

Age-Related Development of Canopy Structure and Its Ecological Functions

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and Nalini M. Nadkarni

Structural complexity embodies not only particular types of stand attributes, but also the way they are spatially arranged within stands.

—Lindenmayer and Franklin, *Conserving Forest Biodiversity*, 2003

Perhaps the word most used in ecology with different meanings is "structure"... Integrative concepts cannot be measured directly, and both their definition and detailed description must be synthesized from studies of a number of systems.

—Ford, *Scientific Method for Ecological Research*, 2000

Introduction

For many years our view of forests has been two-dimensional and the structure and dynamics of forest ecosystems have been studied and analyzed using data expressed as stem maps that indicate the X and Y coordinates of individual trees along with species and size information (e.g., diameter at breast height). In research that moved toward documenting the three-dimensionality of forests, the vertical variable (Z-coordinate) most often considered was tree height. "Stand structure" usually referred to the species composition and tree size distribution of forest stands and sometimes included information on the two-dimensional spatial distribution of trees and tree height. Because humans are confined to the ground, we have been unable to study in detail the three-dimensional (3-D) structure of forests, including the forest canopy. Instead, we inferred tree growth from diameter increment at breast height, and competitive interactions among trees from analysis of the relationship between horizontal spatial distribution and diameter growth or mortality patterns (e.g., Kenkel 1988; Duncan 1991; Stohlgren 1993; Biondi et al. 1994). However, we have always known that the dynamics of forest ecosystems, including growth and competitive interactions among individual trees, occur in the canopy and not at breast height (Krajicek et al. 1961; Hix and Lorimer 1990; Bravo et al. 2001).

Currently, there are techniques that enable safe and repeated access to the forest canopy to study the 3-D structure of forest ecosystems and ecological processes occurring in the canopy (Moffett and Lowman 1995). The 3-D distribution of tree crowns reflects how trees occupy space in the canopy to capture light resources and drives critical ecological processes such as stand

productivity and forest presents a great challenge young stands and plan old-growth stands (see of two-dimensional stand diverse with increasing snags characterize old-growth forests. However, "structural complexity" was coined to describe the complexity of old-growth forests. How complexity such as species debris are derived from Spies and Franklin 1998, 2001). One of the objectives of old-growth forest stand management is to provide wildlife habitat (Kohn 1998). Lindenmayer and Franklin (2002) integrate various aspects of ecosystem management

In this chapter, we explore complexity with increasing of temperate forest dynamics of tree cro

1. Height-growth rate
2. Expansion growth rate and spatial distribution.
3. With increasing effects of small-scale disturbance enhance structural

Developmental processes as community dynamics diversity of forest ecosystems and other organisms.



Figure 5-1 Contrast of Douglas-fir (a) and a

productivity and forest community dynamics. However, measurement of forest canopy structure presents a great challenge (see Box on p.104–108). Visual observation suggests that the canopy of young stands and plantations are structurally homogeneous and simple compared with that of old-growth stands (see Figure 5-1). This difference has been shown through comparative studies of two-dimensional stand structure. Species composition and tree size distributions become more diverse with increasing stand age, and specific structural elements such as large, old trees and snags characterize older stands (reviewed by Franklin et al. 2002). The term “structural complexity” was coined as an integrative concept to represent the complex 3-D structure of old-growth forests. However, many of the measures and indices used to characterize structural complexity such as species composition, tree-size distribution, and abundance of snags and woody debris are derived from two-dimensional, ground-based measurements (e.g., Franklin et al. 1981; Spies and Franklin 1991; Wells et al. 1998; Solomon and Gove 1999; Staudhammer and LeMay 2001). One of the objectives for developing indices of structural complexity is to distinguish quantitatively old-growth forests from younger stands and to establish criteria for enhancing old-growth forest structure in managed stands for conservation purposes, such as creating wildlife habitat (Kohm and Franklin 1997; Smith et al. 1997; Carey et al. 1999b; Hunter 1999; Lindenmayer and Franklin 2002). In order to meet such management objectives, we must integrate various aspects of forest structure, including canopy and below-ground processes, into future ecosystem management strategies.

In this chapter, we review the canopy processes that drive the development of structural complexity with increasing stand age and present a 3-D canopy perspective of structural development of temperate forest ecosystems. Because trees form the basic framework of canopy structure, dynamics of tree crowns define structural development of the forest canopy (see Figure 5-2):

1. Height-growth rate and maximum attainable height of species determine vertical structure.
2. Expansion growth and interactions among individual tree crowns determine horizontal spatial distribution.
3. With increasing stand age, aging and maintenance of individual tree crowns, as well as the effects of small-scale disturbances such as individual tree mortality, crown damage and die-back enhance structural complexity of the canopy.

Developmental processes of canopy structure drive and enhance various ecological functions such as community dynamics and stand productivity. Development of structural complexity enhances biodiversity of forest ecosystems by creating specific structural elements that provide food and habitat for other organisms.



Figure 5-1 Contrasting simple versus complex canopy structure of a naturally regenerated 20-year-old stand of Douglas-fir (a) and a 450-year-old stand (b) in southwestern Washington State.

MEASURING CANOPY STRUCTURE: THE FOREST CANOPY DATABASE PROJECT

Nalini M. Nadkarni and Judy B. Cushing

The increasing interest and realization of the importance of canopy organisms and interactions in whole-forest ecology has generated an unprecedented amount of canopy data (Lowman and Wittman 1996). Both the types and amounts of canopy structure data are changing rapidly. In the past, scientists working alone with simple rope-climbing techniques generated studies that produced fairly small datasets. However, recent access innovations permit multiple teams of scientists to work within the same volume of the canopy. Canopy scientists have to deal with more data, new kinds of data, and the need to share data (Parker 1995). Data collected by canopy research teams will be useful to other scientists (e.g., geographers and land use managers), just as data emanating from allied fields could aid forest canopy researchers (Parker et al. 1992).

Historically, canopy scientists have taken, stored, and analyzed data in independent and idiosyncratic ways. In 1993, a team of forest canopy ecologists and computer scientists received a planning grant from the National Science Foundation's (NSF) Database Activities Program. The project brought together forest canopy researchers, quantitative scientists, and computer scientists to work toward establishing methods to collect, store, display, analyze, and interpret three-dimensional spatial data relating to tree crowns and forest canopies.

A survey we conducted on the perceived obstacles to the advancement of forest canopy studies (Nadkarni et al. 1996) revealed that canopy researchers believe that our understanding of forest canopy biota and processes is not limited by canopy access (as we had anticipated), but rather by two characteristics of canopy data:

1. Lack of quantitative tools that allow canopy researchers to analyze the complex three-dimensional spatial data associated with forest canopy studies, and
2. Lack of harmonized datasets—forest canopy researchers have tended to collect data in non-comparable formats.

Few projects have common methodologies or data formats, so their resulting observations are not easily shared and compared. Thus, the study of the forest canopy is perceived as being held back by the lack of data management tools. However, the relative youth of the field—with its lack of entrenched methods, legacy datasets, and conflicting camps of competing groups—provides a unique opportunity for integrating data management and analysis tools into the research process (Lowman and Nadkarni 1995). The sociology of the discipline is conducive to sharing data; researchers appear openly communicative and supportive of each other's work (Nadkarni and Parker 1995). In particular, documenting tree and forest structure is fundamental to describing and understanding forest ecology, physiology, and forest/atmosphere interactions (Parker 1995). However the task of describing, visualizing, and analyzing structure is extremely difficult because trees are large, irregular, dynamic, and operate on time scales that are different from humans. Statistics and visualization have not been worked out. Trees may not be "individuals" from the perspective of their associated organisms (e.g., epiphytes, birds, and microbes). Rather, branches or individual twigs might be the appropriate sampling unit. Historically, researchers who study tree and forest structure have used a large number of different and non-complementary approaches to describe, visualize, and analyze structure. They have used a variety of different tools and approaches that result in a diversity of ways of seeing the structure (Parker 1995). Thus, the state of the art is that although there are many ways of quantifying forest structure, few are compatible with each

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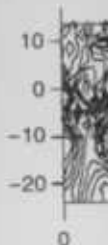


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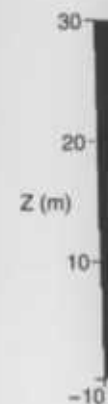


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other. The time is ripe to bring these together, not to impose a single standard or protocol, but rather to present a way in which forest structural elements from different studies can be integrated to foster comparative work.

Here, we describe the development and some of the applications of the Forest Canopy Database Project. In 1998, we were awarded another NSF grant to develop a database and database tools to enhance the ability of researchers in forest canopy studies to collect, analyze, link, and archive data. The computer database has taken three forms. The first piece is our web-based "Big Canopy Database." This database holds information, field data, and images of use to canopy researchers, educators, and conservationists (<http://canopy.evergreen.edu/bcd/>)

The second piece is a web-based program called "DataBank," which allows canopy researchers to search for and download field data submitted by other researchers, design field databases and download them for their own use, and to document and archive their own databases. The system thus builds new databases from database components ("templates") that are designed specifically for canopy data. To submit data to the database, a

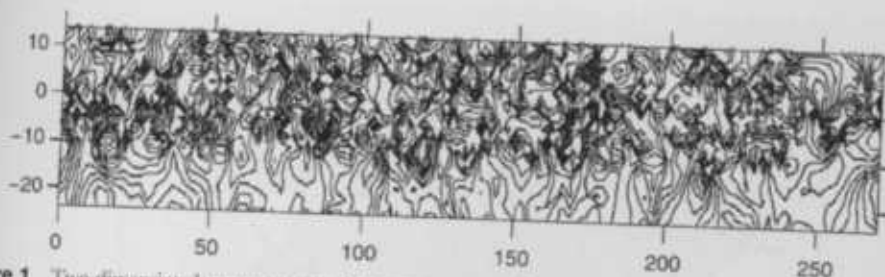


Figure 1 Two-dimensional contour map of the upper canopy from an aerial perspective. The forest is a 950-year-old temperate coniferous forest on Mt. Rainier, Washington State. Graphics produced in Surfer by R. Van Pelt. Data from Van Pelt et al. (in press).

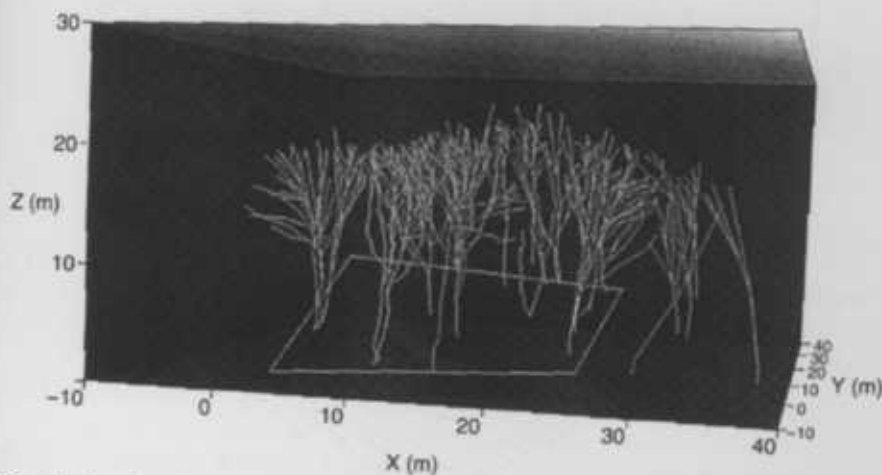


Figure 2 "Suck tree" architecture derived from x,y,z coordinate data from A. Sumida of *Quercus serrata* trees.

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MEASURING CANOPY STRUCTURE: THE FOREST CANOPY DATABASE PROJECT—cont'd

researcher from each study works with a programmer to provide metadata and to structure his or her data to fit one or more existing field data templates, or to generate a new template for novel data types. The current format is implemented in SQLServer, Java, and HTML.

The third component, called "CanopyView," takes data from the database and allows a researcher to select a means of visualizing the data in two or three dimensions. We provide an array of visualization templates and examples from which to choose. For example, we can use simple height and x,y data for branches to create "contour maps" of the forest canopy (i.e., the outer envelope of the trees) (Figure 1). We can also display individual trees as "stick figures" (Figure 2) using the data of A. Sumida (Hokkaido University), in which the x,y,z, coordinates of each node, measured following methods described in Sumida et al. (2002), are connected to provide a schematic of the branching structure of individual trees.

Another approach is to display the distribution of foliage in a forest canopy without regard to which individual tree is attached to a given piece of foliage (Figure 3). Foliar distribution data were provided by G.G. Parker (Smithsonian Environmental Research Center)

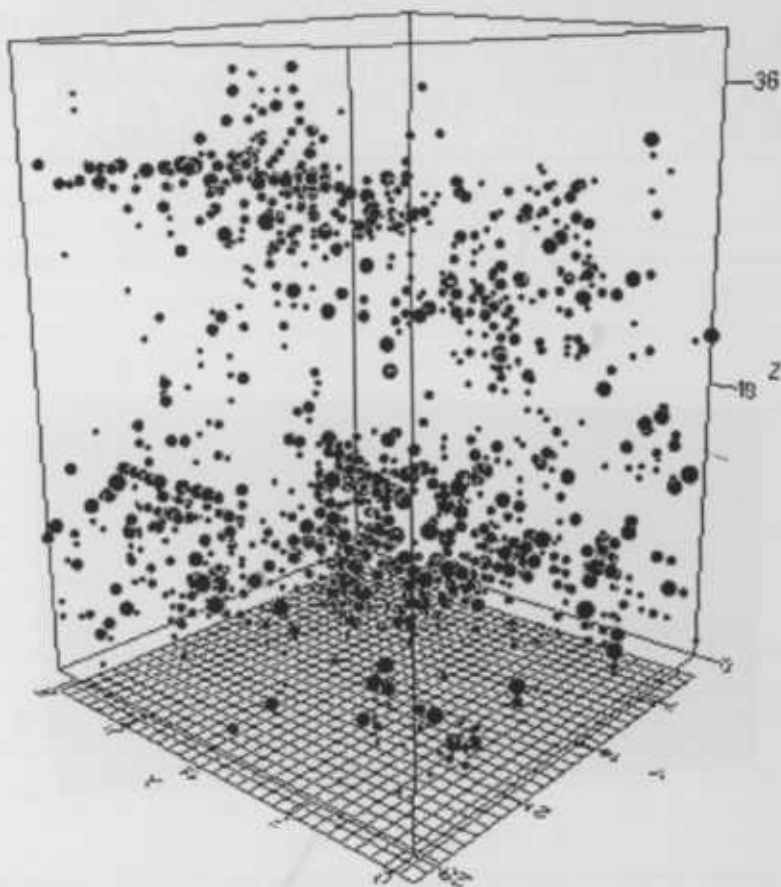


Figure 3 Temperate deciduous old-growth forest stand in Maryland, USA, with foliar density depicted using ArcView. Data from G. Parker.

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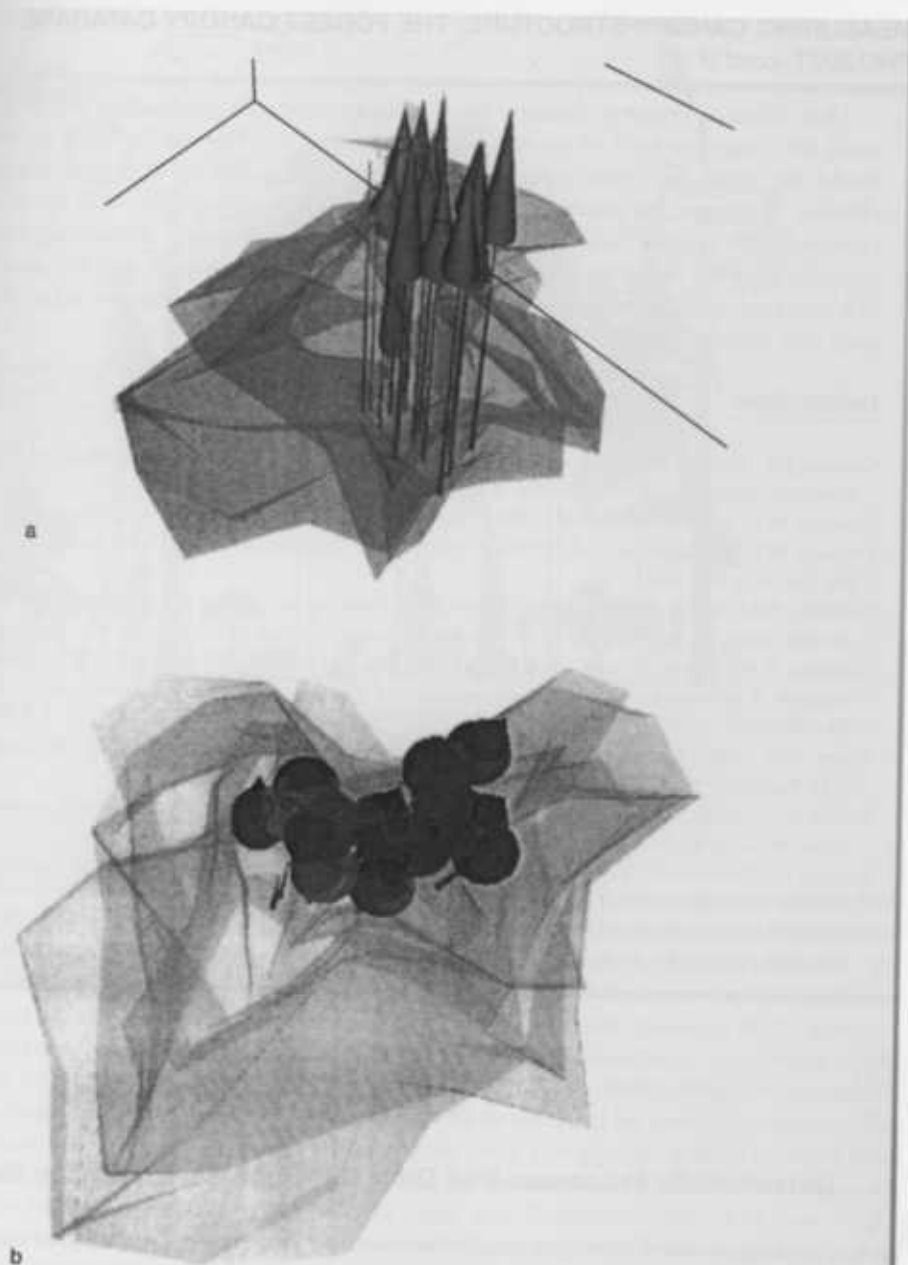


Figure 4 Depiction of trees and airspace around them, side view (a) and aerial view (b). Data are from R. Dial. Graphics produced in *Mathematica* by M. Ficker (Cushing et al. 2003).

using LIDAR technology. Others may be interested in the "airspace" of a forest (i.e., the shape and size of the interstices of air between the solid masses of the forest canopy) (Figure 4), an example of which was created by R. Dial (Alaska Pacific University) for forests of Alaska.

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MEASURING CANOPY STRUCTURE: THE FOREST CANOPY DATABASE PROJECT—cont'd

Our efforts to create a database for the canopy research community will help push forward this emerging field of science. We also believe that our efforts could be viewed as a model for other emerging areas of ecology where data-linking and data-sharing can be effective in integrating results from different studies. This capability will speed the development of the field to more efficiently address both intellectually stimulating and environmentally pressing questions of interest to academics, policy-makers, and the general public. We anticipate that the database and tools can serve as an exemplar for other interdisciplinary and emerging fields of science.

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Deterministic Processes that Drive Development of Canopy Structure

In early stages of stand development, deterministic processes such as timing of establishment following disturbance, height-growth rate, and crown interactions determine canopy structure (Johnson et al. 1994; Dubrasich et al. 1997). In mixed-species natural forests, differences among species in timing of establishment and initial height-growth rates result in vertical stratification of species within the canopy (e.g., Bicknell 1982; Palik and Pregitzer 1991). Early-successional, fast-growing species can establish soon after disturbance, reach the upper canopy, and dominate during early stages of succession. For example, in a 42-year-old forest in Michigan dominated by bigtooth aspen (*Populus grandidentata*) and trembling aspen (*Populus tremuloides*), reconstruction of vertical canopy development revealed that initial height-growth rates were similar among species (Palik and Pregitzer 1991). In this forest, the observed pattern of vertical stratification among species reflected differences in the timing of establishment of each species after disturbance. In a second-

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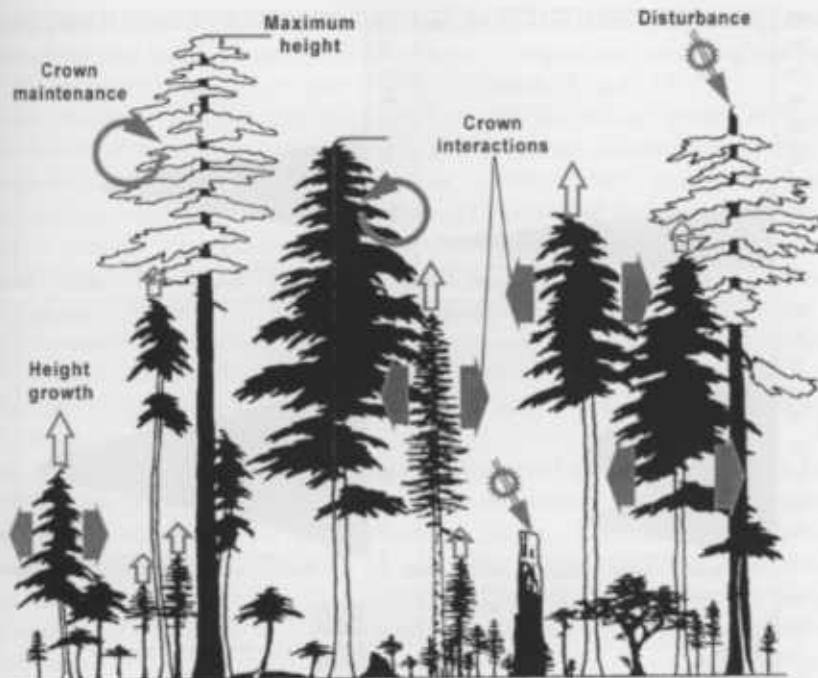


Figure 5-2 Deterministic and stochastic processes that drive development of canopy structure.

ary northern hardwood forest in New Hampshire, early-successional, shade-intolerant species such as pin cherry (*Prunus pensylvanica* L.) had faster height-growth rates and longer growing seasons than the mid- and late-successional species and became the tallest trees within the first six years after the stand was cut (Bicknell 1982). Mid-successional species such as trembling aspen, striped maple (*Acer pensylvanicum*), and yellow birch (*Betula alleghaniensis*) occupied intermediate positions in the canopy.

In mixed-species natural forests, each species has an inherent and site-specific maximum height that determines its canopy position (e.g., Thomas 1999; Ishii et al. 2000). Whether individuals reach their potential maximum height or not may also be determined by their demography. For example, in a warm-temperate forest in southern Japan, most canopy tree species reached their potential maximum heights; however, for some species, the estimated maximum height was much greater than the tallest trees observed in the field (Aiba and Kohyama 1996). This was attributed to early mortality in these species (i.e., many individuals died before reaching their potential maximum height). Thus, in this forest, the relative canopy position of each species is determined by both potential maximum height and mortality pattern.

The vertical development of canopy structure with increasing stand age can be inferred by comparing stands of different ages, i.e., a chronosequence approach (see Figure 5-3). In Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forests of the Pacific Northwest Coast of North America, development of vertical canopy structure during early-successional stages begins with the dominance of the fast-growing, pioneer species, Douglas-fir, in the upper canopy of mixed-species stands (Wierman and Oliver 1979; Larson 1986). In late-successional stands, canopy height reaches over 70 m. Douglas-fir continues to dominate in the upper canopy as more shade-tolerant species such as western hemlock and western red cedar (*Thuja plicata*) invade the mid- to lower-canopy (Gholz

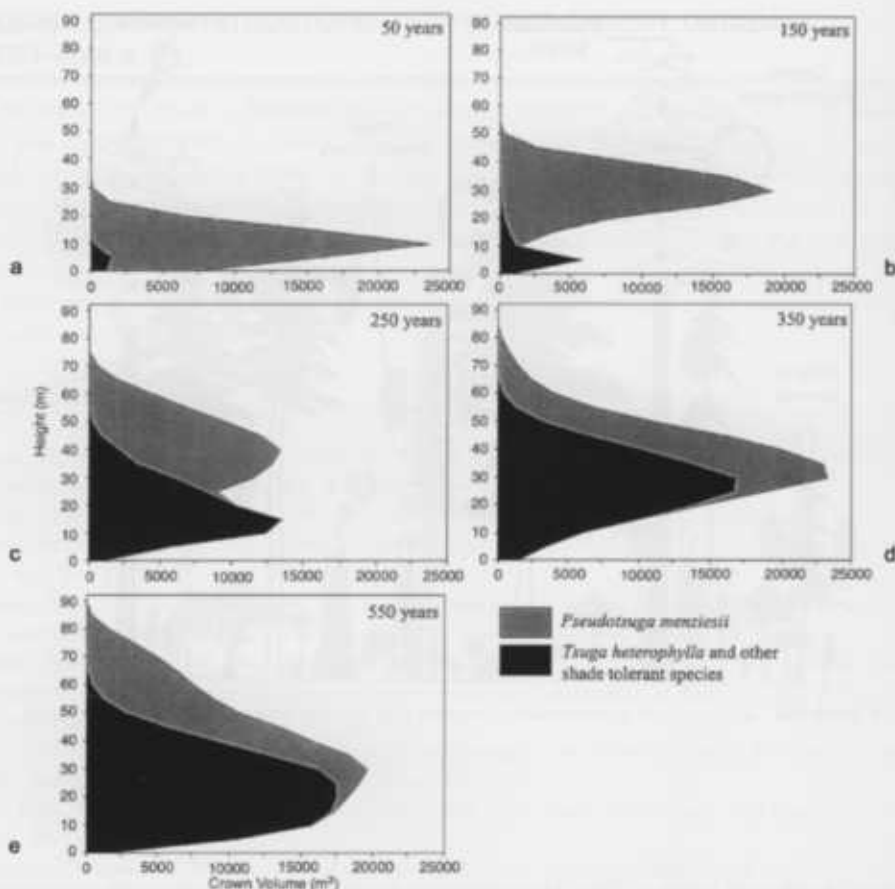


Figure 5-3 Comparison of the vertical distribution of foliage among Douglas-fir-western hemlock forests of different ages in western Washington State. (a) Fifty-year-old stands are nearly pure Douglas-fir. Depending on stand origin and proximity to older stands, shade-tolerant species (largely western hemlock, with vine maple [*Acer circinatum*] present in the understory) may or may not be present at this stage. (b) In 150-year-old stands, the Douglas-fir canopy has a homogeneous and simple structure; most of the canopy trees are nearly the same height and diameter. The understory is more diverse and comprises many shade-tolerant tree species, including western hemlock, western red cedar, and Pacific silver fir. (c) In 250-year-old stands, canopy depth increases and shade-tolerant species are found throughout all canopy heights. (d) In 350-year-old stands, the Douglas-fir canopy is very deep but is only represented by 30 to 60 trees per hectare. Shade-tolerant species represent most of the foliage within all but the uppermost canopy. (e) At 550 years, few large Douglas-fir trees (less than 25 trees per hectare) continue to survive and hold large amounts of foliage in their crowns. Large trees of western hemlock and western red cedar also exist, contributing to increasing stand foliage amount.

et al. 1976; Stewart 1986; Easter and Spies 1994). This results in the development of a deep, continuous canopy comprising both early- and late-successional species.

Crown interactions play an important role in determining the spatial distribution of trees within the canopy (Ford and Sorrensen 1990). "Crown shyness" is a phenomenon where crowns of neighboring trees are separated by small gaps. This has been attributed to mechanical abrasion (Putz et al. 1984; Rudnicki et al. 2003) and to changes in the rate and direction of branch elongation in response to neighbors (Koike 1989; Sumida et al. 2002). "Crown asymmetry," where the crown center is offset from the stem base, results from plasticity in the directional growth of tree crowns. Broad-leaved trees show great plasticity in crown growth, which allows

trees to grow toward gaps in the canopy, increasing the mean crown diameter.

Coniferous trees show a more regular spatial distribution of crowns, and crown competition becomes increasingly important in mortality of saplings as trees increase in size. In a western hemlock forest at Mount Rainier State Park, Washington, tree abundance and the vertical distribution of trees are regular, dispersed (Ishii et al. 2004; Song et al. 2004).

As forests mature, the mortality rate becomes less important than shade tolerance. In a western hemlock forest, trees reach the upper canopy as late successional species. In a Douglas-fir forest, there are few physical or physiological limitations to the tallest trees, allowing late successional species to reach heights over 60 m. In a western hemlock forest, trees attained maximum height in the absence of crown competition. In a Douglas-fir forest, coexistence of a long-lived species (Douglas-fir) with late successional species (western hemlock, western red cedar, and Pacific silver fir) is common in the canopy (Lindenmeyer et al. 2002).

Stochastic Processes

With increasing stand age, gaps in the canopy become increasingly important. The maximum size, life span, and complexity of the canopy increase after initiation. The canopy surface becomes more complex, and the processes and phenomena that occur within the canopy become more diverse.

Many trees in a forest have crooks and irregular crowns in the canopy, frequently affected by wind (Brokaw 1989; Coomes and Brokaw 1992). In a Douglas-fir forest, trees can also cause

trees to grow toward open areas of the canopy and avoid competition from neighboring crowns. Crown asymmetry can buffer negative effects of crown competition, reducing tree mortality and increasing the mean and variation in tree size within stands (Umeki 1997).

Coniferous trees have less plasticity in crown form and directional growth of the crown. The spatial distribution of coniferous tree crowns is more strongly determined by the outcome of crown competition. In a western hemlock forest in northern Idaho, spatial distribution of trees became increasingly regular with increasing diameter, indicating that crown competition results in mortality of spatially aggregated young trees, leading to increasingly regular spatial distribution as trees increase in size (Moer 1993). Similarly, in the 450-year-old Douglas-fir-western hemlock forest at the Wind River Canopy Crane Research Facility in southwestern Washington State, tree abundance decreases markedly with increasing canopy height, and horizontal spatial distribution of trees changes from aggregated distributions in the lower canopy to increasingly regular, dispersed distributions with increasing canopy height (Van Pelt and Franklin 2000; Ishii et al. 2004; Song et al. 2004).

As forests mature, canopy height reaches its maximum and species differences in height-growth rate become less important in determining structural development. Species with similar levels of shade tolerance will occupy similar positions in the canopy. Late-successional species that can reach the upper canopy eventually catch up and take the place of less shade-tolerant, early-successional species in the upper canopy (Guldin and Lorimer 1985). However, in regions where there are few physical limitations to canopy height (e.g., typhoons and poor soil conditions), physiological limitations to height growth and crown expansion may reduce competition among the tallest trees, allowing early successional species to coexist in the upper canopy with the late-successional species. For example, in the old-growth Douglas-fir-western hemlock forest at the Wind River Canopy Crane Research, mild climate and abundant rainfall allow canopy trees to reach heights over 60 m. In this forest, upper-canopy trees (tree height >40 m) of all species have attained maximum crown size and show very little crown expansion growth (Ishii et al. 2003). In the absence of crown competition, long-lived pioneer species such as Douglas-fir may be able to coexist with the late-successional species in the upper canopy (Ishii and Ford, 2002). Similarly, persistence of a long-lived, emergent pioneer species, *Eucalyptus regnans*, is observed in southeastern Australia and the Western Pacific where mild climatic conditions allow for development of tall canopies (Lindenmayer et al. 2000).

Stochastic Processes and Development of Structural Complexity

With increasing stand age, stochastic processes such as mortality of individual trees that create gaps in the canopy and small-scale disturbances that cause damage and die-back of crowns play increasingly important roles in creating structural complexity of the forest canopy. As trees reach maximum size, limitations to crown expansion in the upper canopy enhance structural complexity of the canopy surface. In Douglas-fir-western hemlock forests, gaps created in the upper canopy after individual tree mortality are not filled by neighboring trees, and the upper-canopy surface becomes increasingly heterogeneous with increasing stand age (see Figure 5-4). This may be a distinguishing structural characteristic of older stands that develops as a result of stochastic processes and physiological limitation to crown expansion.

Many trees in old-growth forests show evidence of past damage and re-growth, such as forks and crooks in the main stem (Ishii et al. 2000). In tropical forests and monsoon regions that are frequently affected by windstorms and typhoons, crown damage is commonly observed (Putz and Brokaw 1989; Coutts and Grace 1995). Droughts, fungal infections, insect outbreaks, and forest fires can also cause defoliation and die-back of the crown and are often followed by re-growth

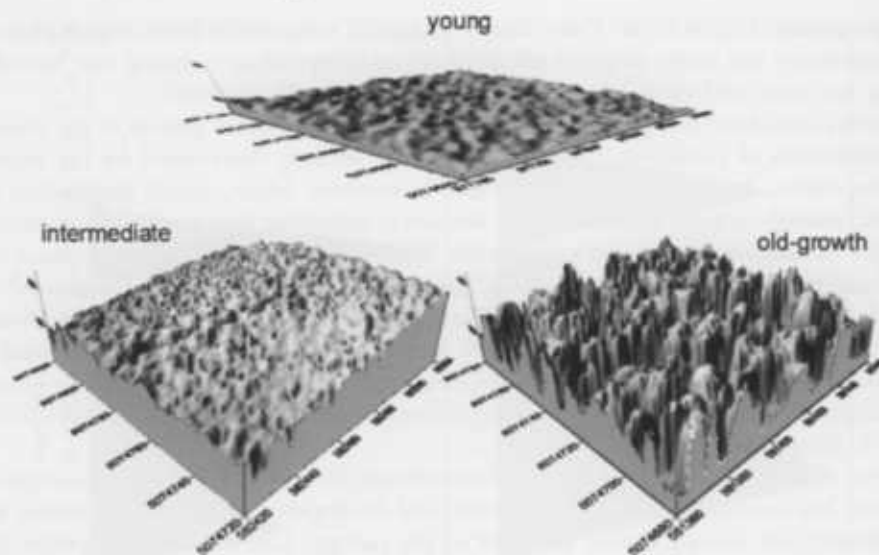


Figure 5-4 Topography of the upper-canopy surface of Douglas-fir forests of different ages. The upper-canopy surface becomes increasingly heterogeneous and rough with increasing stand age. The rugosity, a measure of surface roughness calculated as the standard deviation of outer canopy height, is 4.0 m, 11.5 m, and 15.4 m for young, intermediate, and old-growth stands, respectively.

(e.g., Lanner and Bryan 1981; Piene and Eveleigh 1996; Sharma and Rikhari 1997). Stochasticity of small-scale disturbances followed by re-growth of the crown adds variability to the otherwise deterministic architecture of trees and enhances structural complexity of the forest canopy.

In large, old trees that have reached maximum crown size and foliage amount, the balance between productive and nonproductive organs becomes increasingly important to maintain overall productivity (Remphrey and Davidson 1992). The crowns of large old trees are maintained by "reiteration," where architectural units are duplicated within the tree from suppressed buds (proleptic reiteration) or from growing axes (sylleptic reiteration) (Hallé et al. 1978; Bégin and Filion 1999). Reiteration often occurs by epicormic shoot production, where new units are produced when dormant buds in older tissue are released from suppression. Damage and die-back of the crown due to small-scale disturbances or physiological limitations are often followed by reiteration generating productive organs from existing branching structure, thus efficiently maintaining foliage amount without increasing non-productive biomass. Reiteration contributes to prolonging tree longevity by reproducing dead and dying crown components (Bryan and Lanner 1981). Many long-lived, late-successional species can reiterate architectural units and maintain the crown, in contrast to short-lived early-successional species, which tend to have less ability to reiterate crown components (Millet et al. 1998). Reiteration of various architectural units ranging from shoots and twigs to entire branches and vertical axes (reiterated trunks) has been observed in some large, old trees of long-lived species, including redwoods (*Sequoia sempervirens*, Sillett and Van Pelt 2000) and Douglas-fir (Ishii and Ford 2001). Understory trees of European beech (*Fagus sylvatica*), a shade-tolerant, late-successional species, maintain the crown by means of reiteration when growth is suppressed due to limited light conditions (Nicolini et al. 2001). In old Douglas-fir trees, reiteration enhances structural complexity of the crown by increasing branch size variability (Ishii and Wilson 2001). Reiteration also contributes to enhancing structural complexity by creating specific structural features such as reiterated trunks, fan-shaped clusters of

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epicormic branches, and platform-shaped forks within branches, making the crown of each tree "highly individualistic and irregular" (Franklin et al. 1981, see Figure 5-5).

Structural Complexity Enhances Ecological Function

One of the most pronounced effects of human activity on the global biosphere is the dramatic change incurred on ecosystem function and the declining biological diversity caused by deforestation (Wilson and Peter 1988; Perry and Maghembe 1989; Kimmins 1997). Humans have simplified ecosystem structure by converting natural forests to young stands, plantation forests, and agricultural fields. Management practices affect the structure (Zenner 2000; Lindenmayer and McCarthy 2002), function (Perry and Amaranthus 1997) and biodiversity (North et al. 1996; Beese and Bryant 1999) of forest ecosystems and simplification of stand structure leads to dimin-

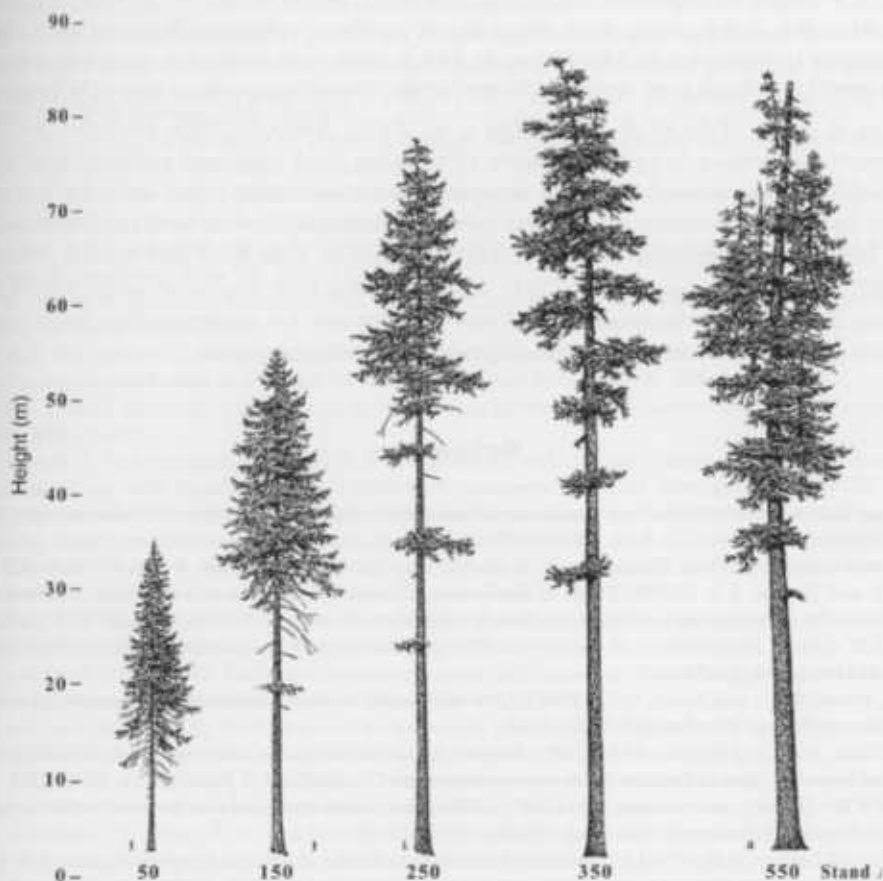


Figure 5-5 Development of structural complexity of the crown of Douglas-fir trees with increasing age. In 50-year-old trees, growth is deterministic and trees show typical conifer tree architecture. Many stands have reached crown closure, and lower branches begin to die. In 150-year-old trees, tree height reaches near 50 m. Further death of lower branches has occurred and the live crown reaches down to about two-thirds of tree height. Branches are reiterated by epicormic branching in the lower crown of some trees. At 250 years, trees are near their maximum height. Epicormic branches can be found in the lower crown of most trees as well as among original branches in the middle to upper crown. At 350 years, epicormic branches in the lower crown have developed into large fan-like clusters, and many of the branches in the main crown are also epicormic. At 550 years, the crown has reached maximum size, suffered several disturbance events, and is being maintained by epicormic branching and reiteration of several vertical axes (reiterated trunks).

ished ecosystem function and biodiversity decline (Bunnell and Huggard 1999). This has raised much debate over future policies for forest ecosystem management. One solution for enhancing ecosystem function and biodiversity of forest ecosystems may be to manage forests to increase stand structural complexity (Onal 1997).

Development of structural complexity, especially that of the forest canopy, enhances stand productivity by promoting complementary resource utilization among species (Ishii et al. 2004). Development of complex canopy structure comprising various species and life forms results in effective packing of biomass in the canopy. This promotes greater spatial and temporal partitioning and more efficient utilization of light resources, leading to increased stand productivity (Kira et al. 1969; Smith and Long 1989; Hartley 2002). Structural complexity of the forest canopy also enhances biodiversity of canopy-dwelling organisms by increasing environmental heterogeneity (e.g., variation of microhabitats and the range of microclimates) (Klopfer and MacArthur 1960; Pianka 1978; Carey et al. 1999a). Structurally complex canopies enhance biodiversity of a variety of organisms, including understory plants (North et al. 1996; McKenzie et al. 2000; Van Pelt and Franklin 2000; Brosfoske et al. 2001), epiphytes (Rhoades 1987; McCune 1993; Lyons et al. 2000), birds (MacArthur and MacArthur 1961; Hansen et al. 1995; Beese and Bryant 1999), small mammals (Emmons 1987; Carey 1996), and arthropods (Schowalter 1995; Ozanne et al. 1997; Halaj et al. 2000; Hijii et al. 2001). Although there are other mechanisms that promote biodiversity (e.g., development of complex food webs and sufficient time for colonization), the development of structural complexity with increasing stand age may be especially important for forest ecosystems where trees predominantly produce the structural framework and create a resource-rich template for biodiversity in terms of both food and habitat (Hunter and Price 1992; Power 1992; Jones et al. 1997). Understanding how structural complexity of the forest canopy develops with increasing stand age is important for understanding forest ecosystem functioning as well as for integrative management of forest ecosystems.

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