseudotsuga* from the stand. These findings are consistent with ecologists' predictions that green-tree retention may be a successful strategy for maintaining structural complexity in managed forests (e.g., Franklin 1988, Swanson and Franklin 1992, Hansen et al. 1995). These findings also support Spies and Franklin's (1991) perceptions of the development of forest structure over time. They predict that structural complexity is at a maximum during the successional stage, that is, transitional between shade-intolerant early successional species and shade-tolerant later successional species. Thus structural complexity would be reduced as old-growth forests change from a canopy still dominated by *Pseudotsuga* to one where *Tsuga* becomes dominant even in the overstory. In this case, standard deviations of tree sizes and size differences among trees may be reduced, and patches of dense, uniformly sized *Tsuga* may be reflected in lower values for the SCIs.

Optimal levels of green-tree retention may, however, depend on local site conditions such as aspect, slope, and elevation. Managers need to recognize the important influence of aspect on forest structure. Due to the potential influence of aspect, different levels of green-tree retention may be appropriate for different aspects. On south aspects, where *Pseudotsuga* is the most abundant and dominant tree species, a greater amount of retained green trees may produce conditions that may be more suitable for *Tsuga* or other more shade-tolerant species, which would increase the structural complexity. On east and north aspects, where *Tsuga* may be more abundant and the dominant tree species, forest managers may have to create conditions, through gap creation, planting of *Pseudotsuga* in natural or artificial openings, and differential thinning of hemlock, to help *Pseudotsuga* survive and maintain its presence, in order to enhance structural complexity. A heavy thinning from above and retaining smaller trees may ensure fast growth of dominant and codominant trees with large crowns, but also ensures the survival of suppressed trees. Underplanting *Pseudotsuga* dominated stands with shade-tolerant species such as *Tsuga*, or *Thuja* in the absence of natural seedling establishment may be a successful strategy to provide more structural heterogeneity in young, managed stands. Silviculturists need to explore the horizontal pattern and spatial extent of species mixtures that allow shade-tolerant trees to thrive without endangering the future crop species. Also, the relationship between thinning intensity, tree species composition, and structural complexity needs to be further investigated.

Forest managers, charged with creating old-forest conditions in short times, need objective criteria to evaluate the success of management strategies. Both SCI-ht and SCI-dbh can be used in this context to compare different management alternatives and evaluate their performance. Investigating structural complexity with these indices highlights different mechanisms that may help to understand how residual trees are associated with structural complexity.

The index most preferable to the evaluation of structural complexity depends on the objective of the study. If, for instance, the objective is to describe wildlife habitat, researchers should use the SCI-dbh, which measures the conditions created by residual trees. It is evident from this study, however, that active management strategies for second-growth forests are required to hold the structure at the intermediate successional stage, maximizing structural complexity.

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