AN ABSTRACT OF THE THESIS OF

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Abstract approved:

David E. Hibbs

Despite the critical ecological roles of structural features in forests, ecologically relevant quantitative measures of structure that allow comparisons among forest stands are still limited. A new index, the structural complexity index (SCI), was developed to characterize and compare the structural complexity of different forests. Point patterns of stem-mapped trees were converted into nearest neighbor triangles (with x, y, and z coordinates) by spatial tessellation, where x and y represent horizontal spatial location of points, and z represents a character of the point like height or diameter. The SCI was defined as the sum of the surface areas of a network of non-overlapping triangles, which form a continuous faceted surface in 3-D. Structural gradients were defined as the maximum size difference among the trees forming a triangle, with greater differences indicating higher structure. To compare structure at different vertical scales, size differences among neighbors that are below a certain magnitude (grain) are considered similar, trees sizes are set equal, giving a lower SCI limit of 1. The SCI was found to be strongly related to tree size variation, tree density, density of emergent canopy trees (> 100 cm dbh), and species mixture in multiple-aged stands. Different structural conditions were simulated by randomly assigning values of the tree size distribution to

each tree position while holding the tree positions fixed, allowing an assessment of the maximum possible structural complexity (potential structure) given the observed tree size distribution. Based on the observed or effective structure and the potential structure, the "maximum structure hypothesis for natural mixed conifer forests" was proposed, stating that in the absence of large-scale, stand replacement disturbances and in the presence of small-scale disturbances associated with mortality and replacement of individual trees, the effective structure is near the potential structure. There was strong evidence in young and mature stands in favor of the maximum structure hypothesis, but stands resembling old-growth structures had effective structures less that their potential. Although rejected in its simplistic form, the maximum structure hypothesis may prove to be a powerful concept in the analysis of forest ecosystems.

A New Index for Describing the Structural Complexity of Forests

by

Eric K. Zenner

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Doctor of Philosophy thesis of Eric K. Zenner presented on April 27, 1998.
APPROVED:
Signature redacted for privacy.
Major Professor, representing Forest Science
Signature redacted for privacy.
Head of Department of Forest Science
Signature redacted for privacy.
Dean of Graduate School
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You have taught me something, maybe three things, rabbit footling mine.

Three things will never be believed - the true, the probable, and the logical.

John Steinbeck.

The Winter of our Discontent (1961).

A New Index for Describing the Structural Complexity of Forests

Chapter 1. Introduction

BACKGROUND AND HISTORICAL PERSPECTIVE

Policy objectives in a pluralistic society are general, complex, and sometimes inconsistent compromises derived by the competing interest groups. Preferences among people within any society vary greatly and this complexity is reflected in decisionmaking processes that respect multiple viewpoints. Since the late 1960's, public concerns and awareness of environmental problems have increased substantially (FEMAT 1993 a, b). The increasing diversity of social values has resulted in society's demand that forest management objectives reflect the complexity and differences of values inherent in society. Forests, like other natural resources, are typically managed for multiple objectives. Management objectives may include the maintenance of biological diversity, the production of timber, aesthetics, outdoor recreation, or the welfare of those who tend the forest or are otherwise dependent upon it (Castle 1993). That the system being managed should be guided toward an equilibrium condition that unites the existing diversity of viewpoints into one generally agreed upon philosophical system seems highly questionable. No one philosophical system is sufficiently broad to encompass the diversity of viewpoints (Castle 1993), nor is it very likely that an allencompassing environmental ethic will be discovered (Stone 1988).

Since pluralism allows policy inconsistencies and fails to guarantee conflict resolutions (Callicott 1990), a pluralistic, pragmatic and evolutionary approach to resource management would allow policies to be evaluated on the basis of their capacity to adapt and change in response to new information (Castle 1993). As with natural environments, social systems are subject to constant change. Relative weights given to, for example, timber production and habitat preservation change over time and society has to continuously renegotiate the relative importance associated with either preservation or utilization, recognizing the future as being inherently unpredictable (Castle 1993).

Until recently, a broad social consensus lent support to the primary forest management objective to convert older unmanaged forests to intensively managed plantations. Silvicultural technology for establishing and managing stands sought to enhance timber production and maximize returns from timber on rotations of 40 to 60 years (Swanson and Franklin 1992). Silvicultural techniques included clearcutting, site preparation, replanting of genetically selected nursery stock, fertilization, early shrub and hardwood control, and one or two commercial thinnings (Bailey 1996). These techniques tend to increase structural homogeneity within stands and minimize the time a stand remains in the stand initiation stage (Oliver 1981). Short rotations result in large proportions of the forest area in stand initiation and stem exclusion stages and preclude or reduce the development of complex late-seral forest conditions. Values such as aesthetics and wildlife habitat associated with horizontal and vertical diversity in stand structures are minimized by conventional short-term rotation management applied

uniformly over large areas. As a consequence, millions of acres of what were formerly mature and old-growth forests in western Washington and Oregon are now dominated by young, homogeneous Douglas-fir plantations. Such forests may not provide the diverse, heterogeneous habitats required to sustain the flora and fauna of the Pacific Northwest associated with mature forests.

Questions about possible negative effects of forest management practices on wildlife, fisheries, watershed values, recreational and aesthetic potential, and long-term productivity of forests, however, have raised questions in the general public about the adequacy of even-aged, timber-oriented forestry to address other social values. Fueled by the widening gap between an increasing diversity of social values and the strong historic commitment of the Forest Service and BLM to intensive timber management, the social consensus that once gave the Federal managers a clear mandate to define desirable forest management objectives has eroded. The assumption that professionals could be entrusted with drafting forest management policy objectives is no longer generally accepted (Castle 1993). Forest management has become increasingly political and silviculture is driven by social, economic, and management considerations outside the forestry profession (Tappeiner et al. 1986, FEMAT 1993). In particular, concerns for maintaining and restoring habitat for species associated with mid- to latesuccessional forests while still producing wood have illustrated the need to refine silvicultural systems that can successfully implement complex management objectives. Land managers and silviculturists are challenged to come up with alternative

silvicultural systems that allow for timber extraction while maintaining biological diversity by meeting habitat needs of native species.

In an effort to regain public trust in their ability to manage the Federal forested lands in compliance with the law and society's demand for multiple objectives, the federal agencies have embraced the concept of ecosystem management (Grumbine 1994). Ecosystem management, which recognizes that people and their values are part of the system that is to be managed for long-term integrity (Lertzman et al. 1997), fundamentally differs from conventional silvicultural planning systems. Two of several important differences are a focus on management strategies at multiple scales, and the production of heterogeneous stand structures.

IMPORTANCE OF SCALE

Whereas the domain of conventional silvicultural activities has been at the stand level, where management activities that sought to maximize timber production were most easily implemented, habitat needs of different wildlife species vary across a spectrum of scales. The spatial and temporal scales at which species perceive and respond to environment and habitat changes varies among species. Functionally relevant scales from an organism's perspective are known as grain and extent, i.e., the smallest and coarsest scales of habitat heterogeneity, respectively, to which an individual or a population responds. Functionally relevant scales are thought to influence a species' distribution and population dynamics (McGarigal 1995). Since habitats with suitable conditions for some organisms are distributed heterogeneously

within landscapes, spatial patterns may exert a strong influence on the abundance, distribution, and dynamics of populations (Wiens 1989 a,b). Consequently, habitat patterning such as habitat subdivision or fragmentation, habitat interspersion or juxtaposition, and connectivity between habitat patches may be critical components for the viability of a species (Kareiva 1990, Gilpin and Henski 1991). For example, the probability of persistence of wildlife species associated with late-successional forests is usually greater in larger patches of unfragmented, late-successional forest than in smaller, unfragmented patches (Rosenberg and Raphael 1986, Thomas et al. 1990, Lehmkuhl and Ruggiero 1991). Since home ranges and dispersal capabilities vary with body size and habitat specificity, distances and connectivity between suitable habitat patches determine if organisms can move between patches to ensure genetic exchange and heterogeneity among individuals and populations (USDI 1992). How much habitat individuals and populations need, how heterogeneous habitat conditions need to be, and what distances between habitat patches can be tolerated varies among species.

The importance of heterogeneity and scale in the structure and function of natural landscapes (Allen and Starr 1982, Kolasa and Pickett 1991) becomes clear in light of habitat variation at a wide range of scales and its effects on ecological processes and wildlife population dynamics (Wiens 1989 a,b). The qualitative behavior of the forest differs according to the scale at which it is referenced. A forest is a dynamic pattern that has been considered constant if viewed over a large area (Watt 1925, 1947). At a large scale, the forest is more or less an equilibrium system. At a small scale, forests are composed of patches that undergo characteristic dynamics based on

demographic mechanisms and life history traits of the species involved (Huston and Smith 1987, Smith and Urban 1988), but are also affected by microhabitat, seed dispersal and vegetative regeneration, and species interactions. Whereas physical patch structures are often related to gap sizes and distributions, compositional patch structures may not express the same relationships (Busing and White 1993). Attributes such as stand biomass, diameter distributions, and species compositions are interpretable as the integration of gap dynamics under given environmental conditions at the stand scale (Smith and Urban 1988). Whether sampling indicates, for example, a forest to be multiple-aged or not may be dependent on the plot size employed (Jones 1945, Goff and West 1975), since replacement may occur in clumps (Whipple and Dix 1979). The strength of an association among species abundance and habitat characteristics can be strongly influenced by the types of habitat attibutes considered, and by the spatial and temporal scales over which they are measured (Neilson et al. 1992). It becomes apparent that both patch dynamics and the steady-state forest are scale phenomena.

IMPORTANCE OF STRUCTURE

The structure of a forest is an important factor in the analysis of forest ecosystems. Forest structure has been used to define certain niche requirements of bird species (MacArthur and MacArthur 1961, James and Shugart 1970, Morse 1976) and other wildlife species (Reynolds et al. 1982, Forsman et al. 1984, Smith and Long 1987), to examine successional processes (Horn 1971, 1975, Connell and Slayter 1977,

Pickett 1983), and to predict timber production (Whittaker 1966, Smith and Long 1989, Long and Smith 1992, Buongiorno et al. 1994).

In contrast to intensively managed forests that are more uniform and have a much simpler structure and composition, natural, mixed-species forests are often structurally more complex in the early and late stages of succession or stand development (Franklin et al. 1981, Hansen et al. 1991, Spies and Franklin 1991).

Although the debate over whether or not late-successional species need old-growth for survival is still unresolved, age and species composition alone may not be adequate indicators of suitable wildlife habitat (Meslow et al. 1991). The structure of the vegetation may be used to define specific wildlife habitats (Hall et al. 1979, Thomas 1979, Verner et al. 1986, Hunter 1990) and structural patterns resembling old-growth may be important for habitat suitability of late-successional species (FEMAT 1993 a, b). Distinctive compositional and functional characteristics of late-successional forests are believed to be a direct consequence of their structural features highlighting the pivotal role of forest structure to understanding ecosystem dynamics (Franklin and Spies 1991).

The need for habitat structures of particular densities and sizes to support viable populations of each species may guide silvicultural prescriptions for individual stands (McComb et al. 1993). For example, species associated with mature stands seem to be associated with, or dependent upon, habitat structures such as large trees of several species, multilayered canopies, large snags and logs (Brown 1985, Ruggiero et al. 1991). Silvicultural systems that seek to convert young Douglas-fir forest into structurally more heterogeneous forests in time scales shorter than natural stand

development will thus have to provide many of the features found in comparable natural stands. Assuming that unmanaged mature and old-growth forests today support viable populations of species that are currently associated with these forests, the development, structure, and composition of natural stands can serve as a guide for alternative silvicultural systems (McComb et al. 1993). This notion was adopted in 1993 by the FEMAT-team for federal lands within the habitat range of the northern spotted owl. For these lands the development of silvicultural guidelines for management activities in Late-Successional Reserves, Adaptive Management Areas, and matrix lands to produce stand structures that resemble old-growth conditions, is encouraged. Similarly, the Oregon Department of Forestry (1996) has recently adopted the philosophy of "structure based management" to manage for a variety of objectives on their lands.

In the most general terms, forest structure is the distribution of biomass in space (Goff and Zedler 1968). Structural diversity can be characterized by the variation in species and age classes, the arrangement of species into different canopy layers, and the distribution of individuals among diameter classes (Smith 1986). Recently, forest structure has also been characterized with geostatistical tools (e.g., Pretzsch 1997, Kuuluvainen et al. 1996). Forest structure can thus be defined by a vertical and horizontal spatial arrangement of plant species, plant sizes, or age distributions (McEvoy et al. 1980, Gadow and Füldner 1992, Crow et al. 1994). Stand features such as stem density, basal area, canopy cover, the number of canopy layers, and height and diameter distributions have all been used to describe forest structure (see Jones 1945, Meyer 1952, Goff and Zedler 1968, Franklin et al. 1981, Spies and Franklin 1991). In

particular, research on forest structure has continuously and vigorously focussed on the importance of diameter and age distributions. Stand structural analysis based on relative abundances of trees in different sizes and ages has often been used to reconstruct details of stand development, assess tree population stability, and predict successional trends (Veblen 1986).

DIAMETER AND AGE DISTRIBUTIONS

Diameter distributions have often been used to make inferences about successional trends and the structural development of forests toward late-seral conditions. Despite varying degrees of skewness at young ages, even-aged stands of multiple species typically show unimodal diameter distributions that approach a more symmetric distribution with time (Meyer 1930, Hough 1932, Nelson 1964, Mohler et al. 1978). The heights and breadths of normal diameter distributions are believed to be a consequence of the initial seedling density and synchrony and/or length of the seedling establishment period (Peet 1981) and/or a progressive differentiation of species into distinct size strata in which the least shade-tolerant species occupies the larger size-classes (Smith 1986).

Multiple-aged stands of shade-tolerant species with light past disturbances typically have diameter distributions that can be approximated by a negative exponential or reversed J-shape form (deLiocourt 1898, Hough 1932, Assmann 1970, Leak 1975, Lorimer 1980). Stands exhibiting a reversed J-shape diameter disribution have been considered indicative of sustained replacement (Peet 1981) and thus approach

stable or steady-state forest conditions (Meyer 1952, Leak 1964, 1965). This reversed J-shape distribution results from a constant birth rate and a constant probability across all age-classes of an arbitrary individual dying. If the probability of dying decreases at a constant rate relative to size, the resulting diameter distribution is a power function or more concave reversed J-shape (Hett and Loucks 1971). Goff and West (1975) believed the negative exponential form to be characteristic for large forest tracts having localized patches of even-aged trees. Stable, undisturbed old-growth forests of small area or uniform structure, however, were shown to have rotated sigmoid diameter distributions. In stands having several age-classes, diameter distributions may vary from nearly normal to irregular negative exponential depending on the shade tolerance and age class dispersion in the stand (Hough 1932, Henry and Swan 1974, Lorimer 1983). Whereas diameter distributions of midtolerant species consistently approximated a normal distribution, those of tolerant species were highly variable from unimodal to negative exponential (Lorimer and Krug 1983). Diameter distributions are, however, not solely dictated by life-history traits like shade tolerance; instead they represent the changing response of a population to variation in the physical environment, the pool of species occuring at the site, dispersal potential, and the prevailing disturbance regime (Parker 1988). Bimodality in diameter distributions is thought to be the result of competition for light, a one-sided dominance/suppression competition in which larger-sized individuals or species obtain a disproportionate share of environmental resources at the expense of smaller-sized individuals or species (Ford and Diggle 1981), or age classes representing different partial disturbances.

NATURAL DISTURBANCES AND THE DEVELOPMENT OF FOREST STRUCTURE

Forest structure, including species composition and diameter and age structures, reflects the influence of past and present environmental conditions (White 1979, Oliver 1981, Whitemore 1982) and hence historical events (McCune and Allen 1985) and is, in old-growth forests, largely determined by gap processes (sensu Watt 1947). Over time, structural dynamics within and among stands may be important factors that influence change in the understory vegetation, wildlife habitat, and ultimately, stand succession. Canopy disturbances can occur at a range of spatial and temporal scales in Pacific Northwest forests, with varying importance of fine- and coarse-scale disturbances in controlling community dynamics during stand development (Spies and Franklin 1989). Coarse-scale (>0.1 ha) disturbances (Spies and Franklin 1989), such as crown fires, hurricanes, tornadoes, windstorms, snow avalanches, landslides, mudflows and other severe soil erosion or deposition, and forest clearcutting (Oliver 1981) create canopy openings that assume a wide range of sizes and generally homogenize the structure and restart the succession in the disturbed area. In the Oregon and Washington Cascades, wildfire, occurring at variable intensities and frequencies, has been an important cause of canopy openings (Morrison and Swanson 1990). The size of coarse-scale events affects environmental conditions and heterogeneity within open patches (Pickett et al. 1987) and may influence the composition, structure, and development of post-fire stands (Halpern 1988, Spies and Franklin 1989). Wildfires often leave patches and scattered individuals of live, remnant overstory trees, snags, and logs (Morrison and

Swanson 1990) and subsequent vegetative growth enhances the stand's structural complexity (Hunter 1990, Spies et al. 1990). The large trees and dead wood may persist as biological legacies into the closed canopy stage in the subsequent young stand, providing habitat for mature-forest vertebrates (McComb et al. 1993) and other organisms, such as epiphytes (Peck and McCune 1997). The shape of the disturbance can influence the amount of edge, which has been recognized as an important wildlife habitat (Reese and Ratti 1988). Edges represent abrupt changes in environmental conditions and edge quality for species sensitive to microclimatic conditions is related to the degree of contrast represented by the edge (Thomas et al. 1979).

Post-disturbance change reflects the nature of disturbance, characteristics of the initial community, life history traits, local environmental conditions, and effects of stochastic events, such as limited seed availability or local weather fluctuations (Halpern 1988, Halpern and Franklin 1990). The severity of a disturbance affects the survival of propagules and advanced regeneration, as well as the openness of the site (Pickett et al. 1987). Differences in the severity and frequency of disturbance events can give different species an initial advantage and dominant position in the resulting stand (Grime 1977, Oliver 1981), depending on the particular adaptive mechanisms of each species for development after disturbance (Harper 1977, Grime 1977). Although limited available seed sources of Douglas-fir and western redcedar can sufficiently delay restocking of many stands for decades (Franklin and Hemstrom 1981, Klopsch 1985), there is evidence that most species either survive the disturbance or colonize shortly thereafter (Long 1976, Connell and Slayter 1977, Wiermann and Oliver 1979).

For example, early successional patterns revealed that shifts from herb to shrub dominance occurred earlier on burned than on unburned sites due to rapid development of invading shrubs, and subsequent transitions to tree dominance showed no clear relationship with disturbance intensity (Halpern 1988). The composition and structure of pioneer forest developing after fire can also be a strong determinant of subsequent regeneration (Stewart 1986a). For example, in Douglas-fir dominated post-fire stands, western hemlock invaded the patch at an early stage. If, however, western hemlock dominated, subsequent regeneration was limited by dense canopies and the occurrence of canopy openings (Stewart 1986a).

There is accumulating evidence that multiple successional pathways following coarse-scale disturbances are common and several different forest communities could inhabit the same area for an indefinite period (Egler 1954, Connell and Slayter 1977, McCune and Allen 1985, Connell 1987, 1989). This is contrary to the concept of development toward a unique climax condition in a steady state equilibrium (*sensu* Clements 1916). However, despite the possibility of multiple pathways for succession, there seems to be a general pattern of forest structural development after a coarse-scale disturbance. Oliver (1981) defined general physiognomic stages, which include stand initiation, stem exclusion, understory reinitiation, transition, and steady state, the latter two often termed old growth. The old growth stage has been expanded by Spies (1994) to include maturation, transition, and shifting gap, paying tribute to the protracted nature of stand development in coniferous forests in the Pacific Northwest. Depending on site conditions and stand history, the maturation stage typically begins between 80 and 140

years in Douglas-fir forests west of the Cascades. Maturation is characterized by a slowing of the rate of height growth and crown expansion and the formation of gaps. Beginning between 150 and 250 years and lasting for an additional 300 to 600 years depending on site conditions and species, the transition stage is characterized by multiple understory canopy layers, accumulation of coarse woody debris, and maximum height and crown diameter in overstory trees. In this stage, low to moderate intensity disturbances create patchy openings that will eventually be filled by understory trees. A relatively uncommon stage in Pacific Northwest forests, the shifting-gap stage, forms in the absence of coarse-scale disturbances when the last of the original overstory trees dies.

These general physiognomic stages provide the framework for the development of forest structure. Within this framework, the greatest changes in forest structure and composition occur early in stand development and succession (Spies 1994).

Additionally, the structure of forests also depends on fine-scale (<0.1 ha) disturbances (Spies and Franklin 1989) or perturbations (e.g., surface fires, windthrow of some overstory trees, lightning strikes, insects, root pathogens, small-scale diseases, and competitive mortality; Oliver 1981, Franklin et al. 1984). Fine-scale disturbances occur throughout all stages and break up the relatively uniform coarse-scale patches in a mosaic of canopy openings, thus enhancing structural and species diversity (Spies and Franklin 1989, Morrison and Swanson 1990). Whereas frequent coarse-scale disturbances can delay or preclude the development of mature-forest structures, frequent fine-scale disturbances may enhance the development of multilayered canopies, large

snags, and large logs (Spies et al. 1990). Fine-scale disturbances accelerate the changes from young to mature and old-growth by increasing (1) woody debris in the stand, (2) vertical and horizontal heterogeneity, and (3) the proportion of shade-tolerant trees (Spies and Franklin 1988).

The local tree species composition and structure of forests may be a consequence of the site condition and the distribution of gap sizes (Brokaw and Scheiner 1989). Gaps are created in the forest canopy by the death of one to many trees. Gap size appears to influence species composition through changes in microclimatic conditions (McClure and Lee 1993). Gap disturbances increased species richness and diversity in northern hardwood forests (McClure and Lee 1993). In conifer forests, western hemlock can regenerate without canopy gaps (Stewart 1986a), and small seedlings and very slow-growing saplings of several other shade-tolerant species (e.g. western redcedar) can be found under intact canopies and low light conditions. In Douglas-fir/western hemlock forests, Douglas-fir does not reach the canopy in gaps less than ≈700-1000 m² (Spies and Franklin 1989), probably because most canopy trees die standing or by top breakage (Spies et al. 1990). Consequently gaps are not formed in the lower tree stratum and no mineral soil, which serves as a seedbed for Douglas-fir (Minore 1979), is exposed. Transmitted light levels are also too low for survival of Douglas-fir seedlings (Spies and Franklin 1989). However, on dry sites of the Western Hemlock Zone, Douglas-fir reproduces and reaches the canopy in small gaps (Means 1982). This may be attributed to the lack of a dense understory canopy of western

hemlock and the shorter canopy height than Douglas-fir/western hemlock forests, which permits higher light levels for Douglas-fir regeneration (Spies and Franklin 1989).

Forest structure clearly varies widely across the region as a consequence of variation in stand disturbance and stand history. Structural characteristics of forest stands, such as stand basal area, tree density, species composition, and the distributions of diameter, height, leaf area and crowns can vary considerably even though stands may have been established at the same time. Age has often been used to define old-growth, but age alone may be a poor indicator of old-growth structure (Spies and Franklin 1988). The age at which a forest develops old-growth characteristics varies with forest type, species composition, site conditions, and stand history (Spies and Franklin 1991).

THE STRUCTURE OF OLD-GROWTH FORESTS IN WESTERN WASHINGTON AND OREGON

What structural features do most strongly discriminate young (40-80 years), mature (80-200 years), and old-growth (>200 years) Douglas-fir dominated stands in western Oregon and Washington and southern Oregon and northern California? The strongest discriminators among forest age-classes have been found to be tree density, density of large Douglas-firs, the mean and variation in tree diameter (Spies and Franklin 1991), and features of tree height and diameter distributions (Bingham and Sawyer 1991). For example, in western Oregon and Washington forests, tree density (stems/ha) was about twice as high in young stands as it was in mature and old-growth stands. Basal area increased with age-class. The mean tree diameter was highest in

mature trees, reflecting the lack of smaller diameter classes in mature stands. This contrasts with old-growth stands with more shade-tolerant trees and the highest overall mean and standard deviation in tree diameters. A single canonical variable, related to standard deviation of tree diameter and density of large trees (>100 cm in dbh) explained most of the variance between age-classes (Spies and Franklin 1991).

Old-growth stands from different geographic provinces and relative site moisture classes differed considerably in structure, which was attributed to the variation in densities of shade-tolerant trees and in particular western hemlock (Spies and Franklin 1991). On dry sites, which may also have had a higher fire frequency, overstories generally had a low abundance of shade tolerant and less fire-resistant plants, suggesting more open canopies that allow more understory development. In contrast to moist sites, which had relatively higher cover of herbaceous species, drier sites had a greater density of subcanopy trees (e.g. Castanopsis chrysophylla (Dougl.) A.DC. Golden chinkapin). The increase in the percentage of herb cover with site moisture exhibited a strong trend with stand age-class. Spies and Franklin (1991) speculated that changes in understory light intensity and microclimate may explain higher herbaceous cover in old-growth stands. Old-growth forests dominated by western hemlock have a lower understory light intensity than mature or young forest canopies dominated by Douglas-fir (Spies et al. 1990). A low light environment may favor more shade-tolerant herbs over more evergreen shrubs, which often form dense clonal patches in mature to young forests, thus limiting the development of many herbaceous plants in younger forests (Long and Turner 1975, Spies and Franklin 1989).

However, the opposite was found by Stewart (1985, 1988); whereas Douglas-fir dominated stands often exhibited a lush herbaceous understory, adjacent western hemlock or multilayered Douglas-fir/western hemlock stands had only a trace of understory development. Furthermore, understory cover in old-growth stands varied considerably and was about twice the cover in Douglas-fir than in western hemlock stands (Stewart 1986a). Species richness in the understory was also greater under Douglas-fir canopies and openings than under western hemlock, which may have been due to lower potential direct radiation beneath western hemlock canopies (Stewart 1988, Traut 1994). Overstory canopy structure is often strongly correlated with patterns of tree regeneration (Spies et al. 1990, Stewart 1986 a, b) and directly (Stewart 1988) or indirectly (via tree regeneration; Traut 1994) with herbaceous understory composition.

Old-growth structures vary widely across the region as a consequence of variation in stand disturbance and stand history (Spies 1990), but appear closely related to available moisture (Dyrness et al. 1974, Zobel et al. 1976, Hemstrom et al. 1987) and densities of shade-tolerant species and understory characteristics (Spies 1990). In coastal forests recovering from disturbance, however, structural variation among age-classes appeared to be less influenced by climate than by the normal developmental process related to growth and biomass accumulation (Arsenault and Bradfield 1995), maybe because of a less variable climate in coastal areas. The following major structural characteristics of old-growth forests have consistently been found in western Oregon and Washington: a wide range of tree sizes and ages, a deep multilayered crown canopy, large individual trees, and accumulations of coarse woody debris including

large snags, logs on land and logs in streams (Franklin and Spies 1983). These characteristics are reflected in current "minimum standards for old-growth Douglas-fir forests" (Old-growth Definition Task Group 1986) in the Tsuga-heterophylla Zone (Franklin and Dyrness 1973):

- ≥ two tree species with a wide range of ages and sizes, forming a deep, multilayered canopy;
- ≥ 20 Douglas-fir trees/ha > 81 cm in diameter or > 200 years of age;
- ≥ 30 trees/ha of associated species (e.g., western hemlock, western redcedar, bigleaf maple, Pacific siver fir, grand fir) > 41 cm in diameter;
- ≥ 10 conifer snags/ha > 51 cm in diameter and 4.6 m in height;
- ≥ 34 metric tons/acre of downed logs, including 10 pieces > 61 cm in diameter and > 15 m in length.

Structural complexity is a key ecological feature of old-growth forest ecosystems (Spies and Franklin 1991) and is hypothesized to promote habitat diversity for forest organisms, nutrient cycling, beneficial predator-prey relationships among forest invertebrates, refugia and inocula for nonvagile mycorrhizal-forming fungal species and invertebrates, and dispersal opportunities for species that avoid forest openings (Franklin 1992, Swanson and Franklin 1992, Hansen et al. 1995). The degree of spatial variation in available habitats (e.g., niche diversification, Connell 1978) or resource availability (Tilman 1982) may control species diversity (Halpern and Spies 1995). For example, some lichen species occur only in older stands that provide stable and appropriate substrates with associated canopy microclimates and have not experienced major disturbances for centuries (FEMAT 1993 a, b). It may take over 200 years for late-successional lichens to become established following a coarse-scale disturbance (Lesica et al. 1991). Higher biomass (McCune 1993) and a more diverse species composition of epiphytic bryophytes (Lesica et al. 1991) was also noted in older forests. Wildlife examples include the association of large Douglas-fir (>100 cm dbh) with marbled murrelets (Singer et al. 1991), northern spotted owls (Forsman et al. 1984), bark-foraging birds (Peterson et al. 1989), and northern flying squirrels (Maser et al. 1981); snags with spotted owls (Carey 1985) and cavity nesting birds (Neitro et al. 1985, Nelson 1989, Marcot 1991); and log densities and litter depth with marsh shrews (Corn et al. 1988).

SPATIAL CONSIDERATIONS

The spatial pattern of trees in a forest reflects the disturbance and developmental history of the stand (Bradshaw and Spies 1992, Moeur 1993). Mechanisms influencing tree spatial patterns are likely complex and not mutually exclusive. For example, spatial patterns are influenced by the complex historical and environmental mosaic imposed by initial establishment and growth patterns, microenvironmental differences, interactions and chance successes of individuals and groups of trees with different life history characteristics (Moeur 1993) and past stand management (Schoonderwoerd and Mohren 1987). Structural complexity of stands has been related to spatial variability in topographic and substrate conditions, variability in fire regimes, post-fire stocking densities, and variability in pest-infestation patterns (Parker and Parker 1994).

Growth and establishment of individual trees are influenced not by the population density *per se*, but rather by the proximity, size, and activity of immediate neighbors (Mack and Harper 1977). Since the position of a tree with respect to nearby trees determines the space available for an individual (Weiner 1984), the spatial pattern

controls growth and establishment of the understory (Bradshaw and Spies 1992). Trees are generally clumped rather than uniformly distributed (Cooper 1960, Bonnicksen 1975, Greig-Smith 1979), but this is dependent on age (Stohlgren 1993) and scale (e.g., Moeur 1993). Younger trees tend to be more clumped than larger, older trees (Cooper 1961, Bonnicksen 1975, Stuart 1983). Since trees primarily compete with their neighbors and self-thinning increases the distance between trees, competition-induced mortality drives spatial patterns from clusters toward uniformity (Kenkel 1988, Moeur 1993). Differential thinning and complex patterns of survivorship around large individuals would overcome initial patchiness of establishment, resulting in less clumped, more uniform spacing (Laessle 1965, Kenkel 1988, Rebertus et al. 1989). Given patchy establishment, stand development can be expected to proceed from clumped to uniform, through differential self-thinning in the most crowded patches, and then from uniform to random, through random mortality in medium- or large-sized trees (Stohlgren 1993). Over time, seedling aggregations would tend to become less distinct as individuals within clumps grow together, thus creating complex spatial patterns in old-growth forests (Stohlgren 1993, Duncan and Stewart 1991).

PROPOSED ALTERNATIVE SILVICULTURAL SYSTEMS

Silviculture is the manipulation of forest structure to achieve various objectives.

Structural parameters such as tree density or basal area are amenable to manipulation during harvesting or thinning (Muir 1993). Currently, alternative silvicultural systems that can be used to create old-forest structures sooner than through natural stand

development are in high demand. What can silviculture do to hasten the development of more structurally heterogeneous stands?

Although the individual forest stand may still be an important management and planning unit for alternative silvicultural systems, objectives for individual stands must be regarded as integrated parts of a landscape-level management approach. Since no single stand management system will precisely match the variability inherent in natural stands, a combination of several silvicultural systems across the landscape may promote heterogeneity and diversity of forest conditions (McComb et al. 1993). Considering size and connectedness of mature stands over landscapes, harvest of stands could be planned to guarantee at least a minimum amount of unfragmented old-forest habitat.

Reviewing silvicultural techniques to meet northern spotted owl habitat,

Tappeiner (1992) suggested early thinnings in addition to, if needed, killing larger trees to provide for large snags and downed logs. Thinnings would provide small-scale disturbances required to create multi-storied canopies. Responses to thinning that have been reported are (from Bailey 1996): (1) for overstory trees; increased tree diameter, increased merchantable volume accumulation, reduced mortality, stimulation of branch size and live crown development, (2) for understory trees; establishment of new cohorts of conifers and hardwoods and increased height growth, (3) for shrubs and vascular plants; increased shrub and herbaceous cover and frequency, e.g., salmonberry, vine maple, grasses, sedges, bracken fern, and, in particular, rhizomatous species.

Understory responses to thinning, however, vary inconsistently among different sites and environmental conditions. Generally, the duration of the shrub stage following

thinning seems to be prolonged while the stem-exclusion stage seems to be reduced (Alaback 1984). Knowledge about long-term responses of understory vegetation to thinning is still incomplete.

Swanson and Franklin (1992) proposed silvicultural practices such as selective cutting or green-tree retention systems that are based in part on the natural disturbance regime of individual sites in that biological legacies are retained (Franklin 1990).

Green-tree retention is entirely different from traditional selection cutting that is designed to create uneven-aged stands (Franklin 1990). The effectiveness of green-tree retention systems providing habitat and refugia for species and ameliorating negative impacts of clearcuts is currently being tested in the Pacific Northwest (Hansen et al. 1995, McGarigal and McComb 1995, Aubry et al. 1998).

The effects on stand structure of several silvicultural approaches that seek to imitate large-scale disturbances, which result in single- and few-storied stands and fine-scale disturbances, which result in many-storied stands have been simulated and discussed by McComb et al. (1993). Single-storied stands were based on either clearcutting, or shelterwood and deferred rotation (Smith et al. 1989) with emphasis on retention of green-trees and snags and variable intensity thinnings. Compared to other techniques, single-storied stands are expected to provide the lowest levels of patch size variation, canopy cover, and large live-tree survival. Few-storied stands developed as the result of regenerating two or more age classes (shelterwoods with reserves; Long and Roberts 1992) or a single age class composed of species with differential growth rates and size potentials (mixed-species clearcuts). These techniques imitate relatively

even-aged patches of Douglas-fir and western hemlock which naturally establish through coarse-scale disturbances. Underplanting with shade-tolerant species in existing young even-aged plantations after thinning or planting mixed species such as Douglas-fir with red alder or western redcedar would produce few-storied stands. Many-storied stands could be created through group- or single-tree selection systems that would mimic small-scale disturbances. This system would have high within-stand variability in tree sizes and vertical complexity, but its implementation is more dependent on harvesting technology than the previous alternatives. Although manystoried stands provide some old-growth structures, they should not be considered a replacement for old-growth (Hunter 1989). The main differences are in the lower structural complexity and stocking levels in many-storied stands following cutting of primarily commercial species and reduced mortality through thinning (McComb et al. 1993). It is, however, uncertain to which degree and for what wildlife species actual old-growth is needed to ensure their survival.

There seems to be consensus among silviculturists and ecologists that alternative silvicultural practices that seek to incorporate natural ecosystem dynamics to balance timber extraction, habitat restoration and maintainance, and human values, need to consider ecosystem-specific information. Silvicultural practices would thus be based on the knowledge and understanding of effects of local and regional disturbance patterns on stand structure, differences and changes of stand structure (dynamics) over time and space, and the relationship of stand structure and landscape patterns to forest ecosystem functions, and thus manage for values and functions desired of structural characteristics.

CONTEXT FOR THE CURRENT STUDY

Processes that operate at different spatial and temporal intensities and scales can influence the complexity of structural, compositional, and functional characteristics of natural Douglas-fir forests in western Washington and Oregon. In this context, climate, local site potential, regional flora, disturbance history and patterns, tree regeneration dynamics and life-history traits of species, and chance have all been implicated as players in creating the continuum of forest structures existing today, each at their own temporal and spatial scale. Research on forest structure in the Pacific Northwest has focused primarily on the reconstruction of the size and age structure of trees (e.g., Stewart 1986 a,b, Morrison and Swanson 1990, Wilson 1991), the structure of vascular plants in relation to temperature and moisture stress (e.g., Zobel et al. 1976, del Moral and Long 1977, del Moral and Fleming 1979), structural changes in stand development (e.g., Spies and Franklin 1989), and the description of structural features in old-growth forests (e.g., Franklin et al. 1981). Recently, the importance of structural features as habitat for wildlife species has been explored in several studies (e.g., Hansen et al. 1995, McGarigal and McComb 1995).

If silvicultural manipulation is intended to mimic natural stand development, determination of characteristic patterns of old-growth stand structure is useful for enhancing and restoring old-growth ecosystems within managed landscapes (Mladenoff et al. 1993). Structural changes after natural disturbance in the Douglas-fir region follow two general pathways in time (after Franklin and Spies 1991). The first pathway has a U-shaped pattern and includes the amount and percentage of total ecosystem

biomass of coarse-woody debris, the number of large snags, the heterogeneity of the understory, and plant and mammal species diversity. High values immediately after a catastrophic disturbance in old-growth decline to lowest values midway through the succession and increase again to moderately high levels in old-growth forests, where levels may decline somewhat as Douglas-fir is being lost from the forests. The second pathway has an S-shaped pattern and includes the average and diversity of tree sizes, the incidence of broken tops, forest floor depth, surface area of boles and branches, and wood biomass. Low values early in succession increase asymptotically until the oldgrowth stage is reached, where levels may stay high for several hundred years. Franklin and Spies (1991) suggest the development of an index for "old-growthness" or a structural diversity index that captures these pathways in such a way that latter stages of Douglas-fir stand development receive the highest values. Developing other indices where important habitat structures would receive different weights may aid wildlifehabitat management.

Based on Spies and Franklin's (1991) identification of four variables that best discriminated among young, mature, and old-growth forests (e.g., mean tree dbh, standard deviation of tree dbh, density of Douglas-fir > 100 cm dbh, and the number of trees/ha), Acker et al. (1998a) evaluated the similarity of successional stands to old-growth stands. They developed an index that gives equal weight to all four variables. The index calculates the sum of the ratio of differences between the difference in means of the observed stand and young stands (from Spies and Franklin 1991) to the difference in means of the old and young stands (from Spies and Franklin 1991). Based on their

index, Acker et al. (1998) found that development towards old-growth structure was rapid up to about 80 years and gradual thereafter, reaching about one-half the transition from young to old-growth forest structure by age 100 years. The major limitations of this index are, however, its dependence on average values of young and old-growth stands, which ignores the wide range of "old-growthness" in the region (Spies and Franklin 1991) and its neglect of spatial distributions.

The distribution and diversity of diameters as an indicator of stand structure and a determinant of biological diversity has long been recognized (Buongiorno et al. 1994). Several problems with endangered species can be related to stand structures and the lack of trees in large size classes. Although different stands may have the same mean and total basal areas and identical diameter distributions, Pretzsch (1995 a, b) demonstrated in a simulation study that the spatial distribution of trees has a remarkable influence on the resulting stand structure.

The structure of a patch is a function of the variation in two basic components of heterogeneity: contrast and aggregation (Kotliar and Wiens 1990). Contrast refers to the degree of difference between patches or between the patch and the surrounding matrix at a given scale and are a function of the relative sizes of the individual patches (Greig-Smith 1952, Hill 1973, Wiens 1976, Forman and Godron 1986, Dale and MacIsaac 1989, Wiens 1992). As contrast increases, the discreteness of patch boundaries increases. Aggregation refers to the spatial distribution (i.e., clumped, random, or uniform) of patches at a given scale (Kotliar and Wiens 1990). Aggregation transfers "among-component" variation to "within-component" variation when

changing scales, until, at the coarsest scale observed, all the variation is contained within that scale (Smith and Urban 1988). The structure of patches is thus a function of hierarchies (Allen and Starr 1982, O'Neill et al. 1986), whereby the context of a patch in the larger mosaic is constrained by patchiness at higher levels and the structure of a patch is influenced by heterogeneity at lower levels (Kotliar and Wiens 1990). More than one single scale of patchiness must be considered to understand its consequences on habitat selection (Wiens 1985, Morris 1987) or on structural developmental processes, which involves differential responses to patch structure at a series of hierarchical levels.

OBJECTIVES OF THE CURRENT STUDY

Only recently have researchers begun to recognize how patterns and processes interact and how local site potential, ecological factors, such as elevation, aspect, topographic position, and soil type, and chance affect patterns and processes, and are ultimately responsible for the structure of these forests. It seems, indeed, imperative that alternative silvicultural practices that seek to incorporate natural ecosystem dynamics consider the patchy nature of tree distributions not only at several spatial and temporal scales, but also the internal heterogeneity of individual patches at a variety of contrast-scales. The range of sizes, shapes, and horizontal distribution, as well as the internal heterogeneity, of patches may more completely characterize forest structures at different scales. Comparing the internal structural heterogeneity of patches (i.e., vertical contrasts among the patch elements) and horizontal variability of tree distributions

within a chronosequence of natural stands and between natural and managed stands would aid managers in designing thinning strategies that take different scales into account. Although research on patterns and processes at scales from landscapes to regions is becoming more common (Spies et al. 1994, Wallin et al. 1994) and research must focus on processes that integrate ecosystems across large scales (Lertzman et al. 1997), the implementation of silvicultural systems occur one tree at a time. Developing different thinning alternatives and management strategies to enhance the development of structural complexity in managed stands would clearly aid managers in monitoring and evaluating the success of "ecosystem management". This research was formulated to address the following objectives:

- develop an index that characterizes the 3-dimensional heterogeneity of forest structure at different scales to compare different forests (Ch. 2);
- apply the index in forest management (Ch. 3).
- characterize the internal heterogeneity of patches at a variety of scales (Ch. 4);
- characterize the spatial distribution of different tree species and sizes (Ch. 4);

Chapter 2

Much Ado About Forest Structure - A New Methodology for Modeling the Heterogeneity of Forest Structure Across Scales.

Eric K. Zenner and David E. Hibbs

ABSTRACT

Despite the critical ecological roles of structural complexity, ecologically relevant quantitative measures of structural complexity that allow comparisons among forest stands are still lacking. The primary objective of this study was to develop a methodology that allows comparisons of structural heterogeneity among stands across spatial scales. First, three horizontal spatial patterns were simulated for tree size distributions taken from each of five natural stands. Point patterns of tree sizes were converted into nearest neighbor triangle areas (with x, y, and z coordinates) by spatial tessellation. A structural complexity index (SCI) was defined as the sum of the areas of the triangles, which related closely to conventional descriptors of forest structure. Structural gradients were defined as the maximum size difference among the trees forming a triangle, i.e., the greater the difference, the greater the structure. To allow comparisons of structural complexity at different vertical scales, size differences among neighbors below a certain magnitude (i.e., the grain) are ignored and the triangle is treated as if all trees had the same size. Successively increasing the vertical grain has a lower limit of 1 for the SCI when the differences between the smallest and tallest tree sizes are smaller than the grain. Patch-types, defined as classes of structural gradients at different positions within the canopy, were compared among the stands. More patchtypes were found in more structurally heterogeneous stands. The applicability of this modeling approach in characterizing the structural heterogeneity of forests across spatial scales is discussed.

INTRODUCTION

The structure of forests has become an important factor in the analysis and management of forest ecosystems. Structural characteristics have been used to define niche requirements of wildlife species, to examine spatial heterogeneity and temporal dynamics of understory vegetation, to investigate patterns of regeneration and gap dynamics, to explain microclimatic variation, and to predict timber production (e.g., MacArthur and MacArthur 1961; James and Shugart 1970; Forsman et al. 1984; Spies and Franklin 1989; Runkle 1991; Chen and Franklin 1995; Whittaker 1966; Long and Smith 1992; Buongiorno et al. 1994). In these studies, structural heterogeneity, complexity and diversity are recurring themes in the explanation of the observed ecosystem processes and functions. Structural complexity is also believed to be a key feature and distinctive characteristic of late-successional forests (Franklin and Spies 1991).

The measurement of structural heterogeneity, complexity, or diversity is, however, not as simple as might be expected. Forest structure has been described, in the most general terms, as distribution of biomass in space, i.e., a vertical and horizontal spatial arrangement of plant species, plant sizes, or age distributions (Goff and Zedler 1968, McEvoy et al. 1980, Gadow and Füldner 1992, Crow et al. 1994), characterized by the variation in species and age classes, the arrangement of species into different canopy layers, and the distribution of individuals among diameter classes (Smith 1986). While these definitions recognize the 3-dimensionality of forest structure, quantitative, ecologically relevant measures of the full 3 dimensions of structural complexity that

allow comparisons among forest stands are, however, still lacking. Analyses of forest structure range from qualitative or 0-dimensional descriptions, to 1-dimensional summary statistics (e.g., coefficient of variation of size, foliage height profile), to 2-dimensional investigations of point patterns. Structure at any time is, however, a 3-dimensional phenomenon with horizontal and vertical components.

Zero-dimensional graphical methods (Hallé et al. 1978), including vertical diagrams illustrating crown stratification and crown projection (Kuiper 1988), have been used to elucidate some general patterns of stand development, such as the differentiation of the forest into strata or crown classes, but no quantitative analyses on the structural complexity of different stands are performed.

Several 1-dimensional structural variables have been taken to represent forest structure, including stem density, basal area, canopy cover, the number of canopy layers, the mean and variation in tree sizes (diameters or heights) measured by the coefficient of variation, the gini coefficient, and the Shannon diversity index (see Jones 1945; Meyer 1952; Goff and Zedler 1968; Franklin et al. 1981; Spies and Franklin 1991). Such conventional stand descriptors do not incorporate directly the vertical and horizontal spatial arrangement of the plants, and largely ignore the spatial character of forest structure. For example, whereas the application of the Shannon index (H') may be a reliable measurement for tree height or canopy structural diversity, it ignores the horizontal spatial component (x, y) of structure. These descriptors provide valuable insights into an average structural condition of a stand, but yield-related stand averages and sums, often based on small sample plots, do not capture 3-dimensional structural

complexity (Pretzsch 1997). Although discriminant analyses, performed on conventional structural variables, allow a separation of old-growth from mature and young stands (e.g. Spies and Franklin 1991), quantitative comparisons of structural heterogeneity among stands have not emerged from these studies.

Recently, researchers have begun to investigate 2-dimensional horizontal patterns (x, y) of stem-mapped data (e.g. Moeur 1993; Pretzsch 1995; Kuulivainen et al. 1996) with nearest neighbor analyses, Ripley's K function, or geostatistical tools that incorporate the horizontal distribution of trees into their description of forest structure. The horizontal pattern of tree locations, which are typically classified into regular, random, and clustered patterns, is the outcome of a 2-dimensional point process. For example, observed spatial patterns have been linked to processes (e.g., tree mortality, competitive interaction, regeneration, gap creation) believed to be responsible for the observed pattern and allowed predictions and tests of several hypotheses (e.g., random mortality hypothesis, Kenkel 1988). The weakness of this approach, however, is that spatial point pattern analysis only accounts for locations of trees, without taking their size variation in space into consideration (Kuulivainen et al. 1996), and thus ignores the vertical structure (z) of the forest. The semivariogram also can be used to provide insight into the scales of patchiness of forest stands (x, z) and highlight the scales of spatial dependence of tree sizes (Palmer 1988). It is, however, often difficult to interpret semivariograms, which may suggest the extent of the scales at which patterns operate rather than provide information on the structural complexity of forests.

For watershed and landscape scales, ecologists have developed tools to investigate landscape heterogeneity based on the recognition of the importance of patches (e.g., McGarigal and Marks 1995). Patches occur at a variety of scales (Wiens 1976), and have internal structures that (1) reflect patchiness at finer scales and (2) are the outcome of processes at larger scales (Kotliar and Wiens 1990). Patch-type heterogeneity, patch-size heterogeneity, patch connectivity, or patch-type interspersion are a few variables used to describe landscapes (e.g., McGarigal and Marks 1995). Patches may also be regarded as building blocks of structural complexity in forests.

The goal of this study was to develop an analytical model of forest structure and to test this modelling approach to quantify the 3-dimensional structural complexity of stands by: (1) developing a 3-dimensional model of forest structure; (2) simulating different structural conditions by randomly assigning observed tree heights to three computer-generated point patterns of trees; and (3) examining the horizontal and vertical structural variability generated from the model, using the Structural Complexity Index (defined below). In this paper we present a methodology that allows the use of tools developed by landscape ecologists at the stand, patch, and tree levels for describing and comparing the structural heterogeneity among stands. We also propose an index that is sensitive to both horizontal and vertical components of forest structure at the same time and explore the possibilities of its applications.

MODELING APPROACH

Suppose different forest stands have the same tree densities, basal areas, and frequency distributions of heights or diameters at breast height (dbh), but differ in their spatial arrangement of trees. For example, one stand might be composed of a series of adjacent strip-clearcuts, each a different age. There would be a gradual decrease in tree heights from the edges of the oldest to the youngest stands. This structure is very different from that of another stand with the same density and frequency distribution but created by a selection system where single trees or small groups of trees were harvested and regeneration occured in small to medium-sized gaps. From these two examples it is apparent that the spatial arrangement of the trees, not just their size distribution, is also a component of the structural complexity of a stand.

Next, suppose that the spatial arrangement of the trees is held constant, but that different heights from a known tree height distribution are randomly assigned to each tree position within the area. Now the importance of differences of heights among neighboring trees becomes evident. In this study, forest structure was modeled and analyzed by simulating point patterns of stems and constructing triangular networks to connect neighboring tree tops to one another. To compare the structure of different forest stands, necessary stand variables include tree density, the diameter and height distributions, and spatial patterns of the stems.

In this paper, a patch is defined by neighboring trees, whose maximum height differences (Δz) do not exceed a certain vertical difference (i.e., grain). Thus a patch is all contiguous trees whose maximum height differences are less the grain. The spatial

extent of patches thus depends on the magnitude of the admissible maximum Δz of trees forming a patch and can range from (1) a group of at least three neighboring trees surrounded by differently sized trees to (2) an entire stand of similarly sized trees to (3) an entire stand of differently sized trees with very large admissible maximum Δz of trees forming a patch.

Since patches are defined by similarly sized trees, simply defining patches leaves the position of a patch within the canopy unknown. For example, a patch composed of contiguous small trees is different from a patch of contiguous tall trees. A patch-type is thus defined as a patch at a certain height stratum in the canopy. Vertical structural complexity of a stand is then operationally defined as the number of different patch-types *per* unit area (note the analogy to "species richness").

Stand variables

The stand information chosen for this study was collected in the Demonstration of Ecosystem Management Option (DEMO) study (Aubry et al. 1998). A subset of five stands, located in the Umpqua National Forest, Oregon, were selected to encompass a broad range of structural variation and stand ages (Table 2.1). Each stand was 13 ha in size and contained 32 sample points on a systematic grid (80 m spacing). A pair of nested, concentric plots (0.01 ha for trees dbh < 5cm, 0.04 ha for trees with dbh > 5 cm) were used to sample stand density, tree species composition, and dbh. Tree heights by species were predicted from dbh based on nonlinear regression models

Table 2.1 Stand information for the simulation of the five stands (based on 1.28 ha area). $^{(1)}$ Shannon's diversity index.

Stand	UNO3	UNO1	UDOG	UDIL	UCOG				
Stand age (yrs)	250	300	165	130	80				
Slope (%)	10	10	50	5	40				
Aspect	S	W/SW	SW	flat	SE				
Elevation (m)	1340	1265	1615	1310	790				
Tree density per ha	350	295	297	310	294				
Douglas-fir	144	35	198	162	198				
Western hemlock	114	238	0	19	15				
Trees > 100 cm dbh	68	40	15	5	0				
Basal area (m²) per ha	123.6	90.2	90.1	43.7	37.6				
Douglas-fir	112.0	58.0	80.4	29.4	33.7				
Western hemlock	8.8	30.7	0	1.8	0.2				
DBH (cm)									
Mean	51.4	40.1	53.7	34.7	35.5				
Douglas-fir	96.2	141.7	67.8	39.9	43.2				
Western hemlock	24.6	27.1	0	30.8	14.2				
_ Standard deviation	43.1	47.8	31.2	24.4	19.2				
Height (m)									
Mean	29.6	21.6	33.8	24.4	26.2				
Standard deviation	19.2	18.6	16.5	13.2	11.5				
_ Maximum	69.1	71.1	63.9	63.6	51				
# trees in height class				-					
0-16 m	174	217	95	118	95				
16-32 m	81	70	28	164	144				
32-48 m	57	42	192	99	134				
48-64 m	134	31	65	16	3				
>64 m	2	18	0	0	0				
H' for tree heights (1)	1.32	1.23	1.19	1.20	1.12				
Aggregation index R (Clark and Evans 1954) for the three spatial patterns									
Regular	1.69	1.62	1.62	1.63	1.61				
Random	1.04	1.06	1.06	1.06	1.06				
Clustered	0.92	0.91	0.91	0.92	0.92				

developed by Garman et al. (1996) for the southern Cascade Range. Since all 32 sample points covered a total of 1.28 ha for trees > 5cm, the density for trees < 5 cm dbh, which only covered 0.32 ha was expanded by a factor of 4 to the 1.28 ha level. All trees were then used to predict several spatial patterns in a 1.28 ha area. General inclusion criteria for stands in the DEMO study, experimental design, and sampling methods can be found in Aubry et al. (1998).

Point pattern

To illustrate the importance of both the horizontal and vertical components of structure, three different spatial patterns were created with the pattern-generating program PATTERN (Moeur 1993): (1) random, (2) uniform with a 4 m inhibition distance between trees, and (3) clustered with 40 clusters of 10 trees with 30 m cluster diameters. Different structural conditions were simulated by randomly assigning a value from the actual tree height distributions to each tree position while holding the tree positions fixed. This process was repeated 100 times for each of the three simulated horizontal patterns for each of the five stands. Results of the simulations are thus averages based on 100 runs. The ranges, means, and standard errors for the "Structural Complexity Index" (defined below) are based on 10000 simulation runs for each of three spatial patterns in each of the five stands.

An index of aggregation, R, (Clark and Evans 1954) was used to evaluate the generated horizontal tree distribution patterns. The aggregation index relates the

observed average distance of all trees to their respective nearest neighbors to the average distance expected under a random or Poisson spatial distribution.

$$R = \frac{r_{observed}}{r_{expected}} \tag{1}$$

The aggregation index ranges from 0 (max. clustering) to 2.1491 (regular hexagonal pattern). Values below 1.0 indicate a clustered pattern, values around 1.0 are a random pattern, and values above 1.0 are a regular pattern. R is based on the average distance $r_{i,\,i=1,\dots,N}$ to their nearest neighbor for each of the N trees by:

$$-\frac{1}{r_{observed}} = \sum_{i=1}^{N} \frac{r_i}{N}$$
 (2)

where r_i = distances of trees i = 1,...,N to their nearest neighbor on the test plot and N = total number of trees on the test plot.

The expected average distance r_{expected} for a random tree distribution is related to the actual number of trees in the test area by:

$$\overline{r}_{\text{expected}} = \frac{1}{2\sqrt{\frac{N}{A}}} \tag{3}$$

where A =area of the test plot in square meters.

Simulation methods

A finite number of points of various spatial distributions within a rectangular area of 1.28 ha were used in this study as a test data set. Interest is focussed mainly on the interior 1 ha core area, with the additional 13.14 m around the core area serving as a

buffer area so that no boundary or edge correction in the search for nearest neighbors was necessary.

To develop a 3-dimensional model of forest structure, three neighboring trees were connected to form a triangle. Trees can be represented as three dimensional irregularly spaced data points (x, y = spatial coordinates, z = an attribute of the point such as tree height or dbh) (Fig. 2.1). Three adjacent points in this x, y, z-space can be connected to form a triangular surface; this surface can be visualized as connecting the tops of three adjacent trees. 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. 2.2). This approach allows the comparison of stands based on the distribution of height differences of neighboring trees as well as the size distribution of triangles.

A simulation program was written (Matlab 1994) that created such a network of non-overlapping triangles. The nearest neighbor of the tallest tree in the stand was found to create the first pair of points. The first and subsequent triangles were established by finding the nearest neighbors to both trees. If both trees were in the 1 ha core area, and no nearest neighbor could be found within a search radius of 20 m, a nearest neighbor with height zero was defined at a distance of 10 m perpendicular to the mid-point of the corresponding pair of points for which the nearest neighbor was sought. In other words, one corner of the triangle went into the ground. If one of the trees was outside the 1 ha core area and no nearest neighbor could be found within the

Figure 2.1. Example of a spatial tree distribution.

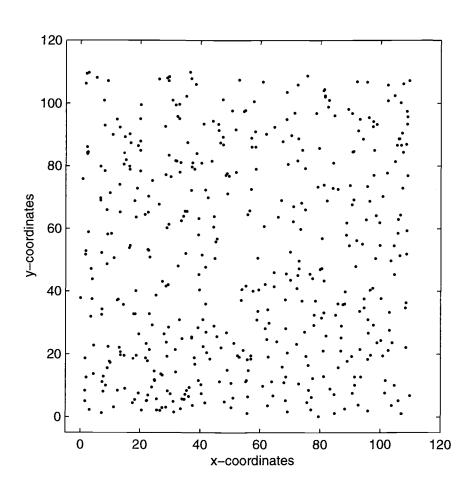


Figure 2.1

Figure 2.2. Example of a triangular irregular network (same stand as above).

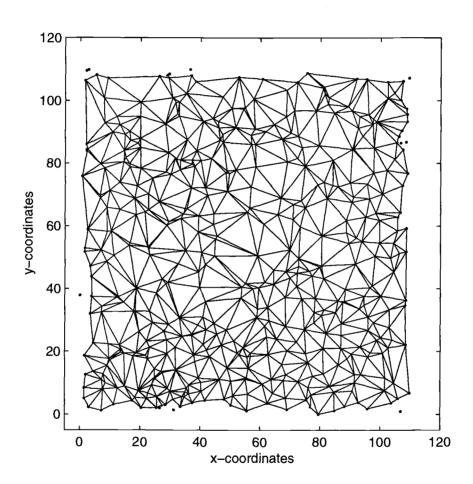


Figure 2.2

search radius, the existing pair then became part of the boundary triangle and no adjacent triangle was connected with that pair. The ground area thus covered by triangles is generally somewhat greater than 1 ha.

An index that is based on vertical gradients and distances of neighboring trees was created to directly compare the structural variability among stands. This "Structural Complexity Index" (SCI) is defined as the sum of the surface areas of the TINs for a stand (SCI*) divided by the ground area covered by all triangles:

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

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

$$SCI^* = \sum_{i=1}^{N} \frac{1}{2} \left| a_i x b_i \right| \tag{5}$$

where i=1,...,N is the number of triangles in the test plot, $|a_i \times b_i|$ is the absolute value of the vector product of the vector AB with coordinates $a_i = (x_{ib} - x_{i\omega} \ y_{ib} - y_{i\omega} \ z_{ib} - z_{ia})$ and the vector AC with coordinates $b = (x_{ic} - x_{i\omega} \ y_{ic} - y_{i\omega} \ z_{ic} - z_{ia})$. The sum of one-half the vector products gives a surface area in 3 dimensions by connecting the z-coordinates of trees with spatial coordinates x and y (Fig. 2.2).

The SCI was also calculated across vertical scales. For example, if the maximum height difference (Δz) of trees in a triangle was less than a certain value for the grain, the triangle was said to be "horizontal". The area of the horizontal triangle was calculated by setting z equal to zero and thus ignoring the z-component. This procedure was repeated with different grains, in increments of 1 m, until triangles with the greatest height differences were set to horizontal triangles and the value for the SCI

was equal to one, the lower limit of the SCI. At each increment of Δz , adjacent horizontal triangles (i.e., triangles having a common side) merged into larger patches if the differences between the minimum and maximum heights of the trees within the triangles were less than the grain. The SCI, the number of horizontal triangles, the sum of the areas of horizontal triangles, the mean number of triangles per patch, and the number of spatially distinct patches (i.e., the number of patches after some triangles were merged with their neighbors into a bigger patch) were recorded at each increment of Δz .

Fourty-four patch-types were defined based on the height class to which the triangle belonged, and the maximum height difference (vertical gradient: Δz_{max}) of the trees in the triangle (Table 2.2). Again, adjacent triangles belonging to the same patch-type merged into patches. The number of patch-types present, the frequencies of each patch-type, and the number of distinct patches in each patch type were recorded.

Tree height diversity and patch-type diversity were quantified with the Shannon-Weaver formula (e.g., MacArthur and MacArthur 1961):

$$H' = \sum_{i=1}^{N} p_i \log_e p_i \tag{6}$$

where p_i is the proportion of trees in the i^{th} height class, the proportion of triangles in vertical gradient class i, or the proportion of triangles in patch-type i.

Table 2.2. Patch-type definitions. Vertical gradient classes: 1: $\Delta z = 0-2$ m, 2: $\Delta z = 2-4$ m, 3: $\Delta z = 4-8$ m, 4: $\Delta z = 8-16$ m, 5: $\Delta z = 16-32$ m, 6: $\Delta z = 32-48$ m, 7: $\Delta z = 48-64$ m, 8: $\Delta z = >64$ m; height strata: 1 = 0-16 m, 2 = 16-32 m, 3 = 32-48 m, 4 = 48-64 m, 5 = >64 m;

Patch	Height	Vertical	Patch	Height	Vertical		
Type	Stratum	Gradient	Type	Stratum	Gradient		
1	1	1	20	1	4		
2	2	1	21	1-2	4		
3	3	1	22	2	4		
4	4	1	23	2-3	4		
5	5	1	24	3	4		
6	1	2	25	3-4	4		
7	2	2	26	4	4		
8	3	2	27	4-5	4		
9	4	2	28	5	4		
10	5	2	29	1-2	5		
11	1	2 3	30	1-3	5		
12	1-2	3	31	2-3	5		
13	2	3	32	2-4	5		
14	2-3	3	33	3-4	5		
15	3	3	34	3-5	5		
16	3-4	3	35	4-5	5		
17	4	3	36	1-3	6		
18	4-5	3	37	1-4	6		
19	5	3	38	2-4	6		
			39	2-5	6		
			40	3-5	6		
			41	1-4	7		
			42	1-5	7		
			43	2-5	7		
			44	1-5	8		

MODEL APPLICATION

Horizontal and vertical patterns

The aggregation indices for the spatial patterns (Table 2.1) ranged between 0.91 and 1.69 and were consistent with the objective to create three different spatial patterns for each stand. Since the tree positions were generated for a 1.28 ha unit, however, the number of trees in the core area varied somewhat among the spatial patterns for each stand (Table 2.3). Horizontal positions are shown for stands UNO3 and UCOG, which had the highest and lowest tree density values, respectively (Fig. 2.3). With the exception of stand UNO3 that had slightly more trees than the other stands, tree densitites were very similar for the other four stands. There were, however, marked differences in the diameter and height distributions among the stands (Table 2.1). For example, average stand diameters varied from 35.5 (UCOG) to 53.7 (UDOG) cm, the standard deviations of the dbh ranged from 19.2 (UCOG) to 47.8 (UNO1) cm, and the density of Douglas-fir with dbh > 100 cm ranged from 0 (UCOG) to 87 (UNO3) trees. Note that the highest values among the several structural variables are achieved by different stands. The distribution of tree heights (Table 1) shows a distinctive bimodal structure in stands UNO3 and UDOG, and a less differentiated height structure in stands UNO1, UDIL and UCOG. The Shannon index (H') for tree height diversity, however, does not reflect these differences in height distributions among the stands well (Table 2.1), despite the remarkable interstand structural differences, particularly in the upper

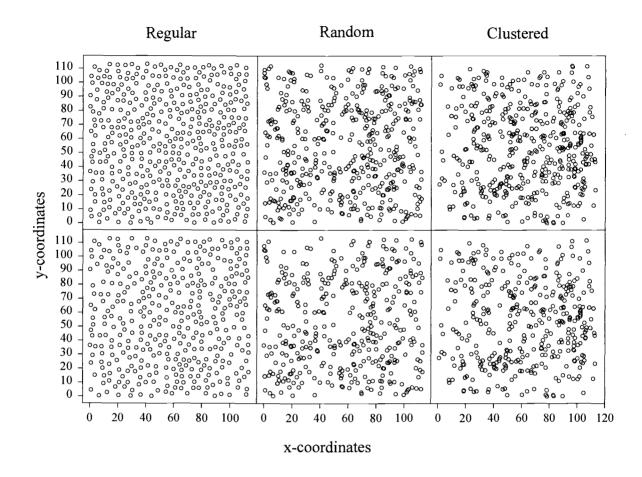


Figure 2.3. Simulated regular, random, and clustered spatial patterns for the stands with the highest and lowest densities per 1.28 ha (row 1 = UNO3: 448 trees/ha; row 2 = UCOG: 376 trees/ha).

Table 2.3. Structural information for the five simulated stands and spatial patterns. (1) the number of triangles that make up the tessellated area, (2) the number of trees inside the core area of 1 ha, (3) standard deviation

Stand		UNO3			UNOI		_	UDOG			UDIL			ÜCOG	
Pattern	reg	rand	clust	reg	rand	Clust	reg	rand	clust	reg	rand	clust	reg	rand	Clust
# triang(1)	760	793	827	651	668	710	659	671	711	676	701	744	650	669	703
# inside ⁽²⁾	337	357	386	288	301	334	290	303	336	300	317	348	286	301	332
Area (m ²)	11308	11496	10704	11524	11687	10515	11586	11612	10476	11377	11529	10650	11573	11709	10476
Distance bet	ween neares	t neighbors ((m)												
Mean	4.51	2.77	2.46	4.70	3.08	2.65	4.69	3.07	2.64	4.64	3.01	2.60	4.70	3.09	2.67
Std ⁽³⁾	0.47	1.45	1.32	0.64	1.57	1.45	0.64	1.58	1.43	0.59	1.54	1.41	0.64	1.57	1.47
Min	4.00	0.41	0.39	4.00	0.41	0.39	4.00	0.41	0.39	4.00	0.41	0.39	4.00	0.41	0.39
Max	6.64	9.66	8.58	7.13	10.60	5.87	7.13	10.60	8.58	7.13	10.60	8.58	7.13	10.60	8.58
SCI (based o	on 10000 sim	nulations)												10.00	0.50
Mean	6.780	7.302	7.645	5.333	5.648	6.237	5.048	5.307	5.734	4.188	4.411	4.809	3.662	3.870	4.173
Std	0.150	0.175	0.196	0.138	0.162	0.198	0.119	0.137	0.187	0.087	0.096	0.117	0.075	0.087	0.100
Min	6.208	6.571	6.811	4.823	5.028	5.585	4.566	4.793	5.191	3.840	4.054	4.353	3.387	3.558	3.749
Max	7.390	7.923	8.298	5.879	6.198	7.048	5.578	5.857	6.331	4.525	4.768	5.316	3.924	4.206	4.550
Average ratio	o of surface	area and pro	jected groun	d area of all	triangles		_							1.200	7.550
Mean	7.57	26.16	27.17	6.03	13.45	23.77	6.66	12.86	52.17	4.60	10.58	18.36	4.42	9.68	24.43
Std	6.98	7.32	7.30	5.29	5.62	6.33	5.18	5.11	5.92	4.15	4.55	4.95	3.67	3.96	4.17
Height differ	ences (vertic	cal gradients)				_						2.07		
Mean	34.65	34.65	34.76	29.00	29.08	28.93	27.38	27.48	27.26	22.41	22.43	22.40	19.84	19.91	19.94
Std	15.64	15.66	15.61	18.88	18.93	19.94	14.20	14.27	14.22	10.85	10.91	10.91	9.07	9.03	9.05
Min	0.47	0.48	0.51	0.15	0.14	0.13	0.73	0.67	0.58	0.68	0.65	0.48	0.74	0.75	0.67
Max	59.22	59.34	59.44	65.06	65.23	65.16	55.72	56.41	55.68	55.58	55.90	55.40	42.06	42.09	42.17
Mean H'	1.527	1.528	1.521	1.781	1.783	1.784	1.491	1.495	1.488	1.329	1.335	1.336	1.227	1.217	1.221
Std H'	0.036	0.033	0.035	0.024	0.024	0.023	0.036	0.040	0.040	0.039	0.041	0.040	0.047	0.049	0.042
Patch-types														0.017	0.072
Mean	28.16	28.32	28.30	25.94	26.52	26.57	24.43	24.46	24.52	25.16	25.22	25.46	22.43	22.05	22.44
Std	1.73	1.80	1.67	1.69	1.94	1.74	1.39	1.35	1.29	1.23	1.23	1.26	1.26	1.21	1.23
Min	24	24	22	21	22	23	22	21	21	21	22	22	1.20	1.21	1.23
Max	32	32	31	29	33	31	28	27	27	28	28	28	26	25	25
Mean H'	2.471	2.474	2.471	2.651	2.660	2.658	2.493	2.492	2.494	2.537	2.542	2.549	2.333	2.314	2.325
Std H'	0.050	0.055	0.056	0.044	0.036	0.036	0.049	0.053	0.050	0.045	0.047	0.046	0.052	0.059	0.053

height classes among the stands. Note, furthermore, that the spatial arrangement of trees and size differences between neighboring trees is not taken into account in describing the structural heterogeneity using H'.

Structural complexity and the SCI

The values for the SCI revealed clear differences among the five stands (Table 2.3). Stand UNO3 showed the highest SCI values, followed by UNO1, UDOG, UDIL, and UCOG. For example, UNO3 had a 31% higher SCI than UNO1 and a 90% higher SCI than UCOG. Although the 100 simulations generally show consistent patterns for each stand with increasing grain values for the maximum height differences in triangles, individual stands showed a 15.9 to 26.2 % difference in SCI values in the simulations (Fig. 2.4). These differences reflect the random assignments of tree heights to stem positions and thus show the influence of the size differences among neighboring trees on the SCI.

A correlation analysis for the average SCI for the five stands and three patterns showed strong correlations with tree density (r=0.738, p=0.002), the density of trees > 100 cm dbh (r=0.934, p<0.001), basal area (r=0.940, p<0.001), Douglas-fir basal area (r=0.934, p<0.001), mean dbh (r=0.703, p=0.004), the standard deviation of dbhs (r=0.808, p<0.001), maximum stand height (r=0.754, p=0.001), and the number of trees above 48 m in height (r=0.939, p<0.001). The single best predictor for the SCI is the maximum height difference within the triangles (r=0.961, p<0.001). Several regression

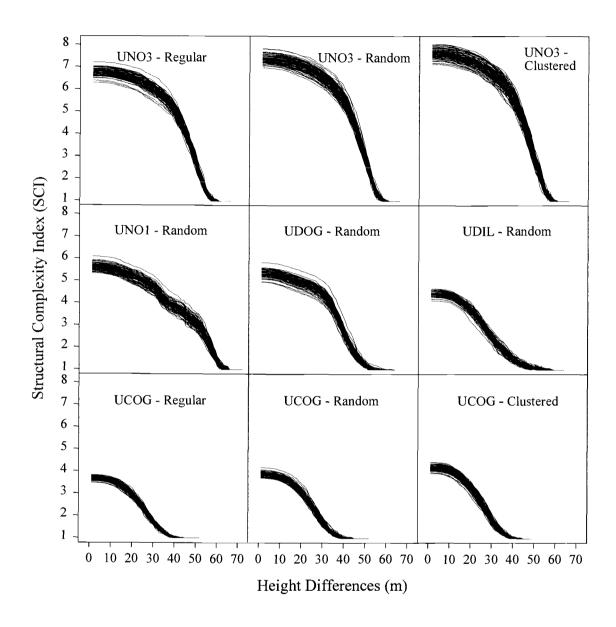


Figure 2.4. Trajectory of the structural complexity index (SCI) over a range of height differences (delta z) for 100 random assignments of tree heights to stem positions for selected sites and spatial patterns. Stands are ordered from highest to lowest SCI. All three spatial patterns (regular, random, and clustered) are given for the stands with the highest and lowest tree densities (UNO3 and UCOG, respectively).

models were tried that gave nearly the same fit to the data. Fitting the average SCI to either (1) tree density, mean dbh, and dbh standard deviation, or (2) the number of trees above 48 m in height and the coefficient of variation of heights explained most of the variation in the data (both R²=0.930). After including the number of trees that were inside the test plot in the previous regression model, nearly all of the variation in the data could be explained (R²=0.995). No differences in these regressions, however, were seen among regular, random, and clustered spatial distributions after accounting for differences in the density of trees in the core areas among the three spatial patterns (p>0.08 for the index of aggregation). Given that the SCI related very closely to several independent variables that have previously been used to describe the structural heterogeneity of forests, the SCI may be used to integrate these structural variables into one index that may prove to be a good surrogate for forest structure in future studies.

The trajectory of the SCI along increasing Δz (Fig. 2.4) shows distinct differences between stands and between simulations for the same stands. Generally, as the grain for Δz within a triangle increases, the reduction of the SCI increases. This is because the area reduction of a triangle with fixed x and y coordinates increases more when a greater Δz is set to zero. The steepness of the ascent of the SCI along the Δz -axis (Fig. 2.5) reflects the number of triangles with maximum height differences that are gradually set to horizontal triangles. The steepness and trajectories of the ascent in the proportion of horizontal triangles also reflects differences among stands and simulations. Depending on the random assignment of heights to spatial coordinates

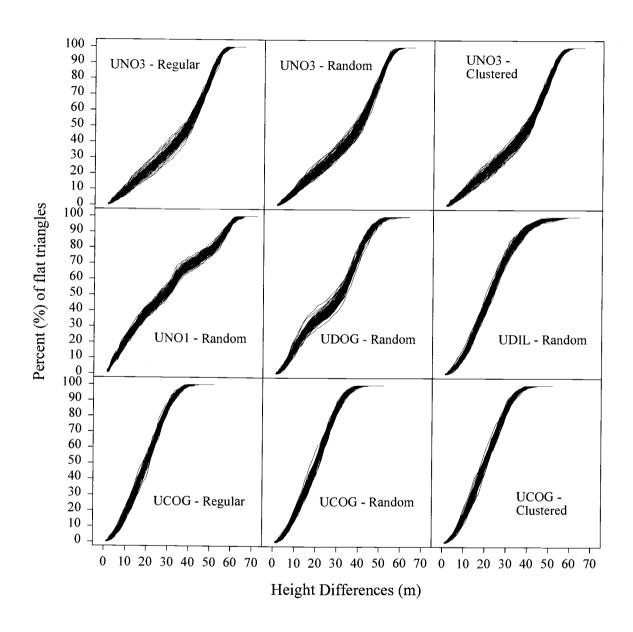


Figure 2.5. Trajectory of the percent of flat triangles over a range of height differences (delta z) for 100 random assignments of tree heights to stem positions for selected sites and spatial patterns. Stands are ordered from highest to lowest SCI. All three spatial patterns (random, regular, and clustered) are given for the stands with the highest and lowest tree densities (UNO3 and UCOG, respectively).

there can be a difference of up to 15% between simulations for the proportion of horizontal triangles at a given Δz (Fig. 2.5).

After collapsing some of the Δz into eight vertical gradient classes (Table 2), differences among the stands and simulations become even more apparent. Gradient class box plots (Fig. 2.6) reveal differences among simulations similar to those in Figures 2.4 and 2.5. For example, only a few triangles are in the first three vertical gradient classes (0-2 m, 2-4 m, and 4-8 m) in all five stands. Whereas the majority of triangles in UCOG belonged to gradient classes 4 (8-16 m) and 5 (16-32 m), most triangles in UNO3 were in gradient classes 6 (32-48 m) and 7 (48-64 m). This difference reflects a greater Δz between neighboring trees and thus more canopy heterogeneity in UNO3 compared to UCOG (Fig. 2.6). Compared to the other four stands that show a peaked gradient class distribution in gradient classes 5 or 6, UNO1 shows a plateau from gradient classes 5 through 7 (Fig. 2.6). The reason for this is the lower proportion of trees in the upper height classes (4 through 7) compared to the other stands. This lack of trees in the upper height classes is also reflected in the more moderate decline in the SCI (Fig. 2.4) and a more moderate increase in the proportion of horizontal triangles (Fig. 2.5). Also, the average Δz within triangles shows the greatest height differences in UNO3 (34.65 m) and the least height differences in UCOG (19.91 m) (Table 2.3). Ranking stands by SCI resulted in the same order as when stands were ranked by the average Δz of all triangles. There were no noticeable differences between spatial patterns on the SCI for all stands (Fig. 2.6).

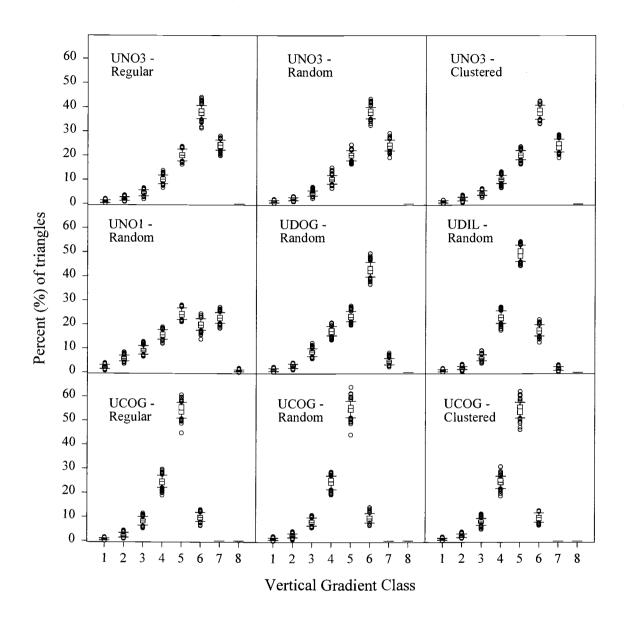


Figure 2.6. Percent of triangles in vertical gradient classes. Vertical gradient classes are defined by the maximum height difference (delta zmax) within a triangle. Box-and-whisker plots show the median within the box, whiskers at the 5th and 95th percentiles, and circles below the 5th and 95th percentiles.

Patch-types

Whereas the gradient class distribution gives a general description of height differences (Δz) among the trees that belong to the same triangle (Fig. 2.6), for a more complete description of structural heterogeneity it may be important to know in what layer of the canopy these height differences among neighboring trees were found. Patch-types, defined on the basis of the magnitude of Δz among neighboring trees and the height classes to which the neighboring trees belong, are shown in Figure 2.7 for the random spatial patterns of all five stands. As with the vertical gradient classes, no differences were seen among the spatial distributions of the five stands.

The frequency distribution of the patch-types (Fig. 2.7) revealed distinct differences in the vertical structural complexity among the five stands. Generally, there were low proportions of patch-types across all vertical gradient classes in the height classes 4 (48-64 m) and 5 (>64 m). This is due to the generally low proportion of trees in the upper height classes and the low probability that three tall trees would form a triangle. Both UCOG and UDIL had trees mainly in height classes 1 through 3 (<48 m), and thus show the highest frequencies in patch-types reflecting these height classes with Δz mostly between 2 and 48 m. UDOG and UNO3 have the majority of patch-types in high vertical contrast patches (vertical contrasts from 8-64 m). UNO1 with the most trees in the lowest height class among all stands shows elevated frequencies in patch-types that involve height class 1 across all vertical gradients (0-64 m).

Figure 2.7. Percent of triangles in patch types. Patch types are defined as a combination of height stratum and vertical gradient (see Table 2.2). Box-and-whisker plots show the median within the box, whiskers at the 5th and 95th percentiles, and circles below the 5th and above the 95th percentiles.

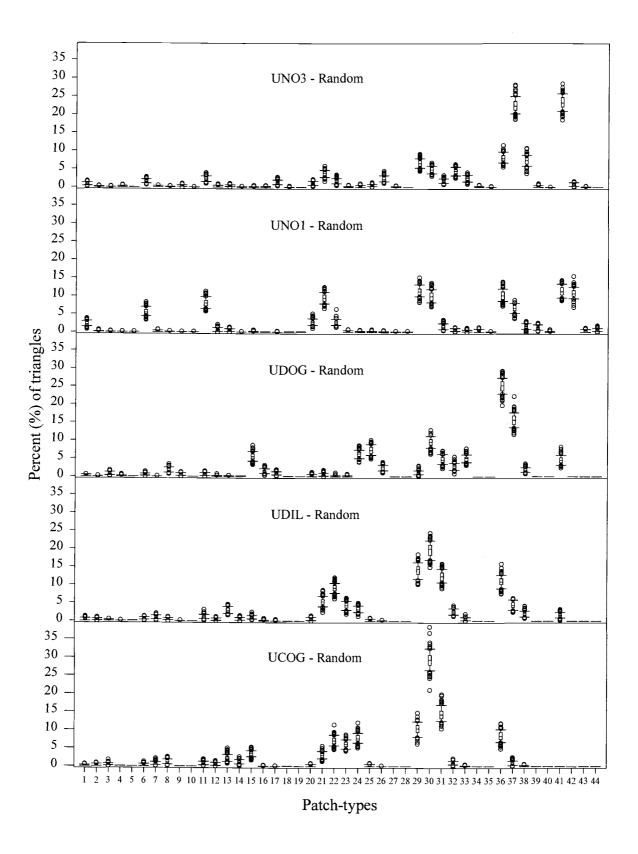


Figure 2.7

Diversity indices

Diversity indices for tree heights (Table 2.1), vertical gradients, and patch-types (Table 2.3) indicate different stands as the most structurally heterogeneous. Using tree height diversity, the stands are ranked in the same order as with the SCI. Differences among the stands, however, are generally very small. The diversity index for vertical gradients shows UNO1 as more diverse than UNO3 due to a more even proportion of higher gradient classes (Fig. 2.6). Although UNO3 and UNO1 have on average the highest number of patch-types ("patch richness"), ranking stands by patch-type diversity gives a different ranking than patch richness. As with tree height diversity, patch-type diversity did not show any significant differences among UNO1, UDOG, and UDIL.

Spatial patterns

The lack of differences in the SCI, vertical gradients, and patch-type distributions among regular, random, and clustered spatial distributions is not surprising. These three variables were defined by the spatial arrangement of nearest neighbors within a 20 m distance, ignoring the particular spatial pattern of the stem positions. Differences may have been found if search radii for nearest neighbors were set to smaller values such that clustered spatial arrangements had more triangles between clusters that would go into the ground. Also, the search for nearest neighbors could be restricted to a certain minimum distance such that smaller trees immediately beneath the crowns of taller trees would be excluded as nearest neighbors. Although the

area of triangles formed by trees close to one another only contribute a small proportion to the SCI, many small trees underneath the canopies of taller trees may have a strong influence on the SCI. For example, the average ratio of surface area and projected ground area of all triangles was usually much higher in clustered spatial patterns than in regular or random patterns, since the distances between neighbors could be extremely small (Table 2.3). Finally, the calculation of the SCI could be restricted to overstory trees only, such that small trees in the vicinity of tall trees do not increase the SCI to a point where the intensive mixture of very small and very tall trees becomes the most important feature of structural heterogeneity.

DISCUSSION

Analogous to landscapes, forest stands can be considered as an area of land containing a mosaic of habitat patches or a population of patch-types (*sensu* Urban et al. 1987). Patch-types represent discrete areas of relatively homogeneous structure where the boundaries of a patch-type are defined by discontinuities in the tree heights. Patches are dynamic and occur on a variety of scales (Wiens 1976), having internal structures that reflect the patchiness of finer scales and, in turn, the structure of the mosaic containing that patch is determined by the patchiness at broader scales (Kotliar and Wiens 1992).

Forest stands can be distinguished by particular spatial relationships among patch-types. Again, analogous to a landscape, forest composition and forest pattern can be distinguished (*sensu* Dunning et al. 1992). Forest composition refers to the types and

amount of patch-types within the forest, but without being spatially explicit about the relative locations of patch-types to one another in the forest. Quantitative measures that can be used to describe forest composition include the proportion of the forest in each patch-type (Fig. 2.6) and patch-type richness, diversity, and evenness. Forest pattern refers to the spatial distribution of patch-types within the forest. Quantitative measures that describe the forest patterns include average patch characteristics such as patch-type sizes and variability in these characteristics, or interspersion and juxtaposition of patchtypes. Because both the proportions in each patch-type and heterogeneity in the sizes of different patch-types (area occupancy, horizontal forest structure) characterize forest structure, it becomes apparent that increasing patch-type heterogeneity implies compromising patch-size heterogeneity for a fixed area, since both components cannot be maximized at the same time. The greater the area necessary to encounter most patchtypes, the more homogeneous the structure of the stand. Investigating the balance between patch-type and patch-size heterogeneity in natural stands may offer an alternative avenue for habitat-type analyses.

The conversion of a point pattern into triangular areas based on spatial tessellation enables the definition of patch-types and the comparison of structural heterogeneity among forest stands at different scales. The hierarchical definition of patch-types in this paper is reflected in the trajectory of the SCI as the vertical gradient changes. As the vertical gradient changes, patches of trees with similar height increase until, when the gradient encompasses the height of the tallest tree, there is only one patch left. The new methodology for describing and comparing the structural

complexity of forest stands (i.e., forest composition and forest pattern) presented in this paper enables the use of many indices and metrics developed in landscape ecology, many of which are based on areas. Examples of such metrics include patch richness, patch richness density, relative patch richness, patch density, mean patch size, patch size coefficient of variation, and largest patch index (see McGarigal and Marks 1995). Some knowledge about the size and spatial distribution of patches is thus imperative.

Patterns of patch-type distributions, including canopy gaps at various heights and the SCI, can be incorporated into habitat studies across scales or to growth-andyield models. Gaps, areas within the forest with a noticeably lower canopy than in adjacent areas (Runkle 1985), can be delineated by finding patch-types with small vertical gradients surrounded by high-gradient patch-types. In forest management, thinning has been proposed as the main tool to create and maintain structural heterogeneity and diversity, to create old-growth structures, to promote tree growth, and to facilitate ecosystem diversity and stability (McComb et al. 1993, Koop 1989). The methodology described in this paper could be used to describe the development of the structural complexity of forests over time and to evaluate the influences of different silvicultural treatments (e.g., the intensity and form of thinning, partial harvests, greentree retention aggregated or dispersed) that seek to speed up the development of old forest structures. Further use of this methodology could lie in the link with other ecological models to study the relationship between forest structure and growth and yield, habitat-type analyses, and other ecosystem processes.

Currently, a study is in progress that will use mapped stands to investigate patch-type sizes and numbers of triangles within a patch-type that can then be compared with simulated random height allocations to stem positions. For example, the maximum or 95th percentile of 10000 simulations could be used to test whether the observed SCI was bigger than the maximum value from random height allocations to stem positions. This would enable a test of the hypothesis whether, given the observed spatial pattern, tree sizes, species mixture, and the scale used for the study, tree sizes are spatially allocated to stem positions such that the structure of a forest is at a maximum ("maximum structure hypothesis of undisturbed natural mixed-conifer forests").

CONCLUSION

Whereas the conventional descriptions of forest structure typically ignore the 3-dimensional character of structural heterogeneity, the structural complexity index (SCI) presented in this study, in contrast, incorporates both the spatial distribution of neighboring trees and their vertical complexity. Although the SCI is not sensitive to differences between random, clustered, and regular patterns *per se*, size differences among neighbors are at the center of the SCI. Patch-types, defined by height differences of neighboring trees and their canopy position, also show clear differences among stands and between simulations. The SCI is strongly associated with conventional structural descriptors such as tree density, density of trees > 100 cm in dbh, mean dbh, standard deviation of the dbhs, and maximum stand heights and integrates their respective contributions to structural heterogeneity into one index. SCI

and patch-types may be useful in growth and yield or wildlife habitat studies, which typically focus on the within-patch scale at the size of forest stands. Actual stem mapped data of natural, undisturbed forests need to be compared to simulated SCI and patch-type values to test whether and how much the spatial pattern may influence the structural complexity of natural forests.

Chapter 3

Do Residual Trees Increase Structural Complexity in Coniferous Forests in the Pacific Northwest?

Eric K. Zenner

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 planted stands after clearcuts. To evaluate if and how overstory residual trees that survived fires that initiated the young tree cohort between 55 and 236 years ago, were associated with a higher structural complexity than in similar, 15 stands with and 15 nearby stands without residual trees were investigated. The young-to-mature young cohorts regenerated naturally and were not managed in any way. The 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 the tree height variation, was negatively associated with residual trees up to 40 residual trees/ha. The SCI-dbh, which is based on the tree diameter variation, was positively associated with residual trees up to 40-60 residual trees/ha. These differences were due to a lower density of dominant and codominant trees in the young cohort, particularly of Douglas-fir, in the vicinity of residual trees, and a different weighting of large residual trees by both SCIs. Generally, stands with intermediate densities in the young cohort and a mixture of about equal proportions of Douglas-fir and shade-tolerant tree species such as western hemlock had the highest structural complexity. Substantial differences were also observed among north, east/west, and south aspects. The most structurally complex stands were generally on east/west aspects. These results suggest that residual trees may enhance the structural

complexity at small scales, but may homogenize the structure of young-to-mature cohorts at intermediate to large scales. At high densities of residual trees, areas of high structural complexity may coalesce to form areas of high structural complexity even at larger scales. Both species mixture and differences among aspects need to be considered when managing stands for 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 legacies such as large residual trees, create snags and logs, and facilitate subsequent regeneration that can enhance the vertical complexity of the forest (Spies et al. 1990). Young natural forests that show a high variability in tree sizes and canopy layers are frequently contrasted with intensively managed, mono-specific

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 1996). Silvicultural systems are being designed that aim to mimic closely the frequencies, shapes, sizes, intensities, and patterns of natural disturbances in PNW-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, 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 focussed 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 1996, Zenner et al. 1998, Acker et al. 1998),

but the relation of green-tree retention levels to structural complexity has not been tested in field studies.

Adaptive forest management, charged with creating old-forest conditions in short times, needs 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 dbhs, tree density *per* unit area, or the density per unit area of large 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 is used for evaluation. Although 1-dimensional stand parameters may provide some insights into an average 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 2-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, Goslin 1997, Kuuluvainen et al. 1996). 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 1-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-s*-space to form a rough surface area that may be used to quantify and compare the 3-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 1-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 is 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 3-dimensional structure associated with residual trees and to test the hypothesis that

residual trees enhanced the structural complexity of forests. More specifically, I address the mechanisms that may be responsible for the observed structural complexity in two-and multiple-storied stands in this study and provide a framework for structural development in green-tree retention stands.

METHODS

Fifteen pairs of plots were established in the lower and mid-elevations of the Tsuga heterophylla (western hemlock) and Abies amabilis (Pacific silver fir) zones (Franklin and Dyrness 1973) in the Willamette National Forest in Oregon's western central Cascade Range. Eleven of the sites were "low elevation" (520-855 m), located in the Tsuga heterophylla zone. Dominant species in the these stands included Pseudotsuga menziesii (Mirbel) Franco (Douglas-fir) and Tsuga heterophylla (Raf.) Sarg. Thuja plicata Donn. (western redcedar), Libocedrus decurrens Torr. (incense cedar), Cornus nutallii Audubon (Pacific dogwood), Acer macrophullum Pursh. (bigleaf maple), and Castanopsis chrysophylla (Dougl.) A.DC. (Golden chinkapin) were often present in the understory. Four of the sites were "mid-elevation" (1220-1340 m), located in the Abies amabilis zone with Abies amabilis Dougl. ex Forbes (Pacific silver fir) and Abies procera Rehd. (noble fir) being the dominant species.

Paired plots were established to compare the structure of naturally developed stands with residual trees to adjacent 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 m²) slope-corrected circular plot, nested in a 30.9 m (3000 m²) slope-corrected plot, 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 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 average breast-height age of dominant and codominant trees. Aspect readings were transformed to a more biologically meaningful continuous variable that equals 0 for north, 90 for east and west, and 180 for south. Aspect was further transformed into three discrete aspect classes (north, east/west, 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 3.1.

An index of aggregation (R, Clark and Evans 1954) was used to characterize the horizontal tree distribution pattern. The aggregation index relates the observed average

Table 3.1. Site and stand characteristics.

Stand	Age (yrs)	Elev. (m)	Aspect	Slope (%)	Clark- Evans index	Density (trees/ha)						Basal area (m²/ha)		
						residual trees	young cohort	PSME ¹	TSHE ²	ABAM³	ABPR ⁴	hard- woods	all trees/ha	young cohort
BR07-R	108	823	Е	85	0.99	20	860	0	820	0	0	0	43.8	35.6
BR07-N	121	823	N	60	1.05	0	1380	500	800	ŏ	ő	ŏ	79.7	79.7
BR08-R	108	823	Е	75	1.00	80	1480	160	1260	ő	o o	0	82.4	42.8
BR08-N	111	823	Е	80	1.08	0	1920	340	1580	ő	0	ő	61.0	61.0
BR17-R	65	853	s	73	0.99	20	900	880	0	0	0	20	70.9	46.7
BR17-N	58	853	S	77	0.90	0	1040	840	0	0	0	160	63.3	63.3
DE06-R	81	640	S	30	1.11	20	680	640	0	0	0	20	77.6	64.0
DE06-N	67	640	S	40	1.09	0	860	840	20	0	0	0	68.6	68.6
LO01-R	61	731	S	62	1.10	80	940	400	540	0	0	0	107.0	39.9
LO01-N	61	731	S	55	0.82	0	1240	920	60	0	0	240	56.4	56.4
LO05-R	83	701	Е	28	1.32	60	460	160	240	0	0	60	96.6	38.1
LO05-N	85	701	Е	17	1.10	0	840	420	420	0	0	0	65.1	65.1
LO06-R	84	701	S	50	1.06	20	480	160	300	0	0	20	112.0	47.3
LO06-N	89	701	S	35	1.14	0	920	260	660	0	0	0	65.6	65.6
LO07-R	92	518	S	10	1.14	60	660	260	400	0	0	0	148.0	47.4
LO07-N	87	518	S	17	1.06	0	800	360	380	0	0	0	82.0	82.0
LO08-R	83	792	S	60	1.14	20	860	420	440	0	0	0	80.2	52.0
LO08-N	85	792	Е	57	1.24	0	680	680	0	0	0	0	74.5	74.5
MC04-R	88	671	S	33	1.33	20	620	560	60	0	0	0	81.6	58.6
MC04-N	94	671	S	25	1.20	0	740	640	60	0	0	40	86.5	86.5
SH13-R	74	640	S	30	1.14	40	1200	500	660	0	0	40	106.0	47.2
SH13-N	77	640	S	30	1.00	0	860	520	260	0	0	40	60.2	60.2
DE02-R	82	1219	N	62	0.97	20	1860	60	1300	280	220	0	79.2	69.2
DE02-N	83	1219	N	60	0.88	0	2880	380	1660	500	300	0	64.9	64.9
DE05-R	233	1341	N	40	1.06	40	2520	0	620	1900	0	0	52.8	33.7
DE05-N	236	1341	N	38	0.97	0	4680	0	2440	2240	0	0	46.0	46.0
DE08-R	88	1280	N	43	1.05	40	980	0	0	340	640	0	96.8	65.2
DE08-N	72	1280	Е	42	1.10	0	1980	160	180	560	1080	0	77.0	77.0
SH12-R	100	1219	S	30	1.24	20	700	440	180	80	0	0	92.9	69.1
SH12-N	107	1219	S	33	1.19	0	780	480	220	80	0	0	88.2	88.2

¹⁾ PSME = Douglas-fir, 2) TSHE = western hemlock, 3) ABAM = Pacific silver fir, 4) ABPR = noble fir

distance of all trees to their respective nearest neighbors to the average distance expected under a random or Poisson spatial distribution.

$$R = \frac{\overline{r}_{observed}}{\overline{r}_{expected}} \tag{1}$$

The aggregation index ranges from 0 (maximum clustering) to 2.15 (regular hexagonal pattern). Values below 1.0 indicate a clustered pattern, values around 1.0 are a random pattern, and values above 1.0 are a regular pattern. R is based on the average distance $r_{i,j}$

$$_{i=1,...,N}$$
 to their nearest neighbor for each of the N trees by: $\bar{r} = \sum_{i=1}^{N} \frac{r_i}{N}$ (2)

The expected average distance r_{expected} for a random tree distribution is related to the actual number of trees in the test area by:

$$\overline{r}_{\text{exp}\,ected} = \frac{1}{2\sqrt{\frac{N}{A}}} \tag{3}$$

where A =area of the test plot in square meters.

Determination of the Structural Complexity Index used a 3-dimensional model of forest structure, where three neighboring pairs of trees were connected to form a triangle. 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. 3.1). This approach allows the comparison of stands based on the distribution of size differences of neighboring trees (Zenner 1998).

A simulation program was written (Matlab 1994) that created such a network of non-overlapping triangles. The nearest neighbor of the tallest tree in the stand was found to create the first pair of points. The first and subsequent triangles were established by finding the nearest neighbor to both trees. An index that 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 "Structural Complexity Index" (SCI) is defined as the sum of the surface areas of the TINs for a stand (SCI*) divided by the ground area covered by all triangles:

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

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

$$SCI^* = \sum_{i=1}^{N} \frac{1}{2} |axb| \tag{5}$$

where i=1,...,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 $a=(x_b-x_{\sigma},y_b-y_{\sigma},z_b-z_a)$ and the vector AC with coordinates $b=(x_c-x_{\sigma},y_c-y_{\sigma},z_c-z_a)$.

Different structural conditions were then simulated by randomly assigning a value of the tree height and diameter distribution to each tree position while holding the tree positions fixed. This process was repeated 10,000 times for each stand and the range for the simulated SCI-ht and SCI-dbh were recorded.

Figure 3.1. Visual representation of a triangular irregular network.



Figure 3.1

Multiple linear regression analysis was used to test which variables were associated with 1-, 2-, and 3-dimensional structural characteristics (Table 3.2). 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. Since regression models are maximum likelihood models, I was able to illustrate how much each independent variable in the regression models influenced the SCI and at what density green-trees would most likely maximize the SCI by using the developed models. Predicted values of the density of the young cohort and proportion of Douglas-fir in the young cohort, and the standard deviations of the tree heights and dbh from the regression models were used to predict the most likely SCI for each combination of aspect and residual tree density.

Table 3.2. Multiple linear regressions for the 1- and 2-dimensional structural characteristics and the SCIs. ^L Natural log transformed, std_{ht} = standard deviation for heights, std_{dbh} = standard deviation for dbh, SCI_{max}-ht = maximum simulated SCI based on heights, SCI-ht = observed SCI based on height, SCI_{max}-dbh = maximum simulated SCI based on dbh, SCI-dbh = observed SCI based on dbh.

Dimensions					Full M	lodel	
Response	Variable	b	F	p	R^{2} (%)	p	
One-dimensional		_		r	(/)	P	
$\operatorname{std}_{\operatorname{ht}}$	Young cohort density ^L	+	6.2	0.020		< 0.001	
	(Young cohort density ^L) ²	-	8.9	0.006		-0.001	
	Proportion Douglas-fir	+	17.2	< 0.001			
	(Proportion Douglas-fir) ²	_	23.8	< 0.001			
std _{dbh}	Residual density	+	24.5	< 0.001	90	< 0.001	
	(Residual density) ²	_	10.8	0.003			
	Young cohort density ^L	_	22.0	< 0.001			
	Proportion Douglas-fir	+	23.4	< 0.001			
	(Proportion Douglas-fir) ²	-	28.4	< 0.001			
Young cohort density ^L	Residual density	_	5.6	0.026	58	< 0.001	
	(Residual density) ²	+	4.5	0.045			
	Aspect	+	15.1	< 0.001			
Proportion of Douglas-fir	Elevation	-	7.0	0.014	81	< 0.001	
	Slope	+	6.6	0.016			
	Aspect	+	67.3	< 0.001			
	Aspect*Residual density	-	9.2	0.006			
Two-dimensional	•						
Clark-Evans index	Young cohort density ^L	_	13.0	0.001	32	0.001	
Three-dimensional	roung conort density		15.0	0.001	32	0.001	
SCI _{max} -ht	Residual density		4.5	0.046	00	-0.001	
SCI _{max} -III	Young cohort density ^L	-	4.5	0.046	98	< 0.001	
	(Young cohort density ^L) ²	+	51.4	< 0.001			
	Proportion Douglas-fir		38.8	< 0.001			
	(Proportion Douglas-fir) ²	+	9.1 11.5	0.006			
	std _w	- +	288.1	0.003			
	Clark-Evans index	- -	12.2	<0.001 0.002			
SCI-ht	Residual density ^L	-	12.2	0.002	90	< 0.001	
Del III	Young cohort density ^L	+	30.2	< 0.002	90	<0.001	
	(Young cohort density ^L) ²	-	24.5	< 0.001			
	Proportion Douglas-fir	+	4.0	0.057			
	(Proportion Douglas-fir) ²	т-	7.9	0.037			
	std _h	+	34.6	<0.010			
SCI _{max} -dbh	Residual density	_	25.8	<0.001	98	< 0.001	
- C-max don	(Residual density) ²	+	18.8	< 0.001	96	\0.001	
	Young cohort density ^L	+	28.9	< 0.001			
	(Young cohort density ^L) ²	-	26.7	<0.001			
	Elevation	+	8.6	0.001			
	std _{dbh}	+	495.1	< 0.001			
	Clark-Evens index	-	10.0	0.001			
SCI-dbh	Young cohort density ^L	+	28.4	< 0.003	89	< 0.001	
Ber den	(Young cohort density ^L) ²		26.1	<0.001	89	<0.001	
	Proportion Douglas-fir	+	34.6				
	(Proportion Douglas-fir) ²			<0.001			
	Elevation	<u>-</u>	30.3	< 0.001			
		++	13.1	0.001			
	std _{dbh}	+	45.9	< 0.001			

RESULTS

One-dimensional summary statistics

Means and standard deviations of tree heights and dbhs. - Means and standard deviations of tree heights and dbhs showed clear differences both within paired plots and among pairs, with greater differences among pairs than within pairs (Fig. 3.2 A, B). Average tree heights and their standard deviations ranged from 5.6 m to 33.5 m and from 3.0 to 15.4 m, respectively. Average dbhs and their standard deviations ranged from 10.1 to 40.4 cm and from 4.9 to 38.1 cm, respectively. Neither mean tree heights, nor tree dbhs were associated with residual tree densities (both p>0.2).

The standard deviation of tree heights, std_{ht} (Table 3.2), was associated with the density of the young cohort and the proportion of Douglas-fir in the young cohort, but was not directly related to the density of residual trees (p=0.927). Both the density of the young cohort and the proportion of Douglas-fir in the young cohort had a curvilinear association with std_{ht} and the greatest positive association with std_{ht} occurred at about 650 trees/ha (95 % CI of 370- 1140 trees/ha) in the young cohort, and when about 47 % (95 % CI of 40-54 %) of these trees were Douglas-fir. The standard deviation of tree diameters, std_{dbh} (Table 3.2), was associated with the density of the residual trees, the density of the young cohort, and the proportion of Douglas-fir in the young cohort.

Both residual tree density and the proportion of Douglas-fir in the young cohort had a curvilinear association with std_{dbh} with a maximum at 57 residual trees/ha (95 % CI of 36-78 trees/ha) and 53 % (95 % CI of 46-60 %) Douglas-fir in the young cohort.

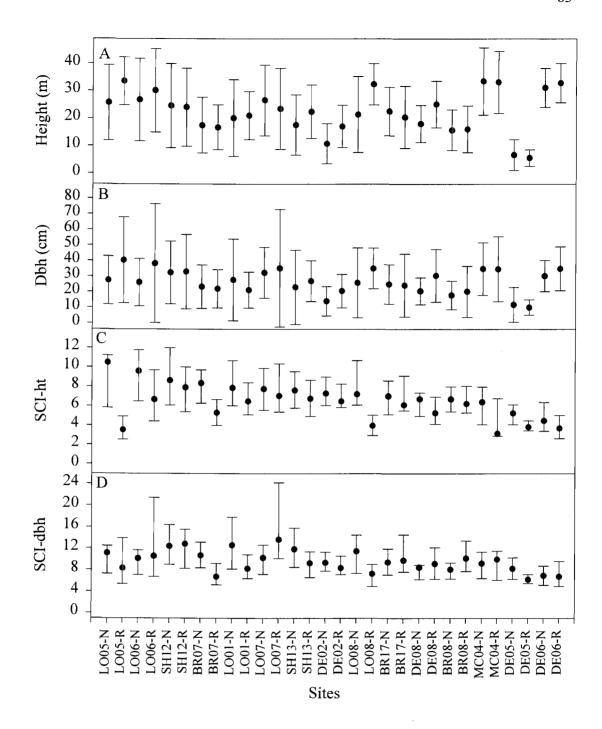


Figure 3.2. Summary statistics for means and standard deviations of tree heights and tree diameters and SCIs. For the SCIs the error bar refers to the minimum and maximum SCI based on 10,000 simulations. Stands are ordered by pairs from highest to lowest SCI-ht. The extension -N refers to stands without residual trees, -R to stands with residual trees.

Density of the young cohort. - The density of the young cohort was strongly associated with the density of residual trees and the aspect of the stand (Table 3.2). Residual trees had a curvilinear association with the density of the young cohort with a minimum at 40 residual trees/ha. South aspects had the lowest, east/west aspects had intermediate, and north aspects had the highest young cohort densities. Density was also related, in turn, to the tree species composition: stands on south aspects were dominated by Douglas-fir (r=0.634) and had lower young cohort densities than stands on north aspects dominated by western hemlock (r=0.648).

Proportion of Douglas-fir in the young cohort.- Residual trees and elevation were negatively, and aspect and slope were positively associated with the proportion of Douglas-fir in the young cohort (Table 3.2). South aspects had the highest, east/west aspects intermediate, and north aspects had the lowest proportion of Douglas-fir in the young cohort. Low-elevation had higher proportions of Douglas-fir than midelevations.

Predictions for the std_{ht} and std_{dbh} - Using predicted densities and tree species composition as input variables in the regression equations for the standard deviations allows the most likely standard deviations for a range of residual tree densities and different aspects to be found. Regression models predict that residual trees up to 40 trees/ha would be associated with a reduction in the density of the young cohort; then the density of the young cohort would increase again. South aspects would have the lowest, east/west aspects intermediate, and north aspects the highest young cohort densities, but differences between east/west and south aspects would be small (Fig. 3.3

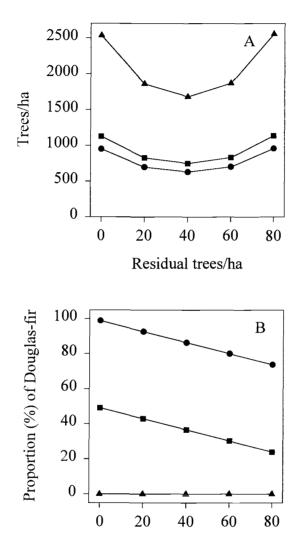


Figure 3.3. Response of tree density/ha (A) and proportion of Douglas-fir in the young cohort (B) to a range of residual tree densities for north (triangles), east/west (squares), and south (circles) aspects.

Residual trees/ha

A). The proportion of Douglas-fir (Fig. 3.3 B) would generally decline with increasing residual tree densities, but even at very high retention levels, the proportion of Douglas-fir in the young cohort would still be very high at south aspects. The proportion of Douglas-fir would also be very low on some north aspects even in the absence of residual trees. Both std_{ht} and std_{dbh} of young cohort and residual trees are predicted to have maxima on east/west aspects, with south aspects being intermediate, and north aspects having the lowest standard deviations. The std_{ht} for east/west aspects would have a maximum at about 20 residual trees/ha, north aspects around 40 residual trees/ha, and south aspects would still increase at 80 residual trees/ha (Fig. 3.4 A). The std_{dbh} would show a maximum for east/west and north aspects at about 40 residual trees/ha, and for south aspects at 60 residual trees/ha (Fig. 3.4 B).

Two-dimensional spatial structure

Stands in this study exhibited a variable spatial structure (Table 3.1): some stands showed a clustering (lowest Clark-Evans index R=0.82), some a random pattern, and some a regular pattern (highest Clark-Evans index R=1.32). Overall, the Clark-Evans index was negatively related to the density of the young cohort (Table 3.2), indicating a tendency for more clustering at higher densities.

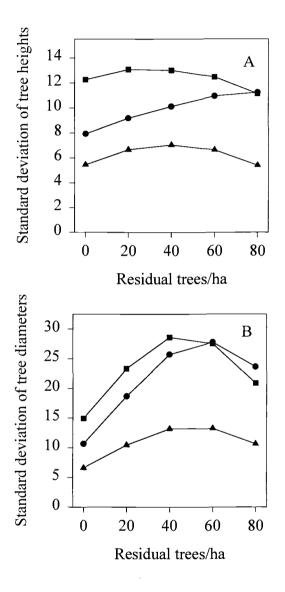


Figure 3.4. Response of standard deviation of tree heights (A) and standard deviation of tree diameters (B) to a range of residual tree densities for north (triangles), east/west (squares), and south (circles) aspects.

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

Based on 10,000 random allocations of measured tree sizes to the observed tree positions, differences of 23-69 % between simulated minimum and maximum SCI values were observed, with observed SCI values ranging from 3.14 to 10.48 and 6.20 to 13.64, based on height and dbh, respectively (Fig. 3.2 C, D). Two stands had an observed SCI-ht values that fell below the 2.5th and two that were above the 97.5th percentile of the simulated SCI-ht distribution; the same two stands also fell above the 97.5th percentile of the simulated SCI-dbh distribution, respectively. The only variable associated with these four stands was aspect; the two stands below the 2.5th percentile were both on south aspects and the two stands above the 97.5th percentile were on east aspects.

Maximum simulated SCI-ht (SCI_{max}-ht). - The SCI_{max}-ht was positively associated with the std_{ht} (partial $R^2 = 0.69$), but negatively with the density of residual trees and the Clark-Evans index for spatial aggregation (Table 3.2). The density of the young cohort and the proportion of Douglas-fir in the young cohort had curvilinear associations with the SCI_{max}-ht. The SCI_{max}-ht was at a maximum with 47 % (95 % CI of 38-56 %) Douglas-fir in the young cohort.

Observed SCI-ht.- The observed SCI-ht was also positively, but less strongly, associated with the std_{ht} (partial $R^2 = 0.40$). Although residual trees were tall and contributed positively to the std_{ht} , their overall influence on the SCI-ht was negative. The density of the young cohort and the proportion of Douglas-fir in the young cohort

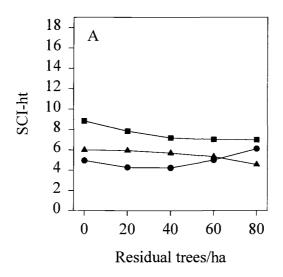
also had curvilinear associations with the SCI-ht. The SCI-ht was at a maximum with 38 % (95 % CI of 23-52 %) Douglas-fir in the young cohort.

Maximum simulated SCI-dbh (SCI_{max}-dbh). - The SCI_{max}-dbh was positively associated with the std_{dbh} (partial $R^2 = 0.86$) and elevation, but negatively associated with the Clark-Evans index for spatial aggregation. The SCI_{max}-dbh had a curvilinear association with the density of residual trees and the young cohort. Low-elevations had lower SCI_{max}-dbh values than mid-elevations. It is estimated that densities up to 45 residual trees/ha (95 % CI of 37-53 trees/ha) were associated with a decrease in the SCI_{max}-dbh, but at densities above 45 trees/ha residual trees contributed enough to the SCI_{max}-dbh that they could compensate for the loss in structural complexity in the young cohort.

Observed SCI-dbh.- The observed SCI-dbh was associated with the std_{dbh} (partial R² = 0.48), the density of the young cohort, the proportion of Douglas-fir in the young cohort, and elevation. Low-elevations had lower SCI-dbh values than mid-elevations. SCI-dbh had a curvilinear association with the density of the young cohort and the proportion of Douglas-fir in the young cohort. SCI-dbh was at a maximum with 57 % (95 % CI of 50- 63 %) Douglas-fir in the young cohort.

Predictions for the SCI-ht and SCI-dbh. - Using predicted densities and tree species composition, as well as the tree size standard deviations, as input variables in the regression equations for the SCIs allows the most likely structural complexity for a range of residual tree densities and different aspects to be found. Stands on east/west aspects generally would have the highest structural complexity among the different aspects. Based on the SCI-ht (Fig. 3.5 A), south aspects would show a minimum

structural heterogeneity at about 40 residual trees/ha, which parallels stands on east/west aspects. While east/west aspects would have a higher structural complexity than south aspects for residual densities ≤ 60 residual trees/ha, at higher residual tree densities stands on south aspects would show an almost equal structural complexity to stands on east/west aspects. North aspects would have intermediate SCI-ht values up to 60 residual trees/ha, beyond which they would have the least structural complexity. Whereas values for the SCI-ht would generally decline with increasing residual tree densities with the exception of south aspects at residual tree densities above 40 trees/ha, the SCI-dbh (Fig. 3.5 B) would generally increase with a higher residual tree density on all aspects. Stands on north aspects would always come out with the least structural complexity, south stands would have an intermediate complexity until residual tree densities are above 60 trees/ha, whereupon stands on south aspects would surpass stands on east/west aspects. Both north and east/west aspects would show highest SCI-dbh values at about 40 residual trees/ha, but stands on south aspects would continue to increase in structural heterogeneity beyond the range of residual trees in this study. Both SCI_{max} show similar associations with residual trees and aspects as their corresponding SCIs (Figs. 3.6 A, B).



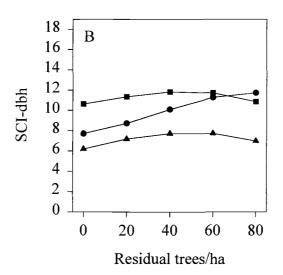
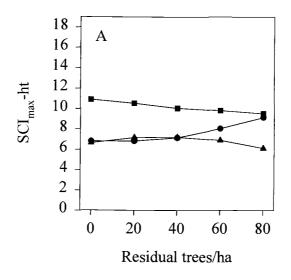


Figure 3.5. Response of SCI-ht (A) and SCI-dbh (B) to a range of residual tree densities for north (triangles), east/west (squares), and south (circles) aspects.



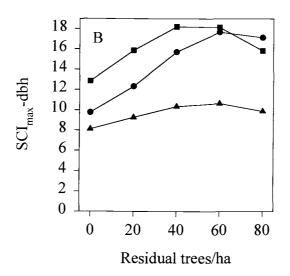


Figure 3.6. Response of SCI_{max} -ht (A) and SCI_{max} -dbh (B) to a range of residual tree densities for north (triangles), east/west (squares), and south (circles) aspects.

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 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. Determining the impact of residual trees on the structural complexity of a stand varied, depending on which criterion was used to evaluate structural complexity: some 1-dimensional structural variables (standard deviation of tree dbhs, young cohort density) showed an curvilinear association with increasing densities of residual trees, and some (proportion of Douglas-fir in the young cohort) showed a negative association with residual trees. Other 1-dimensional variables (mean and std of tree heights and mean dbh) plus the two-dimensional Clark-Evans index for spatial aggregation had no association with residual trees. Using several 1-dimensional structural summary statistics as independent variables for the SCI, the 3-dimensional SCIs were successful in detecting the impact of residual trees on the structural complexity of the stands in this study.

The expectation that structural complexity would be a linear function of residual tree density did not hold. With increasing residual tree densities, std_{ht}, std_{dbh} and SCI-dbh slowly increased, primarily due to an increase in the tree size standard deviations and a reduction in understory density. At low residual tree densities the young cohort

consisted almost entirely of large Douglas-fir of more or less uniform size arranged in 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 had about an equal proportion of Douglas-fir and shade-tolerant species. With fewer dominant Douglas-fir in the young cohort (Zenner et al. 1998), residual trees took the place of dominant young cohort Douglas-fir trees, and with an increasing abundance of suppressed, shade-tolerant western hemlock, western redcedar, bigleaf maple, and dogwood formed a multi-tiered canopy and thus maximized structural complexity. This is 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 oldgrowth 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). Stands with high residual tree densities were associated with high densities in the young cohort, which were mostly small, shade-tolerant western hemlock that show little size differentiation and, through elimination of most dominant and codominant Douglas-fir, a two-tiered structure was reached that is less complex than a multi-tiered canopy.

The SCIs and both standard deviations for tree heights and dbhs were positively related to the species composition in the young cohort. Mixed species stands in this

study that were generated after fires some 60-120 years ago generally had a multi-tiered canopy with the highest structural complexity. This may be the consequence of interactions of large- and small-scale disturbances and successional patterns (e.g., Oliver and Stephens 1977, Veblen et al. 1981, Stewart 1986 a, b). In the Oregon Cascades, the relatively shade-intolerant P. menziesii and A. procera (Minore 1979) usually regenerate in relatively even-aged stands after major fires. In contrast, the shade-tolerant T. heterophylla and A. amabilis (Fowells 1965) can regenerate in even-aged patches after catastrophic events, but also in canopy openings created by partial burns and small windfalls (Stewart 1986 a, b). Such differences in regeneration patterns result in patches of different sizes and ages within a forest, creating a mosaic of more or less even-aged patches of similar tree sizes (e.g., Bonnickson and Stone 1981), which are often composed of only a few tree species. Patterns of initial colonizers after disturbance may have important ramifications for the subsequent tree regeneration. Regeneration patterns after disturbances in the Cascades seem to indicate that if Pseudotsuga establishes first after a disturbance, regeneration of Tsuga and often A. amabilis may occur (Stewart 1986 a. b), thus exhibiting a mixed species composition and a potential for high structural heterogeneity. In contrast, if Tsuga dominates early after fire, regeneration may be excluded or remain at a low levels until canopy openings are formed in later developmental stages through small-scale disturbances (Stewart 1986 a, b). Whether Pseudotsuga or Tsuga dominate the regeneration may also depend on seed source availability and the aspect of a stand, as was observed in this study. In the case of a mixed species composition, stand development is usually characterized by

a progressive differentiation of species into distinct size strata, in which the least shadetolerant species occupied the larger size classes and species of increasing shadetolerance occupying successively smaller size-classes (Smith 1986), thus having a multi-layered canopy and high structural complexity.

Relationships between residual trees and the SCIs suggest that there may be an optimal density of, and perhaps spatial distribution, of residual trees that maximizes the SCI-ht and SCI-dbh by optimizing the stds, density, and the proportion of Douglas-fir in the young cohort. 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. Different structural complexities were found at a given residual tree density depending on the aspect. Moreover, both SCIs had greater differences among aspects than across the range of the residual tree densities 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, which 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 Douglas-fir in the understory was still very high on south aspects even at high densities of residual trees, either because western hemlock did not become established or was outcompeted by Douglas-fir. The proportion of Douglas-fir can also be very low on some north aspects even in the absence of residual trees, perhaps because Douglas-fir did not become established due to a lack of a seed source, or was outcompeted by the more shade-tolerant western hemlock. Although the

absence of Douglas-fir on north aspects is specific to the stands in this study and cannot be generalized to north aspects, abundances, proportions, and competitiveness of Douglas-fir in the young cohort may vary substantially among aspects. Goslin (1997) came to a similar conclusion after finding that suppressed Douglas-fir were able to survive on a south aspect where western hemlock was absent, but a stand on a north aspect was dominated by western hemlock and Douglas-fir was almost entirely absent. Greater frequencies of Douglas-fir (Williamson and Twombly 1983) and higher basal area growth on south aspects (Stage 1976, Youngberg and Ellington 1982) have also been reported previously.

In this study the Clark-Evans index of spatial aggregation indicated that the spatial patterns among the stands were highly variable with some stands showing a regular pattern, others a random pattern, and yet others a clustered pattern, reflecting different stages of differentiation among these stands (Zenner et al. 1998). Clustered patterns were related to high densities of the young cohort and reflected ongoing self-thinning. While two-dimensional statistics of forest structure, such as the Clark-Evans statistic or Ripley's k statistic, 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 Chapter 2)? Is the scale at which these patterns are observed

related to the scale at which structural complexity may be high? In both regressions involving the SCI_{max} the Clark-Evans index was positively related to the SCI_{max}, indicating that clustered patterns may have a higher structural complexity. The non-significance of the Clark-Evans index in the regression of the observed SCIs indicates, however, that the spatial pattern was not related to the observed structural complexity at the scale used in this study. This apparent contradiction is not surprising, however, since clustered patterns can show enormous size differences over small distances, thus increasing the structural complexity index more than if the same size differences were observed at progressively larger distances. 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, larger scales than the one used in this study are necessary.

The lowest densities of the young cohort, greatest variation in tree dbhs, and the highest SCI-dbh generally point to the retention of intermediate (about 40 trees/ha) levels of green-trees. These levels are within the reported range of typical densities of 18 to 29 (95 % CI 2-51 trees/ha) Douglas-fir > 100 cm dbh *per* hectare in old-growth forests (Spies and Franklin 1991). However, whereas std_{ht}, std_{dbh} and SCI-dbh had a direct or indirect positive association with residual trees, SCI-ht had a direct negative association with residual trees and was at a maximum in the absence of residual trees, except on south aspects. This difference may relate to and highlight the mechanisms that may be responsible for the observed structural complexity 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 the fact that having additional residual trees comes at the expense of losing more dominant and codominant understory trees in the vicinity of residual trees, which then occupy lower crown classes. Consequently, although residual trees sharply increase the very localized structure, their negative influence on the growth of Douglasfir in the young cohort (Zenner et al. 1998) is reaching further than their immediate neighborhood, thus reducing the structural complexity at larger scales. At high residual tree densities, structural complexity may increase again. The different conclusions based on SCI-dbh and SCI-ht are also 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. For example, whereas a residual tree of 200 cm dbh can create twice the size 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. It is thus essential to investigate structural complexity with both indices to understand how residual trees are associated with structural complexity.

CONCLUSIONS

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 western hemlock, western redcedar, and hardwoods, or Pacific silver fir in higher elevations, as a potential threat to Douglas-fir, management strategies that seek to integrate timber production as well as habitat restoration need to consider shadetolerant 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 seem to promote the development of a shade-tolerant understory, without eliminating Douglas-fir 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, Hansen et al. 1991, 1995, Swanson and Franklin 1992). These findings also support Franklin and Spies' (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 and hence a reduction in structural complexity as old-growth forests change from a canopy still dominated by Douglas-fir to one where hemlock 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 western hemlock 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 the 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 Douglas-fir is the most abundant and dominant tree species, a greater amount of retained green-trees may produce conditions that may be more suitable for western hemlock or other more shade-tolerant species, which would increase the structural complexity. On north aspects, where western hemlock may be more abundant and the dominant tree species, forest managers may have to create conditions, such as though gap creation, planting of Douglas-fir in natural or artificial openings, and differential thinning of hemlock to help Douglas-fir survive and maintain its presence 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 Douglasfir dominated stands with shade-tolerant species such as western hemlock, western redcedar, or red alder 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.

Adaptive forest management, charged with creating old-forest conditions in short times, needs 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. The index most preferable to the evaluation of structural complexity most likely depends on the objective of the study. If, for instance, the index may be used for a description of wildlife habitat, researchers may be interested in conditions created by residual trees, which may favor use of the SCI-dbh. 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 which maximizes structural complexity.

Chapter 4

The Structure of Some Natural Mixed-Conifer Forests in the South-Central Oregon Cascades

Eric K. Zenner and David E. Hibbs

ABSTRACT

A new index, the structural complexity index (SCI), was used to compare the structural complexity of young, mature, and old stands in the south-central Cascades of Oregon and relate the index to commonly measured structural variables and spatial patterns. The concepts of effective and potential structural complexity are introduced and a more operational definition of forest structure is proposed that, together with the SCI and effective and potential structure, comprise powerful new tools to test hypotheses about the complexity of observed structures in forests. In our analysis, we found that structural complexity was highest in stands where both dominant and suppressed trees were randomly distributed at small scales and where these crown classes occurred in close proximity to one another. Where dominant and codominant trees occurred in groups, the structural complexity was somewhat reduced; dispersion of these groups across the stand increased structural complexity, however. The same was true for groups of Douglas-fir, which was found mostly in the emergent and dominant canopy layers. Species composition per se was not associated with structural complexity, probably because all stands were highly mixed. Differences between the effective and potential structural complexity were related to the occurrence of different patch-types and species mixtures, indicating that the observed structural differences among stands were generally the same as between the effective and potential structural complexity within a particular stand. The maximum structure hypothesis was proposed and tested, but despite strong evidence in young and mature stands in favor of the hypothesis, oldgrowth forests generally had effective structural complexities below their potential.

Since the young-to-mature natural, unmanaged stands in this study were at their structural potential, their structures may serve as a guide for managers who seek to enhance the structural complexity of managed stands.

INTRODUCTION

Structure has been defined as the "physical embodiment of a system's pattern of organization" (Capra 1996). The pattern of organization of any system is the configuration of relations that reflect processes taking place in the system. In ecosystems, structure is believed to be tightly coupled to ecosystem dynamics and processes. Structural complexity in forests is a record of interactions with the environment, where over time an individual pathway of structural coupling between the forest and its environment emerges. Definitions of forest structure point out two important components of forest structure: (1) the vertical arrangement of individuals and their foliage, and (2) the horizontal arrangement or spatial distribution of stems (McEvoy et al. 1980). For example, forest structure has been defined as "the distribution of biomass in space" (Goff and Zedler 1968) or as "the variation in species and age classes, the arrangement of species into different canopy layers, and the distribution of individuals among diameter classes" (Smith 1986). Forest structure has also been shown to have a strong relation to species composition, although forests of similar composition can differ quite widely in structure (Goff and Zedler 1968, Kershaw 1973). Forest structure is thus characterized by a vertical and horizontal spatial

arrangement of plant species, plant sizes, or age distributions (McEvoy et al. 1980, Gadow and Füldner 1992, Crow et al. 1994).

Ecologists have used the structure of a forest as an important factor in the analysis of forest ecosystems. For example, the importance of forest structure has been invoked in the definition of niche requirement of wildlife species (e.g., MacArthur and MacArthur 1961, James and Shugart 1970, Forsman et al. 1984), the identification of vertical and horizontal microhabitats (e.g., Franklin et al. 1981), the examination of spatial heterogeneity and temporal dynamics of understory vegetation (e.g., Spies and Franklin 1989), the investigation of patterns of regeneration and gap dynamics (e.g., Runkle 1991), the explanation of microclimatic variation within a forest (e.g., Chen and Franklin 1996), and the prediction of timber production (e.g., Buongiorno et al. 1994). The close coupling between structure and the processes generating it has led ecologists to believe that by maintaining structural characteristics of natural forests, and in particular old forests, ecosystem functions can be sustained (e.g., FEMAT 1993 a, b, Hansen et al. 1991, 1995, McComb et al. 1993). It is assumed that structural complexity of a forest can be used as a surrogate for the "biodiversity value" (Hansen et al. 1991) of a forest stand. Analyses of forest structure could thus be used to guide management strategies that seek a balance between conservation and creation of wildlife habitat and the production of timber. For example, it is believed that structural complexity is associated with habitat quality for many wildlife and the need for habitat structures of particular densities and sizes to support viable wildlife populations may be

assessed from structural characteristics of forests that currently support such populations (McComb et al. 1993).

Structurally complex stands seem to result from natural disturbances that occur over a broad range of spatial and temporal scales, sizes, shapes, and intensities, which often leave legacies such as large residual trees, create snags and logs, and facilitate subsequent regeneration that can enhance the vertical complexity of the forest (Spies et al. 1990). Mortality and replacement of individual trees seem to be a primary source of heterogeneity for structure and composition in forests where small-scale disturbances are dominant and large, stand-destroying disturbances are infrequent (Lertzman and Krebs 1991). Old-growth forests, through exposure to small-scale disturbances that cause mortality and replacement of individual trees, are believed to show the highest degree of structural coupling and complexity (Franklin and Spies 1991). Distinctive compositional and functional characteristics of late-successional forests seem to be a direct consequence of structural features (Franklin and Spies 1991).

The conversion of mature and old forests to young plantations, and disturbances imposed by timber management (e.g., clearcutting), may 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). The lower structural complexity, and the absence of large trees and dead wood in young managed stands, contrasts with young natural forests that show a high variability in tree sizes and canopy layering (Spies et al. 1988).

Currently, new silvicultural systems in the context of "ecosystem management" (e.g., Grumbine 1994) or "structure-based management" (Oregon Department of Forestry 1996) are being designed and tested to create structurally more complex forests in the PNW (e.g., Aubry et al. 1998, Halpern et al. 1998). To evaluate the success of different silvicultural systems in creating forests with a high structural complexity, adaptive ecosystem management needs objective criteria for determining if the created structures resemble the structures managers sought to reproduce. Despite the critical role of structural complexity to habitat diversity, species conservation, and ecological diversity, the lack of quantitative, ecologically relevant measures of structural complexity that allow comparisons of structural complexity among forests (Kuuluvainen et al. 1996) may partly be due to a definition of forest structure that is non-operational and partly due to a failure to incorporate the 3-dimensionality of forest structure in an index used to assess it.

Although the previous definitions incorporate the elements of structural complexity and implicitly recognize the 3-dimensionality of forest structure, they do not provide a quantitative basis for evaluating whether one forest is structurally more complex than another and are thus non-operational.

In lieu of a comprehensive measure of structural complexity, 1-dimensional structural characteristics such as stem density, canopy cover, the number of canopy layers, the mean and the standard deviation of tree size distributions, and various combinations of these characteristics have been used to assess the structure of forests (see Jones 1945, Meyer 1952, Goff and Zedler 1968, Franklin et al. 1981, Spies and

Franklin 1991). Recently, Acker et al. (1998) developed an old-growth index that uses variables that discriminated best between young, mature, and old-growth stands in western Oregon and Washington (see Spies and Franklin 1991). Their index is based on average values for dbh, the standard deviation of the dbh, tree density, and density of Douglas-fir > 100 cm dbh of young and old-growth stands, but does not incorporate the spatial patterns of stems.

The study of 2-dimensional horizontal patterns with stem-mapped data with nearest neighbor analysis, the Clark-Evans index for spatial aggregation, Ripley's K, and the semivariogram enjoy increasing use in describing the spatial pattern of a forest (e.g., Moeur 1993, Pretzsch 1995, Goslin 1997, Kuuluvainen et al. 1996). Results from spatial point pattern analyses have been linked to ecological processes (e.g., gap processes, self-thinning; Kenkel et al. 1988, Kuuluvainen et al. 1996), but they typically ignore the tree sizes or have to be computed for each size class separately (Kuuluvainen et al. 1996) and 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? Is the scale at which these patterns are observed related to the scale at which structural complexity may be high? Thus the limitations of the 1-dimensional structural variables in adequately reflecting structural complexity have essentially not been overcome by these 2-dimensional techniques.

In landscape ecology, structure has been recognized as scale dependent and is measured by the size and distribution of patches (Turner 1989). The term "patch" in this paper is understood to be a spatially discrete and internally homogeneous collection

of neighboring trees. Patches are recognized by their relative differences (Wiens 1976).

To distinguish among patches that have different levels of internal homogeneity,

different "patch-types" that reflect these levels have been defined in this paper.

Analogous to landscapes, forests can, at a smaller scale, also be regarded as a dynamic mosaic of patches of different structure.

A more operational definition of structural complexity in forests may then be based on the spatial arrangement of patches of similarly sized trees rather than individual trees and recognizes the importance of the patchiness of a forest (i.e., the frequency distribution of patch-sizes, the spatial distribution of patches, and the interspersion of different patch-types). In this paper, the structural complexity of a forest at a single time is defined as the scale-dependent, 3-dimensional distribution of tree attributes among neighbors in space, characterized by the spatial arrangement of trees into patch-types based on homogeneous tree attributes at various levels of the utilized attribute or of various combinations of species mixtures. The attribute utilized in this study was tree diameters at breast height (dbh).

Indices that are based on continuous scales of multiple, ecologically meaningful attributes are superior to categorical approaches and definitions that seek to distinguish structurally complex from homogeneous stands, or young from mature from old-growth forests (Franklin and Spies 1991). Furthermore, an ecologically meaningful index used to compare the structural complexity of different forests should (1) reflect the 3-dimensional nature of forest structure, (2) be sensitive to the outcome of small-scale processes such as self-thinning or gap processes, and (3) be sensitive to the habitat

heterogeneity and the dynamic mosaic of patches ("patchiness") of different structures at larger scales within a forest (e.g., tree sizes, species composition). Such 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 structural complexity of forest stands was previously proposed (Zenner 1998).

The objective of this paper was to examine the spatial patterns of the stands used in this study and to test the association of the SCI with 1- and 2-dimensional structural stand characteristics. In particular, the following issues and hypotheses were tested: 1) Does the SCI find a difference in the structural complexity from young to mature to old forests? 2) What 1-dimensional summary statistics relate best to the SCI? 3) Is there a particular species mixture that maximizes the structural complexity of the stands used in this study? 4) What patch-types are associated with the structure of the forests in this study? 5) Do the spatial patterns vary at different scales and how consistent are these patterns across several stands? 6) Are the spatial patterns, particularly at the scale of nearest neighbor distances, associated with the SCI and does the horizontal structure contribute to overall structural complexity at the stand level?

METHODS

Ten plots were established in the lower and mid-elevations of the *Tsuga* heterophylla (western hemlock) zone (Franklin and Dyrness 1973) in the Umpqua National Forest in Oregon's western south Cascade Range. Dominant species in the

these stands included *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir), *Tsuga heterophylla* (Raf.) Sarg., *Thuja plicata* Donn. (western redcedar), and *Libocedrus decurrens* Torr. (incense cedar). *Taxus brevifolia* Nutt. (Pacific yew) also occurred in the understory of some stands.

Only unmanaged, natural stands of various ages were included in the study. Stands with recent excessive mortality or understocked stands were excluded from the study. A 110 by 110 m plot area was established in each stand and a 10 by 10 m reference grid was overlaid on the plot area. Trees were stem-mapped and slope-corrected distances (to the nearest 5 cm) and azimuths (to the nearest 1/10 degree) to the grid points were recorded and later converted to Cartesian coordinates. Species, diameter at breast height (dbh), crown ratios, and canopy class relative to the general canopy for all live trees ≥ 5 cm in dbh, were recorded. Emergent, dominant, and codominant trees were further classified as canopy trees, intermediate and suppressed trees as subcanopy trees. Relevant site and stand characteristics are listed in Table 4.1.

Nearest neighbor analysis in form of the index of aggregation (R, Clark and Evans 1954) was used to characterize the horizontal tree distribution pattern. The aggregation index relates the observed average distance of all trees to their respective nearest neighbors to the average distance expected under a random or Poisson spatial distribution. The aggregation index ranges from 0 (maximum clustering) to 2.15 (regular hexagonal pattern). Values below 1.0 indicate a clustered pattern, values around 1.0 are a random pattern, and values above 1.0 are a regular pattern.

Table 4.1. Stand information for the ten mapped stands (inner 1 ha core area).

Stand	S-001 1)	S-002 1)	S-003 1)	S-004 ²⁾	S-005 ²⁾	S-006 ²⁾	S-007 ²⁾	S-008 1)	S-009 ³⁾	S-010 1)
Tree density (# trees/ha)	379	436	585	520	617	528	571	404	850	349
Douglas-fir	34	131	144	153	241	188	252	137	335	48
western hemlock	300	242	378	221	254	323	259	250	168	259
western redcedar	30	27	32	113	16	6	59	16	344	3
trees > 100 cm dbh	35	19	26	15	4	3	0	27	0	60
Basal area (m ²)	85.6	99.8	106.1	103.2	93.9	86.6	96.2	105.0	76.7	108.0
Douglas-fir	46.6	69.9	80.2	58.0	70.0	60.6	74.2	74.3	46.1	76.1
western hemlock	33.5	26.8	18.7	21.7	22.3	24.6	16.8	27.3	17.1	29.9
western redcedar	5.2	2.8	4.8	14.3	2.7	0.8	4.8	2.9	13.5	0.2
DBH (cm)		_				_				
mean	40.3	42.0	35.9	41.3	37.2	39.3	40.6	48.1	30.2	46.9
Douglas-fir	123.9	66.2	66.0	64.6	60.2	62.9	60.7	47.0	40.5	142.8
western hemlock	32.8	32.9	21.0	31.5	29.0	27.8	24.3	47.6	33.6	33.1
western redcedar	35.6	31.8	31.2	34.3	36.6	36.8	30.4	50.3	21.7	24.3
standard deviation	35.1	31.4	32.2	27.5	24.7	24.3	23.1	32.7	14.8	46.7
Height (m)										
mean	26.4	27.8	23.8	27.2	25.8	27.5	28.2	30.8	22.8	27.3
standard deviation	15.0	16.4	16.2	13.9	14.7	13.8	13.2	16.0	9.6	18.9
maximum	68.9	61.4	64.0	61.7	56.8	55.1	53.0	63.4	47.2	72.1
Aggregation Index (R)	1.03	0.96	0.97	1.00	0.97	0.98	1.12	1.15	1.01	1.04
Distance between neighboring trees (m)		_							
mean	2.7	2.2	2.1	2.2	2.0	2.2	2.4	3.0	1.8	2.9
std	1.5	1.3	1.2	1.1	1.1	1.2	1.2	1.4	1.0	1.4
min	0.1	0.1	0.1	0.2	0.02	0.2	0.3	0.2	0.1	0.2
max	8.0	8.4	10.2	6.4	6.2	8.0	11.4	11.4	5.9	8.2
SCI	10.61	11.13	13.15	11.33	10.67	10.29	10.68	11.44	7.96	13.94
SCI_{max}	11.73	12.64	13.91	11.72	11.68	10.73	10.59	12.42	8.03	15.35
percentile 4)	49.1	1.2	77.7	98.2	10.2	92.9	>100	32.2	99.8	66.9

old-growth, and mature, and ma

A test of spatial segregation (Dixon 1994) was used to test the hypothesis that species labels and crown class labels were randomly assigned to points (random labeling hypothesis). Based on cell counts of a contingency table of nearest neighbors, Dixon (1994) proposed a 2-df chi-square test of spatial segregation, a pair of species/crown class-specific tests, and a pair of species/crown class-specific measures of segregation (symmetry test) for completely mapped data where Pielou's (1961) 1-df chi-square test of independence is inappropriate (Meagher and Burdick 1980, Dixon 1994).

Ripley (1977) proposed an extension of the nearest neighbor statistic to a complete cumulative distribution function, which provides information about an observed spatial pattern relative to randomness as a function of distance (scale). Ripley's K(d) analysis can be applied to stem-mapped data to investigate the distribution of point-to-point distances within the plane considering the distances between all pairs of points in the plane (Moeur 1993). The K(d)-distribution is compared for values of d (distances) from 0 to a maximum of one-half the length of the shortest boundary (e.g., 50 m in this study). An edge correction scheme as reported by Diggle (1983, p. 72) was employed in this study. L(d), a square root transformation of K(d) that stabilizes the variance and has an expected value of approximately zero under the Poisson assumption was used to examine the type of pattern as a function of scale. Negative L(d) values would indicate regularity, inhibition, or repulsion, positive values would indicate clustering or attraction (Moeur 1993). Departures from a random distribution were evaluated with Monte Carlo tests that compared the observed L(d)-distribution to values from multiple spatial patterns generated from a Poisson model. In all examples, 200

spatial patterns were generated in each Monte Carlo simulation to define point-wise 95 % confidence boundaries at distances from 0 to 50 m by 0.5 m intervals.

Ripley's K(d) analysis was also used to analyze the pattern of interactions among more than one type of points. Upton and Fingleton (1985) distinguish several elements of inter-type point patterns that were tested with Ripley's K(t): 1) univariate withingroup patterns of a single point-type, e.g., univariate spatial pattern by species (Douglas-fir and western hemlock) and by crown classes for Douglas-fir and western hemlock; 2) combined between-group patterns of several point-types, e.g., all trees combined, canopy western hemlock (dominant and codominant crown classes) and subcanopy western hemlock (intermediate and suppressed crown classes); 3) the bivariate interaction pattern of two point-types, e.g., canopy trees and subcanopy trees, Douglas-fir and western hemlock, Douglas-fir and canopy western hemlock only, Douglas-fir and subcanopy western hemlock only, canopy western hemlock and subcanopy western hemlock.

A 3-dimensional model of forest structure was used to describe the structural complexity. Trees are represented as 3-dimensional irregularly spaced data points (x, y = spatial coordinates, z = tree sizes such as tree heights or dbh's). Three adjacent points in x, y-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), creating a continuous faceted surface. The Delaunay triangulation routine (Matlab 1997) was used to create a network of non-overlapping triangles, where

the triangulation is independent of the order the points are processed. Delaunay triangles are as equi-angular as possible such that all sample points are connected to their two nearest neighbors to form triangles.

An index that is based on differences in tree attributes (here diameters) and distances of neighboring trees was created to directly compare the structural variability among stands. This "Structural Complexity Index" (SCI) is defined as the sum of the surface areas of the TINs for a stand (SCI*) divided by the ground area covered by all triangles:

$$SCI = \frac{SCI *}{A_T} \tag{1}$$

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

$$SCI^* = \sum_{i=1}^{N} \frac{1}{2} |axb| \tag{2}$$

where i=1,...,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 $b=(x_c-x_a, y_c-y_a, z_c-z_a)$.

In two separate analyses, the proportions of nine patch-types that were defined based on the species composition of the triangles (i.e., Douglas-fir only, western hemlock only, redcedar only, other species only, Douglas-fir/western hemlock mixture, Douglas-fir/redcedar mixture, western hemlock/redcedar mixture, other 2-species mixtures, and 3 species mixtures) and the proportions of ten patch-types that were defined based on the composition of crown classes of the triangles (i.e., dominant trees only, codominant only, intermediate only, suppressed only, dominant/codominant

mixture, dominant/intermediate mixture, dominant/suppressed mixture, codominant/intermediate mixture, codominant/suppressed mixture, and intermediate/suppressed mixture) were recorded. Adjacent triangles belonging to the same patch-type were then merged to larger patches and the segregation of these patch-types was assessed. Patch-type segregation is defined as the ratio (in %) of the number of triangles in a patch-type after adjacent triangles have been merged to larger patches and the number of triangles in a patch-type before the merging.

Different structural conditions were simulated by randomly assigning a value of the tree diameter distribution to each tree position while holding the tree positions fixed. This process was repeated 10,000 times for each stand and the ranges of SCI were recorded. Multiple linear regression analysis was used to test which variables were associated with the SCI. Several sets of independent variables were separately tested for their associations with the SCI. To relate the univariate and bivariate spatial patterns to the SCI, indicator variables were defined for the dominant observed pattern (i.e., 0=random, 1=aggregated, 2=dispersed) for several distances at the scale of nearest neighbors distances (e.g., from 2 to 10 m) and regressed on the SCI. 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. For the regression analysis of the SCI on species composition of the patch-types, stand 9 was deleted as it had more than twice the density of western redcedar than any other stand and proved to be a consistent outlier.

RESULTS

Tree density, species composition, and size distributions of trees

Tree densities in this study ranged from 349 to 850 trees/ha (Table 4.1). Stands 1, 2, 8, and 10 had densities within the range of old-growth forests presented in Spies and Franklin (1991); stand 9 had a density typical for a young stand, and stands 3-7 showed densities typical for mature stands. Densities for canopy trees (trees > 100 cm dbh) ranged from 0 to 60 trees/ha; stands 1, 2, 3, 8, and 10 had densities of canopy trees that were within the range reported for old-growth forests.

Species composition in all 10 stands was highly mixed and quite variable.

Douglas-fir contributed between 10 and 45 %, western hemlock between 20 and 78 %, and western redcedar between 1 and 41 % of the tree density. Stand 9 had more than twice the density of western redcedar than the stand with the next highest western redcedar proportion. Stands 1 and 10 had the highest proportions of western hemlock.

Mean dbhs (Table 4.1) ranged from 30.2 to 46.9 cm, which is within the reported range for mature and old-growth forests (Spies and Franklin 1991). The standard deviations for the tree dbhs ranged from 14.8 to 46.7 cm. These values are typical for unmanaged young (stand 9), mature (stands 4-7), and old-growth (stands 1-3, 8, 10) stands in the Pacific Northwest (Spies and Franklin 1991). In all 10 stands, Douglas-fir was the dominant canopy species with the biggest dbh. Whereas western hemlock and western redcedar generally had smaller dbhs than Douglas-fir, their tree sizes overlapped substantially with one another and to some extent with Douglas-fir.

Both stands 1 and 10 had Douglas-fir mostly in the emergent/dominant canopy layer with tree dbhs generally > 100 cm.

Canopy classes showed clearer size differences than the tree species in each stand, but a substantial overlap in the dbh ranges among the crown classes also occurred in all stands. Stands 1 and 10 had the biggest range in dbh for dominant trees, which encompassed both emergent and dominant canopy trees.

Spatial structure

At the scale of nearest neighbors, stands in this study exhibited mostly random spatial structures (Table 4.1): the Clark-Evans index for spatial aggregation ranged between 0.96 and 1.15. The 2-df test of spatial segregation for Douglas-fir and western hemlock rejected the random labeling hypothesis for stands 7 and 8 (both p < 0.0001). Instead, both Douglas-fir and western hemlock tended to have the respective other species as nearest neighbors (p<0.0001) and nearest neighbor relations tended to be symmetrical (p>0.05); Douglas-fir had western hemlock as nearest neighbors as frequently as western hemlock had Douglas-fir as nearest neighbors. In all other stands, none of the tests of segregation were significant and the nearest-neighbor relationships were not significantly asymmetric. There was very strong evidence from the 2-df test of spatial segregation for emergent/dominant and suppressed canopy classes that labels were not randomly assigned in stands 7 and 9 (p<0.0001). Emergent/dominant and suppressed canopy classes tended to have the respective other canopy class as nearest neighbors (p<0.0001) and nearest neighbor relations tended to be symmetrical (p>0.05).

There was even stronger evidence that labels were not randomly assigned for canopy and subcanopy trees in stands 7 and 9 (p<0.0001). Again, canopy and subcanopy trees tended to have the respective other canopy class as nearest neighbors (p<0.0001) and nearest neighbor relations tended to be symmetrical (p>0.05). In all other stands, none of the tests of segregation was significant and the nearest-neighbor relationships were not significantly asymmetric.

Univariate spatial analyses for Douglas-fir and western hemlock. - Douglas-fir had variable spatial patterns (Figure 4.1) ranging from random (stands 1, 4, 10) to clustered at intermediate and large scales (stands 2, 3, 8) to uniform patterns up to 6 m (stands 5-9). Western hemlock also had variable spatial patterns but was more often clustered at intermediate and large scales (stands 1, 3-5, 8-10) than Douglas-fir and could also be uniform at small scales (stands 5, 7, 8). Moreover, western hemlock had different spatial patterns for different crown classes, with intermediate and suppressed western hemlock often exhibiting clustered patterns across a wide range of scales (e.g., 5-50 m). The spatial patterns of the different crown classes for western hemlock did not show any clear patterns among stands and reflected a unique pattern for each stand. Generally, however, Douglas-fir tended toward more uniform and random patterns, whereas western hemlock showed a more clustered pattern, particularly for the subcanopy trees at small to intermediate scales. Within-group patterns of emergent or dominant Douglas-fir and canopy western hemlock typically exhibited uniform or random spatial distributions at small scales in this study. This pattern was even stronger when all canopy trees where combined.

Figure 4.1. Univariate spatial analyses for Douglas-fir and canopy and subcanopy western hemlock. Stand are ordered from 1 to 10. White bars indicate random spatial distributions, black bars indicate spatially clustered distributions, and gray bars indicate spatially dispersed distributions over a range of distances. PSME refers to Douglas-fir, TSHE to western hemlock. Extensions refer to canopy classes, DC = dominant/codominant, D = dominant, C = codominant, IS = intermediate/suppressed, I = intermediate, and S = suppressed trees.

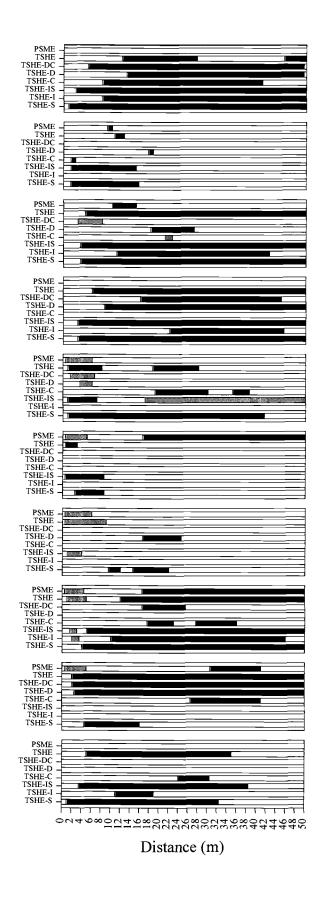


Figure 4.1

Univariate analyses for all trees combined and by crown classes. - As with Douglas-fir and western hemlock individually, the spatial pattern of the entire tree assemblage was highly variable from stand to stand (Fig. 4.2). Whereas some stands were clustered at intermediate to large scales (e.g., stands 1-4, 9-10), stand 6 had a completely random spatial pattern, and stands 5 and 7 were clustered at small scales; stand 8 was clustered at all scales. In general, most stands had uniform spatial patterns for canopy trees (dominant and codominant crown classes) at small scales (e.g., up to 8 m, stand 10 up to 20 m), but random (stand 2) and clustered (stand 9) spatial patterns also occurred. Subcanopy trees were mostly clustered across a range of scales and sometimes up to 50 m, but even sub-canopy trees could have a uniform pattern at small scales (e.g., stand 8). Generally, however, the spatial scales of clustering seemed to increase from canopy to sub-canopy trees.

Bivariate analyses: Douglas-fir vs. western hemlock and canopy vs. sub-canopy trees. As with the univariate analyses, the bivariate analyses revealed unique spatial
interactions and unique scales of interactions for each stand (Fig. 4.3). Douglas-fir and
western hemlock were sometimes independent of one another (stand 10), attracted at
small scales (stands 4, 7), attracted at larger scales (stands 1, 8), or dispersed away from
one another at large scales (stands 5, 9). Differences in the interactions between
Douglas-fir and canopy western hemlock and Douglas-fir and subcanopy western
hemlock were apparent in most stands. Whereas Douglas-fir and canopy western
hemlock were independent in 8 of the 10 stands, Douglas-fir and subcanopy western
hemlock were generally attracted at small distances.

Figure 4.2. Univariate analyses of all trees and trees by crown classes. Stand are ordered from 1 to 10. White bars indicate random spatial distributions, black bars indicate spatially clustered distributions, and gray bars indicate spatially dispersed distributions over a range of distances.

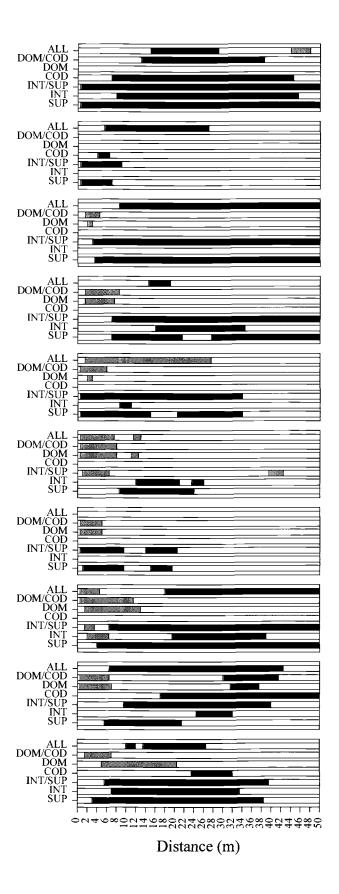


Figure 4.2

Figure 4.3. Bivariate analyses of species interactions and interactions of different canopy classes. Stands are ordered from 1 to 10. DCIS=dominant/codominant vs. intermediate/suppressed crown classes, PSTS=Douglas-fir vs. western hemlock, PSTSDC=Douglas-fir vs. dominant/codominant western hemlock, PSTSIS=Douglas-fir vs. intermediate/suppressed western hemlock, TSDCIS=dominant/codominant western hemlock vs. intermediate/suppressed western hemlock. White bars indicate random spatial interactions, black bars indicate spatial attraction, and gray bars indicate spatial dispersion over a range of distances.

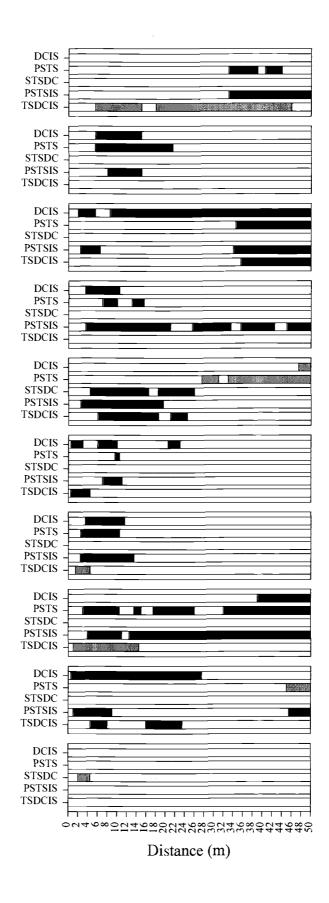


Figure 4.3

Patches and patch-types

Patches based on species composition are single triangles or clusters of triangles (Fig. 4.4). Generally, patches that reflect a mixture of Douglas-fir and western hemlock were dominant (proportions of 30-65 %) in all but stands 1, 9, and 10. In stands 1 and 10 western hemlock patches dominated (proportions of 40 - 50%); in stand 9 a mixture of Douglas-fir and western redcedar patches dominated the stand. Monospecific Douglas-fir patches had proportions of less than 10 % in all stands. Patches composed of 2-other-species (e.g., Pacific yew, incense cedar and their mixtures with Douglas-fir, western hemlock, or western redcedar) and patches with 3-species had proportions between 5 and 30 %. There was no clear pattern in the differences in proportions between the observed patches and those from the simulations yielding the maximum and minimum SCI values (Fig. 4.4). It appears that the simulation with the maximum SCI had fewer patches of pure western hemlock and more patches of other 2-species and 3-species mixtures. The simulation with the lowest SCI did not, however, have the lowest proportion of other 2-species and 3-species patches as might have been expected, but had consistently fewer mixed Douglas-fir/western hemlock patches than were actually observed or occurred in the simulation with the maximum SCI.

The mixed dominant/suppressed tree patch-type (Fig. 4.5) had the highest proportion in all 10 stands. The dominant tree patch-type only occurred between 0 and 12 % and mixed dominant/codominant tree patch-types had only a slightly higher proportion of occurrence than dominant tree patch-types. In general, the simulation with the maximum SCI had higher proportions of patch-types with high contrasts (i.e.,

Figure 4.4. Percent of patch types based on species composition for the 10 sample stands. Stands are ordered by row and column from 1 to 10. DF=Douglas-fir, WH=western hemlock, RC=redcedar, OTHER=incense cedar and Pacific yew, 2spp=mixture of two species excluding DF/WH, DF/RC, and WH/RC, 3spp=mixture of 3 species. Min. SCI refers to the simulation giving the smallest SCI, obs. SCI is the observed SCI based on the actual mapped trees, and max. SCI refers to the simulation giving the biggest SCI.

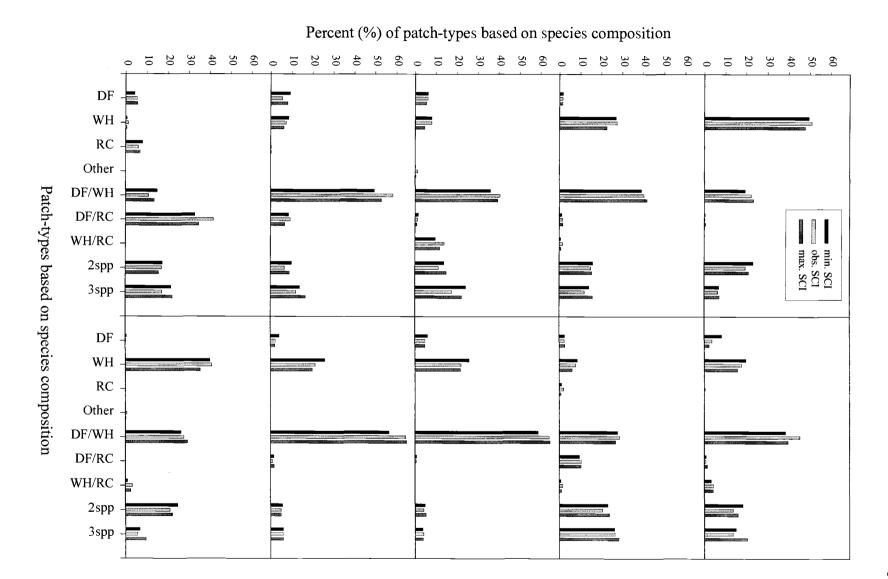
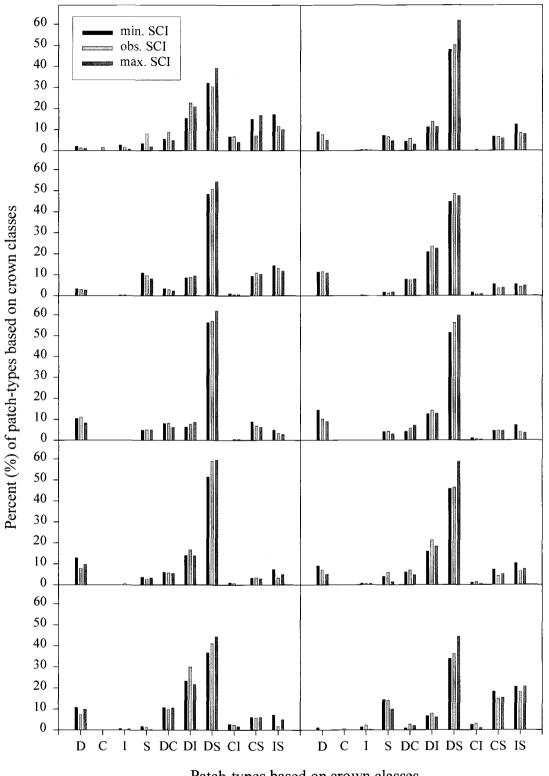


Figure 4.5. Percent of patch types based on crown classes. Stands are ordered by row and column from 1 to 10. D=dominant, C=codominant, I=intermediate, S=suppressed, DC=mixture of dominant and codominant, DI=mixture of dominant and intermediate, DS=mixture of dominant and suppressed, CI=mixture of codominant and intermediate, CS=mixture of codominant and suppressed, and IS=mixture of intermediate and suppressed. Min. SCI refers to the simulation giving the smallest SCI, obs. SCI is the observed SCI based on the actual mapped trees, and max. SCI refers to the simulation giving the biggest SCI.



Patch-types based on crown classes

Figure 4.5

dominant/suppressed patch-types), but exceptions occurred. The simulation with the lowest SCI had generally the highest proportion of dominant tree patch-types and the lowest proportions of high contrast patch-types, but again, exceptions occurred.

Three-dimensional structure

Based on 10,000 random re-allocations of observed tree sizes to the observed tree positions for each stand, differences of 11-28 % between simulated minimum and maximum SCI values were found, with observed SCI values ranging from 7.96 to 13.94 (Table 4.1). Four stands were above the 90th percentile, 3 stands were above the 97.5th percentile, and one stand had observed SCI values below the 2.5th percentile of the simulated SCI distributions.

SCI (Table 4.2).- The observed SCI was only marginally associated with the standard deviation of the dbh (std_{dbh}). Density of trees with dbhs >100 cm had a positive association with the SCI, as did the proportion of Douglas-fir in the stand. Tree density had a curvilinear association with the SCI.

The SCI was not related to the individual proportions of the species that made up the tree assemblage for the stands (all p>0.15). The SCI was only marginally associated with the proportion of Douglas-fir patches, but was positively associated with the level of dispersion of Douglas-fir patches and negatively associated with the level of dispersion of western hemlock patches. The SCI was not associated with the overall level of patch dispersion (p>0.15).

Table 4.2. Multiple linear regressions for the SCI. ^L Natural log transformed, std_{dbh} = standard deviation for dbh, SCI_{max} = maximum simulated SCI based on dbh, SCI = observed SCI based on dbh.

Dimensions					Full Model	
Response	Variable	b	F	p	R^{2} (%)	p
	Structural variables			_	99.6	< 0.001
SCI	Young cohort density ^L	+	68.0	0.001		
	(Young cohort density ^L) ²	-	63.9	0.001		
	density trees > 100 cm dbh	+	15.2	0.018		
	Proportion Douglas-fir	+	43.3	0.003		
	std _{dbh}	+	7.7	0.050		
	Tree species patches				37	0.081
SCI	Proportion Douglas-fir patches	-	22.1	0.081		
	Dispersion of tree species patch	es			80	0.004
SCI SCI	Douglas-fir patches	+	19.8	0.003		
	western hemlock patches	-	21.6	0.003		
	Patch-types				73	0.002
	dominant/codominant crown classes ^L	-	21.7	0.002		
	Dispersion of patch-types				86	0.001
SCI	dominant/codominant crown classes	+	11.7	0.011		
	dominant/intermediate crown classes	+	7.6	0.029		
	Univariate point pattern at nearest neighbor scale				87	0.012
SCI	dominant trees	+	11.4	0.020		
	intermediate/suppressed trees	+	13.4	0.010		
	Structural variables				98	< 0.001
SCI _{max}	Young cohort density ^L	+	23.0	0.003		
	(Young cohort density ^L) ²	-	21.9	0.003		
	std _{dbh}	+	105.2	< 0.001		
	Tree species patches				57	810.0
SCI _{max}	Proportion Douglas-fir patches	-	9.4	0.018		
	Patch-types				81	<0.001
SCI_{max}	dominant/codominant crown classes	-	34.6	< 0.001		
	Differences in proportion of tree	specie	es patches			
SCI _{max} -SCI	Proportion Douglas-fir patches	+	7.7	0.028	52	0.028
	Differences in proportion of patch-types (2 different regressions)					
SCI _{max} -SCI	dominant/intermediate crown classes	+	6.2	0.041	81	0.003
	dominant/suppressed crown classes	+	24.4	0.002		
SCI _{max} -SCI	dominant crown classes	+	35.7	< 0.001	82	< 0.001

The SCI was negatively associated with the proportion of dominant/codominant tree patch-types. The SCI was also positively associated with the level of dispersion of dominant/codominant tree patch-types and the level of dispersion of dominant/ intermediate tree patch-types. As the degree of segragation of low-contrast patch-types increased, structural complexity increased. Structural complexity was high when low-contrast patch-types were intermingled with either high-contrast patch-types or different low-contrast patch-types.

The SCI was not related to any spatial pattern from any of the bivariate point pattern analyses (all p>0.15). The SCI was, however, strongly related to small scale (up to 4-6 m) spatial patterns as measured by univariate point pattern analyses using Ripley's K. The SCI was associated with the spatial distributions of emergent and dominant trees, and random spatial distributions seemed to increase the SCI more than uniform spatial distributions. Furthermore, random spatial distributions of sub-canopy trees were positively, uniform spatial distributions were intermediate, and clustered spatial distributions were negatively associated with the SCI.

 SCI_{max} (Table 4.2).- The SCI_{max} was positively associated with the std_{dbh} . Density had a curvilinear association with the SCI_{max} . The SCI_{max} was also negatively related to the proportion of patches that were composed of only Douglas-fir. Similarly, the SCI_{max} was negatively related to the proportion of low-contrast (dominant/codominant tree) patch-types. The SCI_{max} was not related to the proportion of the species that made up the tree assemblage for the stands (all p>0.15).

Maximum simulated SCI versus observed SCI (Table 4.2).- Differences in structural complexity among stands and between the SCI and the SCI_{max} stands were strongly associated with the spatial distribution of the overstory and with Douglas-fir in particular. In general, structural differences were associated with (1) the proportions of high-contrast overstory patch-types (i.e., the proportion of patch-types composed of a mixture of either dominant and intermediate and dominant and suppressed trees) or low-contrast patch-types (i.e., proportion of dominant/codominant tree patch-types) and Douglas-fir, and (2) the spatial separation of trees into differently sized mosaics of low-contrast overstory patch-types. The difference between the SCI and the SCI_{max} was positively associated with the proportion of high-contrast patch-types, with a preponderance of high-contrast patch-types and fewer dominant/codominant tree patch-types in the simulation with the SCI_{max} than in the observed data.

Stands with a high proportion of low-contrast overstory patch-types generally had lower structural complexity than stands where overstory trees were not arranged in groups, but more uniformly distributed within the stand. This was also evident in the positive association between the SCI and random and uniform spatial arrangements of overstory and understory trees based on Ripley's K analyses. Structural complexity was highest when overstory and understory trees were intermingled at the scale of nearest neighbor distances. Generally, stands that had the highest proportion of unmixed Douglas-fir patches had a lower structural complexity, but the pattern was weak. The simulation giving the SCI_{max} had lower proportions of Douglas-fir patches than the observed data.

DISCUSSION

Components of structural complexity

Forest structure, as measured by the SCI, has two separate components that determine the structural complexity of stands: the frequency distribution of the underlying attribute (e.g., the diameter distribution in this study), and the spatial distribution of that attribute. Legacies of coarse-scale disturbances (e.g., residual trees), stand development, the extent to which species of differential growth rates are present, and timing of their regeneration have been found to affect the diameter distribution (e.g., Lorimer 1980, Peet 1981, Parker 1988). Local disturbance patterns (e.g., mortality, frequency and size of gaps), competition among neighboring trees and self-thinning, presence/absence of shade-tolerant species, and the nature of the species mixture (e.g., single trees of a species intermingled with another species or spatially separate mono-specific patches) affect the spatial distribution of diameters (e.g., Ford and Diggle 1981, Smith 1986).

In this study, the SCI related very strongly to tree density, the density of emergent canopy trees > 100 cm dbh, the proportion of Douglas-fir in the stand, and, marginally, to the tree diameter variability at the 1 ha stand level. Indeed, all of these variables are directly or indirectly related to the diameter distribution of a stand. This result is in keeping with Spies and Franklin (1991), who found that tree density, the density of emergent canopy trees > 100 cm dbh, the mean dbh, and the standard

deviation of the dbh were the best variables for classifying stands as young, mature, or old-growth in the Pacific Northwest.

Species composition, and in particular the proportion of shade-tolerant trees (Spies and Franklin 1988), have been identified as another important contributor to structural complexity, enhancing vertical and horizontal heterogeneity through 1) increasing the size variation in the stand, and 2) the formation of patches composed of shade-tolerant trees as a result of fine-scale disturbances. Stand development of mixedspecies stands is usually characterized by a progressive differentiation of species into distinct size classes (Smith 1986), thus increasing the size variation in the stand. In this study, however, species composition did not enhance the structural complexity of the stands. The reason for this is that all stands were highly mixed, with more than 50 % of the trees being shade-tolerant, and sizes of different species overlapping substantially. Indeed, these results indicate that as long as there is a substantial amount of shadetolerant trees in the stand, it does not matter what the exact species composition may be. This is good news for managers and may encourage the use of various types of species compositions and intensities of species intermingling to create structurally more complex stands. These results also seem to confirm Zenner (1998), who found that the structural complexity in green-tree retention stands was highest when there was about an equal proportion of Douglas-fir and western hemlock in the young cohort. Stands with only Douglas-fir or western hemlock showed lower structural complexity than more evenly mixed stands.

Effective vs. potential structural complexity

The observed or "effective" structural complexity is a record of the coupling between forest structure and ecosystem dynamics and processes. It is the outcome of complex processes influencing the actual spatial pattern, size differentiation, interactions among neighbors, and interactions of a forest with the environment. Over time, an individual pathway of this structural coupling between a forest and the environment may emerge and the sequence of structural changes may be useful to predict the structural development of forests across the region. The effective SCI can be used to compare and rank stands based on their structural complexity. To evaluate and interpret the effective structural complexity of a stand, the "potential" structural complexity for that stand must be known. One approximation of this potential structural complexity is a structural complexity that could have developed, given the observed tree size distribution and spatial patterns, if the processes shaping the structure of the forest had led to a maximum structural complexity. The concept of "effective" and "potential structure" allows an evaluation by ecologists and managers of each stand as to the complexity of the structure of that stand compared to what may have been possible. It also enables tests of hypotheses about the processes and management alternatives that may lead to high and low structural complexity in forest stands.

Potential structural complexity is reflected by the SCI_{max}, and allows a determination whether the effective structural complexity of a stand is high or low relative to its potential. The potential structural complexity and a distribution of structural complexity can be obtained empirically by random assignments of tree sizes

to the observed stem positions. At the 1 ha scale, differences of almost 30 % between the minimum and maximum values in the structural complexity distributions for a given stand in this study reflect size differences among neighbors. The magnitude of these differences seems to be related to the scale used to assess the structural complexity. For example, in a previous study conducted at smaller scales (0.04 ha), differences of almost 70 % were observed between maximum and minimum SCI values (Zenner 1998). As the scale increases, the SCI integrates size differences among patches of trees and is thus less influenced by large size differences at small scales.

The variability of tree sizes is generally regarded as the key element of structural complexity (e.g., Buongiorno et al. 1994), has been recognized as one of the more distinctive features of old-growth Douglas-fir forests, contributing to both horizontal and vertical diversity in microhabitats (Spies and Franklin 1991), and has been found to increase strongly with succession and to possess a high discriminating power for age classes (Spies and Franklin 1988, Franklin and Spies 1991). Whereas the variability of tree sizes dominated the regression models for the SCI_{max}, it was less strongly related to the observed SCI. Greater variability in tree sizes allows greater size differences between neighboring trees. The variation of the trees sizes therefore seems to be indicative of the potential structural complexity, but the variation of tree sizes was not the best indicator and criterion for a comparison of effective structural complexity among forests. Indeed, the variation in tree sizes by itself indicates nothing about the actual height or diameter distribution of a stand (e.g., Lorimer and Krug 1983). In stands having several age classes, diameter distributions may vary from nearly normal

to irregular negative exponential (Figure 4.6) depending on the shade tolerance and age class dispersion in the stand (Hough 1932, Henry and Swan 1974, Lorimer 1983). The variability of tree sizes is also independent of spatial relations among neighbors, but spatial relations among neighbors have been shown to be a critical component of structural complexity (e.g., Pretzsch 1995). The variation of tree sizes may, however, be useful to identify structurally homogeneous stands whose structure could be enhanced by management actions such as thinning and underplanting with shade-tolerant trees.

Patches and patch-types

At scales beyond the distance of nearest neighbors, all 10 stands had unique spatial patterns that may reflect the interactions of previous disturbances and associated stand regeneration patterns with stand development and site characteristics. In mature and old-growth stands in this study, the similar SCI values at the 1 ha scale found among stands with very different spatial patterns of all trees and by species indicate that structural complexity is to some extent independent of the spatial pattern *per se*. Moreover, differences among stands and between the effective and potential SCI, associated with the proportions and spatial separation of trees into mosaics of high- and low-contrast patch-types, indicate that it is the patchiness and perhaps the spatial patterns of species mixture of a forest that largely determine the structural complexity. Patchiness refers to the abundance, spatial extent, and spatial distribution of patches and patch-types (Zenner 1998), i.e., the spatial arrangement of trees into patches of the same

Figure 4.6. Different spatial structures for three stands of different diameter distributions.

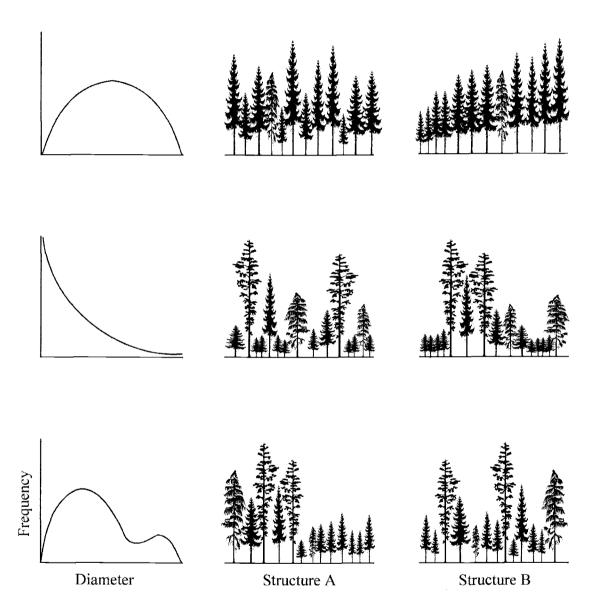


Figure 4.6

species or patch-types of similar sized trees. Structural complexity is high when low-contrast patch-types are intermingled with either high-contrast patch-types or different low-contrast patch-types. Structurally complex stands also seem to have a more uniform spatial distribution of Douglas-fir and a higher level of dispersion of unmixed Douglas-fir patches, where Douglas-fir is mixed with shade-tolerant western hemlock and western redcedar throughout the stand.

The results from this study may be used to extend the notion that two basic components of heterogeneity, contrast and aggregation (*sensu* Kotliar and Wiens 1990), are important components of structural complexity not only at the scale of landscapes, but also at the stand level. Contrast refers to the degree of difference between patches at a given scale (Wiens 1976, 1990), and large between-patch differences enhance heterogeneity through increases in the discreteness of patch-boundaries. Aggregation refers to the spatial distribution of patches, i.e., clustered, random, or uniform (Pielou 1977). The patchiness of an environment is a function of the relative sizes of, and the magnitude of difference between, individual patches (Gillespie 1974), and their aggregation. Structural complexity is then created by the junction of different patchtypes, as was observed in this study.

Maximum structure hypothesis

Do natural stands, in the absence of large-scale, stand-replacement disturbances and in the presence of small-scale disturbances through stand development and mortality of individual trees, and given the observed tree sizes and spatial patterns, tend

towards maximum structure? The maximum structure hypothesis, based on the concepts of effective and potential structural complexity, can be tested by simulating a large number of Monte Carlo randomizations of the observed tree sizes to the spatial stem positions. A p-value can be obtained by finding the proportion of randomizations that produce SCI-values at least as extreme as the observed one. A significant p-value would reveal the presence of processes that caused significant departures from a structural complexity that would be expected if the observed allocation of tree sizes to stem positions was controlled by a random process.

In four of ten stands in this study the effective SCI was above the 90th percentile, and three stands were above the 97.5th percentile of the simulated SCI distribution. These four stands were all young to mature forests that showed a uniform spacing among overstory trees and spatial attraction at the scale of nearest neighbor distances between overstory and understory trees, and between Douglas-fir and understory western hemlock in particular. Two stands also had significantly higher proportions of emergent/dominant and suppressed trees as their respective nearest neighbors than all other stands. This translates into a significantly higher proportion of high contrast patch-types than would be expected by chance alone. Surprisingly, stands that had structures resembling old-growth forests were, without exception, at percentiles that were substantially below the 90th percentile and as low as the 1st percentile, although the absolute value of the SCI may have been higher than in mature stands (e.g., stand 10).

It is important, in this context, to distinguish between the level of the effective structural complexity and the degree to which the effective structural complexity approaches its potential. The level of structural complexity can be used to elucidate general patterns and processes that may be associated with the change of the SCI over time through multiple, but perhaps predictable pathways in the absence of large-scale disturbances. These trajectories may depend on the disturbance regime that initiated the tree regeneration, how many residual trees survived the disturbance, the spatial arrangement of residual trees and the young cohort, the availability of shade-tolerant and shade-intolerant species in the regeneration, and the stand development through competition and self thinning. High levels of structural complexity in this study were associated with variables that reflected the variability of the diameter distribution. Generally, as the range of the diameter distribution increases, so does structural complexity. In a similar study, Zenner (1998) found that the level of structural complexity 55-240 years after the disturbance event that initiated the young cohort was associated with both the number of residual trees, and, more importantly, the species composition of the young cohort. Structural complexity was highest when the young cohort had about equal proportions of shade-intolerant and shade-tolerant species, again reflecting the diameter distributions of the stands.

The degree to which the effective structure is maximized may elucidate specific patterns and processes that may have influenced the structural complexity of a particular stand. Results from this study indicate that old-growth forests in particular may not approach their potential structural complexity or even have altogether lower levels of

structural complexity than expected (e.g., stand 1). Why were the young to mature forests in this study, although at lower levels of structural complexity than old-growth forests, close to their potential structural complexity and old-growth stands were not?

When trees of similar sizes grow together in low-contrast patches in either overstory or understory, effective and potential structural complexities diverge. Processes that result in fine-grained, uniform or random mixtures of species, size classes, and age classes at multiple scales (Frelich and Graumlich 1994) seem to create multi-tiered canopies with high levels of structural complexity across all scales. This is the case where through small-scale, light-intensity disturbances that create abundant small gaps the regeneration of shade-tolerant species is either successfully initiated or released and mixed with larger trees throughout the stand.

Intensive intermingling of species with differential growth potential and complex patterns of self-thinning and surviviorship may lead to a maximum structural complexity. Observed differences in spatial patterns among tree species in this study may be related to their patterns of establishment and hence shade-tolerance. For example, in the central Oregon Cascades patchy patterns of partial fires result in complex and variable spatial patterns for residual trees and the different tree species in the young cohort (Goslin 1997, Zenner 1998, this study). After major fires, the relatively shade intolerant *P. menziesii* and *A. procera* (Minore 1979) usually regenerate in even-aged stands, whereas the shade-tolerant *T. heterophylla*, *Th. plicata*, and *A. amabilis* (Fowells 1965) can regenerate in even-aged patches, but also in canopy gaps created by partial burns and small windfalls (Stewart 1986 a, b). Where both Douglas-

fir and western hemlock occur together in even-aged stands, Douglas-fir usually outcompetes western hemlock. Through more aggressive competition, density-dependent self-thinning, and one-sided competition for light, overstory trees, and Douglas-fir in particular, may arrive at uniform and random spatial patterns sooner than western hemlock, and in particular understory western hemlock. In this case, dominant Douglas-fir are mixed with understory western hemlock, resulting in maximum structural complexity observed in four stands in this study.

Due to the legacies of remnant trees, differential thinning in the most crowded areas, and complex patterns of survivorship around large individuals, complex spatial patterns are often observed in old-growth forests, even when seedlings become established in clusters of similar age (Stohlgren 1993, Duncan and Stewart 1991, Goslin 1997). The level of structural complexity in late-successional and old-growth stands may, however, depend on the size distribution of canopy gaps and the regeneration success of shade-tolerant species. The role of canopy gaps has been stressed in creating fine-scaled clustered patterns (e.g., Stewart 1986 a, b). Small-scale random patterns in older forests may be the result of random events such as mortality of medium- and large-sized trees. Small-scale disturbances and the death of one to many trees may create various-sized gaps in the forest canopy and alter the population structure and species composition of the vegetation in gaps (McClure and Lee 1993). Patchregeneration may result in patches of different sizes, species mixtures, and ages within the forest, creating a patchy mosaic of even- or multiple-aged patches of similarly-sized trees (e.g., Bonnickson and Stone 1981). Old-growth stands with heterogeneous

overstories where various-sized and -aged trees are interspersed with emergent and dominant trees (Hedman and van Lear 1995) may exhibit high levels of structural complexity (e.g., stand 10). Low to moderate levels of structural complexity may be associated with intermediate to large gaps containing similarly-sized trees of perhaps mono-specific tree composition or mixed species with either similar ages and growth patterns or differential ages and growth patterns. This may result in local monolayered canopies at the scale of the gaps, surrounded by high-contrast patches but an overall lower level of structural complexity and large differences between effective and potential structural complexity (e.g., stand 1). Alternatively, small gaps lacking regeneration may also lead to low structural complexity.

Franklin and Spies (1991) surmised that structural complexity may decline in later old-growth stages when canopy Douglas-fir is increasingly replaced by western hemlock. While it may be true that some of the old-growth stands in these studies were already in the later stages of old-growth, that does not hold for all old-growth stands used in this study. A lower structural complexity would be consistent with Franklin and Spies' (1991) conjecture that old-growth forests show a decline in structural complexity only in advanced stages. Results from this study indicate that at the scale of 1 ha this hypothesized decline in structural complexity may depend on the size distribution and regeneration of canopy gaps and that the decline in structural complexity may happen in earlier stages of old-growth than previously believed.

Whether the point of divergence of effective and potential structure is the time when mature forests develop into old-growth stands in this region needs to be further

explored. It appears from this study, however, that unmanaged young and mature stands may, at least during some period in the course of their stand development, develop structures close to their potential structural complexity at the scale used in this study. This raises several research questions about the SCI's trajectory over time. For example, a younger stand with a high SCI may not necessarily, if left alone, develop into a structurally complex old-growth stand. How the SCI's trajectory over time may relate to the local disturbance regime that initiated the stand, to the current stand development, to the proportional species mixture and the spatial pattern of species mixtures (i.e., to the intensity of intermingling of species), to the scale used to assess these patterns, and to the processes responsible for structural complexity are questions still unanswered. What thinning regime may be best suited to first create structurally complex forests in young, managed stands, and then to put these stands on a trajectory that ensures high structural complexity in mature and old-growth stages is a critical question for managers.

Within the framework of effective and potential structure several new questions about the development of structural complexity can be addressed. For example, the maximum structure hypothesis may be tested in more stands and at different scales to identify processes leading some stands to be, and others not to be, at their potential structure. The hypothesis that maximizing structural complexity is an emergent property of natural forest ecosystems at some point in their development and at some scale may be investigated. Furthermore, the hypothesis that fine scale disturbances are an integral part of the ecosystem to the extent that a high structural complexity actually

depends on their periodic occurrences and may be needed for stands to arrive or remain at their potential structure could also be tested. How do disturbances change structural trajectories? How important is the species mixture and the spatial nature of that mixture in creating structurally complex forests? Managers challenged to rapidly create structurally complex forests that resemble old-growth may have good use for that information in their quest to enhance structural complexity and bring structural complexity back into managed forests.

SUMMARY

The new definition of structural complexity, the SCI, and the concepts of effective and potential structure are powerful new tools to test new hypotheses about complexity of observed structures in forests and possibly relate these structures to processes that have generated it. That such processes are most likely not mutually exclusive and may vary from stand to stand and across scales, was reflected in the unique spatial patterns and spatial interactions between different tree species across the stands in this study. Although general trends in spatial patterns for different tree species and crown classes could be observed in this study, exceptions were found and the patterns were generally weak. An intensive species mixture at the scale of individual neighbors generally enhanced the structural complexity of these stands. Structural complexity was highest in stands where both dominant and suppressed trees were randomly distributed at small scales and where these crown classes occurred in close proximity to one another. Where dominant and codominant trees often occurred in

groups, the structural complexity was somewhat reduced, but dispersion of these groups across the stand was beneficial for structural complexity. The same was true for Douglas-fir, which was found mostly in the emergent and dominant canopy layers in this study. Differences between the effective and potential SCI were also related to the occurrence of different patch-types and species mixtures, indicating that the observed structural differences among stands were generally the same as those between the effective and potential structural complexity within a particular stand.

Despite a strong evidence in young and mature stands in favor of the maximum structure hypothesis, old-growth stands generally had effective structural complexities below their potential. Since the young-to-mature natural, unmanaged stands in this study were at their structural potential, their structures may serve as a guide for managers who seek to enhance the structural complexity of managed stands. Since all stands in this study were highly mixed, the species composition per se was not related to the structural complexity. This may have important implications for forest management in that there is not just a single type of species mixture that would guarantee a high structural complexity, while other species mixtures would not. This is good news for forest managers who may use several species to achieve the objective of creating a more structurally complex forest. As long as stands have a mixture of shadeintolerant and more shade-tolerant species, structurally more complex stands can be created. Although a large proportion of groups of big canopy trees that are not interspersed with sub-canopy trees was associated with a reduction in the SCI, it appears that dispersion of such groups across the stand enhance structural complexity. This is

also good news for managers, since that would not preclude a clustered retention of green-trees, but would allow a combination of dispersed and clustered green-tree retention.

Chapter 5. Conclusion

The structural complexity of forests has long been elusive to rigorous. ecologically meaningful quantitative measures that allow structural comparisons among forests. This is despite a large body of ecological literature that relates structural characteristics to wildlife habitat, patterns of regeneration and gap dynamics, spatial heterogeneity and temporal dynamics in understory vegetation, succession and stand development, and timber production. Structural complexity and diversity are often inferred in the explanation of observed ecosystem processes and functions. Structural complexity is believed to be a key feature and a distinctive characteristic of latesuccessional forests in the Pacific Northwest. It is also believed that the conversion of mature and old forests to young plantations and disturbances imposed by timber management may create conditions that deviate to varied degrees from those created by natural disturbances. If these anthropogenic disturbances result in more homogeneous stand structures than natural disturbances, the lack of structural complexity may degrade the habitat quality for many species, in particular late-successional species that are associated with structurally complex forests. Consequently, the close coupling between structure and the processes generating it has led some ecologists to believe that by maintaining and creating structural characteristics of natural, and in particular old forests, ecosystem functions can be sustained. Structural complexity may then be used as a surrogate for the biodiversity or ecological value of a stand and management strategies could be guided by structural analyses.

While this strategy may have some theoretical merit, translating this approach into a practical and operational management action requires structural analyses that consider the 3-dimensional character of forest structure. In particular, an index based on continuous scales of multiple, ecologically meaningful attributes may prove to be superior to commonly used categorical approaches and definitions that seek to distinguish structurally-complex from structural-homogeneous stands by a plethora of individual characteristics. Categorical approaches have the disadvantage of often being quite arbitrary in classifying stands due to conflicting results based on the criteria used in the classification or by imposing sometimes arbitrary weights on different structural components.

The main objective of this dissertation was to develop an index that does not make assumptions about average structural conditions of young, mature, or old-growth stands and that is more objectively guided by the structural condition of a stand to give a continuous structure-score to the stand. The index should also be ecologically meaningful, able to compare the structural complexity of different forests, and reflect the 3-dimensionality of forest structure. The index should be sensitive to different scales and the hierarchical nature of patches, the building blocks of forest structure. A methodology needed to be developed that could capture the dynamic mosaic of patches of different structures (i.e., the patchiness of a forest) within a forest.

The result of this effort was a more operational definition of forest structure and the development of the structural complexity index (SCI) and the use of the method of spatial tessellation to calculate the SCI and decompose the forest structure into different

patch-types. Since trees primarily compete with their nearest neighbors and patches are an assemblage of similarly-sized trees that occur in spatial proximity to one another, it was necessary to use a methodology that recognized size differences among neighboring trees as the building block of patches and hence forest structure.

The ability of the SCI to distinguish different levels of structural complexity among forest stands was tested in a simulation study and a field study with stemmapped data. The SCI was found to be able to characterize the different levels of structural complexity and through the definition of patches and patch-types several important variables that closely related to the SCI and the structural complexity in forest stands could be identified. The SCI related very strongly to the tree size variation, the density of trees, the density of large canopy trees (> 100 cm dbh), and the tree species mixture. Monospecific stands of either Douglas-fir or western hemlock were found to be structurally less complex than stands that had a more even mixture of both species. In mixed stands of several species, the species composition was not related to the SCI, indicating that as long as stands have a mixture of different tree species, many possible species combinations may lead to high structural complexity. Species mixture is, in turn, positively related to the tree size variation in the stands used in this study. Generally, species occupied different crown classes, with Douglas-fir emergent and dominant, and more shade-tolerant species such as western hemlock found in all crown classes, although tree sizes did overlap substantially.

Spatial patterns at the scale of nearest neighbors were also associated with the SCI. The SCI was positively related to a random distribution of emergent/dominant and

suppressed trees at scales up to 6m. This is indicative of a mixture where canopy and subcanopy trees were intensively intermingled. When dominant and codominant trees occurred in aggregated groups, the SCI was lower, but a more dispersed spatial distribution of dominant tree clusters related positively to the SCI.

Different structural conditions were simulated by randomly assigning a value of the tree size distribution to each tree position while holding the tree position fixed.

Repeating this assignment in 10,000 independent runs allowed an assessment of the likelihood of having an SCI value as extreme as the one that was observed for a given stand. The observed or effective structural complexity could then be tested against the SCI distribution to evaluate whether the observed structural complexity could have been observed by a spatial distribution of differently sized trees that depended on chance alone.

Comparing effective SCI's across several stands thus allowed a ranking of stands from structurally most to least complex. Furthermore, comparing the effective SCI to the maximum simulated SCI (the potential structure) allowed an evaluation of what the structural complexity of a stand could have been given the observed tree size distribution.

Based on the concepts of the SCI and the effective and potential structure, the "maximum structure hypothesis for natural mixed conifer forests" was proposed and tested. The maximum structure hypothesis states that in the absence of large-scale, stand-replacement disturbances and in the presence of small-scale disturbances associated with mortality and replacement of individual trees or through the course of

stand development, mixed conifer stands have effective structures close to their potential structure. This hypothesis was strongly supported in young and mature stands, but had to be revised from its current simplistic form. Old-growth stands all had effective structural complexities below the 90th percentile of the SCI-distribution. All but one of the other young-to-mature stands were at their potential structure. Based on these results further research may be warranted to investigate whether stands that are commonly classified as old-growth always show large discrepancies or not between their effective and potential structures and whether that may even be a condition to be classified as an old-growth. Further research may be needed to investigate whether the scales used to assess effective and potential structures may influence the results. At scales of tens of hectares different conclusions may be reached, since it is likely that different processes operate at larger scales and structural complexities that are locally below their potential may still be high when investigated at the landscape level.

The results from this study may have important implications for managers who seek to manage forests on a structural basis. First, species mixture is a very important contributor for structural complexity. A more structurally complex forest may have a mixture of shade-intolerant species such as Douglas-fir and shade-tolerant species such as western hemlock and redcedar, but as long as there are multiple species, many different mixtures can be used to achieve the objective of creating a structurally complex forest. Second, both interspersion of emergent and dominant trees with the lower tree layers as in dispersed green-tree retention, or spatial dispersion of groups of large canopy trees as in aggregated green-tree retention can be used to create

structurally complex stands. However, whereas a dispersed retention may have a high structural complexity at all scales, aggregated dispersion may create local zones of extremely high structural complexity at smaller scales nested within areas that a structurally more homogeneous. This may be due to a zone of influence around residual trees where growth of the young cohort may reduced and the sizes of the young cohort may be homogenized. This was observed in this study as a lack of dominant and codominant trees of the young cohort in the vicinity of residual trees, probably due to the competitive advantage of large residual trees.

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