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Abstract

Forest structure is both a product and driver of ecosystem processes and biological diversity. It has become apparent in recent years that changes in forest structure as a result of management for timber production have undesirable consequences for other components of forest ecosystems. The objective of this paper is to provide an overview of what we have learned about the ecological roles of forest structure in the Pacific Northwest and how forest structure changes as a result of disturbance and succession. Forests are structurally diverse, but many structures derive from the same processes of disturbance and growth. Consequently, measurements on a few structural attributes can be used to estimate many other structural conditions. Particularly important components of forest structure include live-tree sizes, vertical foliage distributions, horizontal variation in canopy density, and coarse woody debris. Knowledge of the ecological roles of these structures has increased in recent years and we now have a general understanding of how these structures change during succession. Although the ecological values of forest structures are now more widely appreciated, we still have many significant knowledge gaps including the ecological roles of belowground structure, woody debris, and landscape pattern.

Introduction

Forests are three-dimensional systems whose biophysical structure plays major roles in ecosystem function and diversity. Forest structure can be thought of as both a product of forest dynamics and biophysical processes and as a template for biodiversity and ecosystem function. Consequently, understanding forest structure can help unlock an understanding of the history, function, and future of a forest ecosystem. The importance of structure is especially apparent in coastal forests of northwestern North America where trees can reach great heights and diameters (Waring and Franklin 1979). In these forests, structures play many roles in the ecosystem, e.g. large leaf areas intercept radiation and precipitation, gaps in dense canopies allow trees, shrubs, and herbs to regenerate, and large live and dead trees provide specialized habitats for many species (Franklin et al. 1981, Spies and Franklin 1988, Franklin and Spies 1991). Forest structure is shaped by natural forces such as wind, fire, and succession. Increasingly, the structure of forests at stand and landscape scales is controlled by forest management (Spies and Cline 1988, McComb et al. 1993). Managers have typically manipulated and restricted variation in forest structure to maximize timber outputs (Franklin et al. 1981 Hansen et al. 1991). However, as the range of forest structures becomes limited, so does the diversity of wildlife habitat and other values. Knowledge of patterns of variation in forest structure over time and space can serve as the basis of forest management strategies that seek to sustain a broad array of forest goods and services (Spies et al. 1991, McComb et al. 1993).

Our knowledge of forest structure, its dynamics, and its significance in ecosystems has advanced considerably since some of the first efforts to understand the ecological importance of forest structure (Franklin et al. 1981, Harmon et al 1986, Spies et al. 1990a, Ruggiero et al. 1991, Spies 1997). However, knowledge gaps remain, leaving considerable uncertainties about the ecological role of forest structure. In this paper I will briefly review some of what we have learned about forest structure in the Pacific Northwest and identify areas where our knowledge is especially deficient. In particular, I will examine what we know about how forest structure changes as a result of disturbance and succession in coastal Douglas-fir/western hemlock forests (*Pseudotsuga menziesii/Tsuga heterophylla*). I will focus on four major components of forest structure: live-tree size distribution; vertical foliage distribution; horizontal pattern; and coarse woody debris.

Components and Patterns

The term 'forest structure' encompasses many things and can be described in numerous ways. Essential attributes of forest structure include: structural type, size, shape, and spatial distribu-

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TABLE 1. Components of forest structure.

Foliage	**Fallen Trees**
Leaf area	Diameter
Vertical distribution	Height
Leaf shape, density	Decay state
Canopy gaps and horizontal pattern	Volume, mass
Tree Crowns	**Shrub, Herb, and Moss Layers**
Shape	Biomass, volume
Length	Height
Life form (e.g. deciduous, coniferous)	Life form
Diameter, area, density	Spatial pattern
Position in stand	**Forest Floor and Organic Layers**
Branch characteristics	Depth
Cavities, breakage, decay	Decay state
Tree Bark	**Pit and Mound Topography**
Texture	Area
Thickness	Height/depth
Tree Boles	**Roots**
Diameter	Size
Height	Density, decay state
Cavities, breakage, decay	Biomass
Gaps and spatial pattern	Spatial pattern
Age distribution	**Soil Structure**
Wood Tissues	Aggregations
Volume	Organic matter distribution
Biomass	**Landscape Structure**
Type (e.g. sapwood, heartwood)	Stand/patch type distribution
Standing Dead Trees	Patch size
Diameter	Patch shape
Height	Habitat connectivity
Decay state	Edge density
Volume, mass	
Cavities	

tion (vertical or horizontal) of components. Forest structure comprises numerous components (Table 1), many of which are fundamental to the functioning and diversity of ecosystems. For example, forest canopies vary both vertically and horizontally and play major roles in intercepting radiation, controlling microclimate, and determining habitat. In addition, the perspective of the observer, (i.e. above canopy, forest interior, or below ground) influences the appearance and kind of ecological functions observed. From above the canopy we can measure the effects of canopy surface structure on reflectance and gas fluxes, and we are able to study epiphytic habitat structure and canopy decadence. From below the canopy, we can study the effect of structure on transmission of light through canopies and gaps, and measure relative crown position and shape. Within stands, measurements of tree sizes, biomass, and distributions of shrub and herb layers are important to understanding forest growth and habitat potential. Forest structure of the soil surface and below ground are not well studied (Spies et al. 1990b, Griffiths et al. 1996) but are very important to forest growth, nutrient cycling, and habitat for vertebrates and invertebrates. In general, our ability to see and measure patterns (e.g. spatial distribution of forest trees and stands) and structure is ahead of our understanding of the role of structure in ecosystem processes.

Quantifying relationships among different forest structures simplifies the process of measuring, understanding, and managing forest structure. For example, scientists have used allometric relationships within trees to predict crown characteristics from stem diameters (Waring and Schlesinger 1985). At the stand level, overstory canopy characteristics such as stem density and gap size have been linked to composition and dynamics of tree regeneration (Gray and Spies 1996, 1997). Structural attributes also change with time. A comprehensive study of stand structure over a 900-year chronosequence of Douglas-fir/western hemlock stands in western Washington and Oregon (Spies et al. 1988; Spies and Franklin 1988, 1991) indicates that two general trends exist (Figure 1, Table 2). One structural trajectory, followed by attributes such as tree size, biomass, and forest floor depth follows an 's-shaped' pattern during succession after stand-replacement disturbances. This pathway is related to stand growth phenomena that occur following stand replacement disturbances. Tree growth and biomass increase slowly at first, then increase rapidly until growth rates and biomass accumulations slow as trees reach maximum size and sites reach maximum capacity to support vegetative growth and biomass. The other trajectory, follows a 'u-shaped' pattern and includes attributes such as amount of coarse woody debris, biomass, and diversity of the shrub and herb layers. This pathway is followed by components that attain high levels in early stages of succession, either because of carryover from the previous mature stand (e.g. woody debris) or because the open conditions are favorable to growth (e.g. shade-intolerant plants). These components then decline with decay or canopy closure and then increase again later in succession as stands produce more dead wood and gaps open in the canopies. Although individual stands develop in a wide variety of ways, general tendencies allow one to predict the characteristics of one type of forest structure from knowledge of another (e.g. foliage height distributions from tree dbh variation) (Spies and Franklin 1991) and to predict future states of a population stands from knowledge of their current forest structure (e.g. knowledge of current size/age distributions and species of live trees can be used to estimate future characteristics of dead trees).

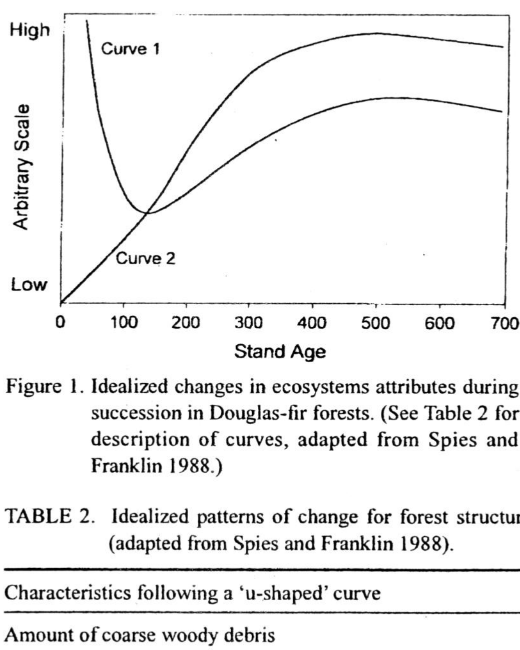

Figure 1. Idealized changes in ecosystems attributes during succession in Douglas-fir forests. (See Table 2 for description of curves, adapted from Spies and Franklin 1988.)

Four Important Components of Forest Structure

Particularly important components of forest structure include: (1) tree size/age distribution, (2) vertical foliage distributions, (3) horizontal canopy distribution, and (4) dead wood. The traditional and most common measures of forest structure are the size and age distributions of the trees (Smith 1986). Size distribution of living trees is closely linked to many other structural features (e.g. foliage distribution, crown attributes) or the potential to produce other features (e.g. dead wood of different sizes). Size distribution and densities per unit area are used to calculate growth and yield

TABLE 2. Idealized patterns of change for forest structural characteristics during natural succession in Douglas-fir forests (adapted from Spies and Franklin 1988).

Characteristics following a 'u-shaped' curve	Characteristics following an 's-shaped' curve
Amount of coarse woody debris	Average size of dominant trees
Number of large snags	Diversity of tree sizes
Dead trees as a percentage of ecosystem biomass	Incidence of broken tops and other signs of decadence
Spatial heterogeneity of herbs, shrubs, and tree regeneration	Forest floor depth
Plant species diversity	Surface area of boles and branches
Vertebrate species diversity	Vertical foliage diversity
Susceptibility to fire	Live biomass

as well as make decisions about harvesting or thinning forest stands. Size distributions are also related to important habitat elements such as canopy layering and nest site availability. Tree size is indicative of age distributions but the relationship between age and size is frequently not very strong. However, even-aged stands tend to have relatively narrow bell-shaped size distributions, whereas in uneven-aged stands, diameter distributions approximate negative exponential functions or exhibit a series of peaks that represent establishment events (Smith 1986).

Size distributions of trees in unmanaged coniferous forests are strongly related to disturbance history and time since the last stand-replacement disturbance. Typical patterns of size distribution can be identified, although many stands will deviate from idealized patterns. In centuries-old, late-successional forests, frequency distributions of trees typically approximate a negative exponential distribution. Intermediate disturbances such as partial fires can remove understory and overstory trees, altering horizontal and spatial pattern of canopy foliage. In some cases, different disturbance histories can produce similar size distributions of trees. For example, where partial fires leave large remnant Douglas-firs, late-successional diameter distributions (negative exponential) can arise in less than 100 years instead of four or five centuries (Spies, unpublished data). Processes or species that are sensitive to conditions in multi-layered canopy forests may not distinguish between the two cases.

If similar forest structures can arise from different stand histories then there may be options to create desired stand structures through silvicultural practices. It is becoming increasing clear that traditional forest management practices will not produce the structures found in old-growth stands or will not produce them at the same rate as in natural stands. For example, Tappeiner et al. (1997) found that growth rates of individual young trees in dense forest plantations are much slower than those of old-growth trees in unmanaged forests when those trees were young. If the objective of management is produce old-growth structures from forest plantations, future forests will probably not have the same structural characteristics as current natural old-growth forests, unless stand densities in plantations are reduced now.

Foliage layering or vertical foliage distribution is another component of forest structure that plays important roles in wildlife habitat, absorption of solar radiation, and in the microclimate of the forest. Forests can have distinctive horizontal layers of vegetation, but typically foliage is distributed more continuously from the forest floor to the upper canopy with peaks in the profile. During succession, forest foliage distributions tend to increase in height and evenness. Evidence is mounting that other forest species such as birds and epiphytic lichens also respond to this vertical gradient of structure and microclimate. For example, vertical foliage diversity may facilitate thermoregulation by northern spotted owls (*Strix occidentalis caurina*) (Gutierrez 1996). Epiphyitic lichen species are distributed at different heights within multilayered Douglas-fir forests (McCune et al. 1997). Until recently, it was nearly impossible to measure foliage distributions directly and most studies had to use surrogates such as tree height and canopy depth to evaluate foliage distributions in stands. New remote sensing tools such as laser altimetry now give us the ability to directly measure this attribute of forest structure and examine its variability across landscapes (Weishampel et al. 1996. Lefsky et al. in review).

Forests are horizontally structured into a mosaic of different canopy densities and gaps. Because light is limited within most forest systems, variation in foliage density plays important roles in regeneration and understory development. Gaps contribute to spatial diversity, facilitate tree regeneration, and enable herb and shrub species to grow and reproduce within late-successional forests (Eck 1984; Stewart 1984; Taylor 1990; Spies et al. 1990a; Lertzman 1992; Gray and Spies 1996, 1997; Van Pelt and North 1996). The role and dynamics of gaps change with succession. Canopy gaps become larger and close more slowly as stands become older (Spies et al. 1990a). In contrast to gaps, patches of remnant canopies help create diversity in early successional forests (Goslin 1997). Remnant trees can retain epiphytic lichen species and become a source of propagules to populate the canopies of younger conifer stands (Sillett and Neitlich 1996).

Coarse woody debris plays many roles in forest ecosystems, including wildlife and fish habitat, water storage, nutrient cycling, and soil development (Maser and Trappe 1984, Harmon et al. 1986). Its role in terrestrial and aquatic habitat is generally understood. Many species of terrestrial vertebrates, invertebrates, plants, and fungi use decaying wood as shelter, as substrate, and as an energy source (Maser and Trappe 1984). In streams, dead wood helps create habitat complexity for salmonids (Sedell et al. 1988). The role of dead wood in site productivity is less clear than its role as habitat. It can contribute nitrogen to soil ecosystems via fixation; however, this contribution may be small relative to other sources (Harmon and Chen 1991). On dry sites, decayed wood may contribute structures to the soil, increasing water holding capacities (Harmon et al. 1986).

The abundance and distribution of dead wood in a forest is strongly controlled by disturbance history. Although old forests typically accumulate relatively large amounts of dead wood, the highest amounts are found in very young forests that originate following disturbances that kill overstory trees (Spies et al. 1988). Consequently, the greatest difference in the structure of managed vs. natural forests is probably in young stands which typically have low amounts of dead wood under traditional timber management systems (Spies and Cline 1988). Coarse woody debris in streams comes from two major sources: (1) streamside disturbances and mortality; and (2) landslides and debris flows in headwall areas, which entrain wood and deliver it to larger stream channels. Management of stream channel structure and watersheds will need to take both sources of wood into account.

Conclusion

Studies over the last 20 years have shown us that forest structure is more than just variation in tree size or age. Forests are a three-dimensional complex of structures, many of which are linked through growth, disturbance, and decay processes. Forest structures vary over time and space and are quite sensitive to disturbance history. Studies of natural forests also indicate that there are many developmental pathways to a particular forest structure. Consequently, it might be possible to use alternative silvicultural practices to imitate the structure and dynamics of natural forests and thereby retain desired elements of biological diversity in managed stands and landscapes. While we know much about the ecological roles of forest structure, there is much we do not know. For example, the role of coarse woody debris in site productivity is not well known and our knowledge of its habitat role comes from only a few localities. Finally, it is below ground and at landscape scales where our lack of understanding of the roles and variability of forest structure is often most apparent. Until we expand the geographic and temporal extent of research on forest structure and conduct more studies of managed forests, we will be unable to provide managers with the specific information they need to sustain and understand forest ecosystems.

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