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Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example

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Abstract

Forest managers need a comprehensive scientific understanding of natural stand development processes when designing silvicultural systems that integrate ecological and economic objectives, including a better appreciation of the nature of disturbance regimes and the biological legacies, such as live trees, snags, and logs, that they leave behind. Most conceptual forest development models do not incorporate current knowledge of the: (1) complexity of structures (including spatial patterns) and developmental processes; (2) duration of development in long-lived forests; (3) complex spatial patterns of stands that develop in later stages of seres; and particularly (4) the role of disturbances in creating structural legacies that become key elements of the post-disturbance stands. We elaborate on existing models for stand structural development using natural stand development of the Douglas-fir—western hemlock sere in the Pacific Northwest as our primary example; most of the principles are broadly applicable while some processes (e.g. role of epicormic branches) are related to specific species. We discuss the use of principles from disturbance ecology and natural stand development to create silvicultural approaches that are more aligned with natural processes. Such approaches provide for a greater abundance of standing dead and down wood and large old trees, perhaps reducing short-term commercial productivity but ultimately enhancing wildlife habitat, biodiversity, and ecosystem function, including soil protection and nutrient retention. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Attributes of forest ecosystems are composition, function and structure. Composition is the variety and proportion of various species present a major aspect of biodiversity. Function is the “work” carried out by an ecosystem, including such processes as productivity, conservation of nutrients, and regulation of hydrologic cycles. Structure includes both the variety of individual structures, such as trees, snags, and logs of various sizes and conditions, and the spatial arrangement of these structures, such as whether they are uniformly spaced or clumped. The importance and inter-related natures of composition, function, and structure have been known for many decades (e.g. Bormann and Likens, 1979). Of course, all three attributes change during the successional development of forest stands.

Structural attributes of forest stands are increasingly recognized as being of theoretical and practical importance in understanding and managing forest ecosystems because:

- structure is the attribute most often manipulated to achieve management objectives following establishment of a forest stand;
- structure is a readily measured surrogate for functions (e.g. productivity) or for organisms (e.g. cavity-dwelling animals) that are difficult to measure directly;
- structures have direct value as a product (e.g. wood) or in providing a service (e.g. in sequestering carbon or influencing hydrologic responses).

Approaches to forest structure have evolved from a near-exclusive focus on live trees (e.g. Oliver, 1981) to consideration of a broad array of forest structures and their importance, such as in providing critical wildlife habitat (e.g. Barnes et al., 1998; Bormann and Likens, 1979; Kimmins, 1996; Perry, 1994) (Fig. 1). Complete conceptual models of forest structural development are required to guide managers in efforts to maintain critical forest functions and the full array of native organisms. The most accurate models—complete as to structures, patterns, and processes—are most likely to come from studies of natural stands.

Detailed synthetic models of natural stand development are not available for many forest types. Generalized models with establishment, thinning,

transition, and steady-state stages have been developed and used by Bormann and Likens (1979) and Peet and Christensen (1987). Oliver (1981) and Oliver and Larson (1990) created a widely-cited stand-structure model of three process-based stages and a fourth structural condition: (1) stand initiation; (2) stem exclusion; (3) understory re-initiation; and (4) old-growth or structurally complex. These are all useful pedagogical models of early development in dense even-aged stands, such as plantations.

These conceptual models have limited usefulness in guiding silviculturalists seeking to imitate natural forests, however. They fail to consider several important variables including: (1) severity of initiating disturbance; (2) coarse woody debris and other residual structures; and (3) the spatial aspect of structure. Fourth, much variability in stand development—especially in later successional stages—is lumped into a few developmental categories. For example, Oliver’s three process-based stages cover only about 10% of the potential life span of a coastal Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) forest.

The structural development of coniferous forest stands in western North America has been the subject of much recent research (e.g. Spies et al., 1988, 1990; Spies and Franklin, 1988, 1991; Cohen et al., 1990; Franklin and Spies, 1991; McComb et al., 1993; Halpern and Spies, 1995; Gray and Spies, 1996; MacKinnon and Trofymow, 1998; Pabst and Spies, 1999; Lefsky et al., 1999; Van Pelt and Franklin, 1999, 2000; Franklin et al., 2000). Our goal in this synthesis is to provide a more complete vision of key processes and stages in the development of natural forest seres using Douglas-fir forests as our primary example. The contrasting influences of disturbances on structural legacies is emphasized along with the global applicability of these concepts in understanding temperate and boreal forests.

Our purpose is to make clear the challenge of managing forest stand-structure so as to maintain biological diversity and sustain forest productivity. Simplistic structural classifications can lead managers to believe that they can easily replicate examples of natural forests through silviculture (Scientific Panel on Ecosystem Based Forest Management, 2000; Aber et al., 2000). Foresters can and must learn to manage forest stands that sustain biological diversity and a range of essential processes, but they will be most



Fig. 1. Natural forests are now known to include a variety of living and dead tree structures as well as vertical and horizontal spatial complexity; structural complexity is very high in old-growth coniferous forests in the Pacific Northwest (Ashael Curtis Nature Trail, Mt. Baker-Snoqualmie National Forest, Washington) (photo by J.F. Franklin).

successful if their efforts are based on a comprehensive understanding of the structures and developmental processes in natural forest stands.

2. Structures and forest structural processes

Before proceeding we will define some characteristic structures of forest stands (Table 1) and developmental processes that operate during forest stand development (Table 2).

2.1. Structural features of forest stands

Both individual structures and their spatial arrangements are relevant when analyzing forest stand-structure (Table 1, Fig. 1). Tree species diversity contributes importantly to ecosystem structure and function particularly when species with different life forms and autecology are included, such as species of both evergreen and deciduous behaviors and shade-tolerant and shade-intolerant habits. Tree species also produce snags and logs that differ widely in decomposition rates and patterns resulting in more structural diversity (Harmon et al., 1986).

Tree size and condition contribute to structural diversity. Large old trees with multiple decadent features (e.g. multiple and dead tops, bole and top decays, and cavities) are an example. Specific features, such as

decay cavities, large-diameter branches, and distinctive bark features (e.g. the bark streamers produced by the exfoliating bark of many *Eucalyptus* spp. (Lindenmayer et al., 2000)), may be explicitly recognized because of unique functional and habitat roles. Larger live trees also generate larger snag and log structures that have distinct ecological roles simply because of their size. Many forests have a lower tree stratum composed of species with limited height potential, such as Pacific dogwood (*Cornus nuttallii* Audubon ex Torr. & A. Gray) and Pacific yew (*Taxus brevifolia* Nutt.) in Douglas-fir forests. The small tree layer may make unique contributions to ecosystem function as exemplified by the role of lower tree layers of *Acacia* spp. and myrtle beech (*Nothofagus cunninghamii* Oerst.) in providing habitat for arboreal marsupials in the mountain ash (*Eucalyptus* spp.) forests of south-eastern Australia (Lindenmayer et al., 2000).

Standing dead trees and coarse woody debris on the forest floor are significant structures (Maser and Trappe, 1984; Harmon et al., 1986; Franklin et al., 1987; Maser et al., 1988; Kirby and Drake, 1993; Samuelsson et al., 1994; Renvall, 1995; McMinn and Crossley, 1996; Hagan and Grove, 1999; Lindenmayer et al., 1999). Much variability results from differences in speed and type of decay related to species and piece size (Harmon et al., 1986) and with disturbance history (Spies et al., 1988). Uprooted trees create additional structural features—root wads (mounds)

Table 1
Some structural features of forest stands including individual structural elements and spatial patterns of structural elements

Important attributes	
Individual structures	
Live trees	Species, density, mean diameter, range in diameter, height, canopy depth
Large-diameter live trees	Species, density, decadence (including presence of decay columns), crown condition, bark characteristics
Large-diameter branches	Species, density, size, individual or arrays, presence of arboreal "soil"
Lower-canopy tree community	Composition, density, height
Ground community	Composition, density, deciduous/evergreen
Standing dead trees (snags)	Species, size, decay state, density
Large woody debris (logs)	Species, density, decay state, volume, mass
Uproots (root wads and holes)	Density, size, age
Organic layers	Depth, chemical and physical properties, biota
Spatial patterns	
Vertical distribution of foliage/canopy	Depth, continuity, cumulative distribution
Horizontal distribution of structures	Spatial pattern (e.g. random, dispersed, or aggregated)
Gaps and anti-gaps	Size, shape, density

Table 2

Some structural processes that are operational during the successional development of forest stands in approximate order of their first appearance

Disturbance and legacy creation
Establishment of a new cohort of trees or plants
Canopy closure by tree layer
Competitive exclusion (shading) of ground flora
Lower tree canopy loss
Death and pruning of lower branch systems
Biomass accumulation
Density-dependent tree mortality
Mortality due to competition among tree life form;
thinning mortality
Density-independent tree mortality
Mortality due to agents, such as wind, disease, or insects
Canopy gap initiation and expansion
Generation of coarse woody debris (snags and logs)
Uprooting
Ground and soil disruption as well as creation of structures
Understorey re-development
Shrub and herb layers
Establishment of shade-tolerant tree species
Assuming pioneer cohort is shade-intolerant species
Shade-patch (anti-gap) development
Maturation of pioneer tree cohort
Achievement of maximum height and crown spread
Canopy elaboration
Development of multi-layered or continuous canopy through
Growth of shade-tolerant species into co-dominant
canopy position
Re-establishment of lower branch systems on
intolerant dominants
Development of live tree decadence
Multiple tops, dead tops, bole and top rots, cavities, brooms
Development of large branches and branch systems
Associated development of rich epiphytic communities
on large branches
Pioneer cohort loss

and pits and mix soil (Bormann et al., 1995). Organic layers on the soil surface are important in cycling of water, carbon and nutrients and as habitat (e.g. North et al., 1997).

The non-arborescent understorey community also can provide structural complexity and diversity in ecosystem function and niches. Tree ferns (Cyathea-*ca*e) are an example from Australian mountain ash forests (Lindenmayer et al., 2000). Competition can also lead to dominance by one or a few species creating distinct structures that exclude or suppress other life forms, the range of structural conditions, and processes, such as nutrient cycling. Examples of such

circumstances are the dense shrub layers formed by salal (*Gaultheria shallon* Pursh.) or salmonberry (*Rubus spectabilis* Pursh.) in coastal forests of the Pacific Northwest (Franklin and Dyrness, 1988; Pabst and Spies, 1999) and dwarf bamboo layers found in many sub-alpine forests in Asia (Franklin et al., 1979) and South America (Zegers, 1994).

The spatial arrangement of structures in stands—the vertical distribution of branches and foliage and horizontal distribution of trees and other structures—is as important as the diversity of individual structures. Young- and old-growth forests offer extreme contrasts in foliage distribution. Foliage is concentrated high in the canopy in dense young stands with little or none lower in the canopy. In many old-growth forests, foliage and live branches are distributed continuously from the ground to the top of the canopy (Parker, 1995, 1997; Parker and Brown, 2000; Lefsky et al., 1999). The shift in foliage distribution with stand development is a complex, long-term process (discussed later) that contributes significantly to the vertebrate diversity of many old-growth forests (see e.g. Ruggiero et al., 1991; Carey et al., 1992, 1999; Carey, 1995; Carey and Johnson, 1995; Lindenmayer et al., 2000).

Spatial patterns in the horizontal distribution of structures, such as trees, snags, and logs significantly influence ecosystem functioning. The foresters' traditional focus on fully stocked, evenly spaced stands implicitly recognizes the relation of spatial pattern to function—in this case, wood production. Canopy gaps created by the death of one or a few trees in an established stand are a widely studied spatial phenomenon in natural stands (Runkle, 1982, 1985; Canham et al., 1990). Establishment of dense cohorts of trees in gaps also produces densely shaded areas within stands. New tools (e.g. GPS) and analytic approaches are greatly improving our ability to measure and analyze structural patterns in forests, such as the degree of randomness, regularity, or aggregation of structures or species (e.g. Freeman and Ford, 2001).

2.2. Processes associated with structural development of forest stands

Our discussion and classification of forest structural development is oriented around processes, such as birth, growth, decadence, and death of trees (Table 2).

These will be discussed as they occur in the developmental stages but some introductory comments are useful.

Most structural developmental processes actually operate throughout much of the sere and not at a single stage. Specific processes are often identified with particular stages in stand development, such as competitive exclusion of organisms and density-dependent tree mortality or “self-thinning” in a period following canopy closure. This is because particular processes may dominate or characterize particular stages in stand development, however, those processes are never confined to those stages.

For example, disturbances that kill trees, generate biological legacies, and establish new cohorts of trees are not confined to the stand-initiating disturbance. Wind, insects, diseases, low-intensity fires, etc. operate throughout succession to generate and maintain spatial heterogeneity within the stand (e.g. the shifting mosaic of Bormann and Likens, 1979).

Similarly, competitive exclusion of organisms through shading, biomass accumulation, and self-thinning among a tree cohort are typically important early in a sere. However, they also operate later in stand development (old-growth forests) albeit at the smaller scale of patches within the stand. When operating at the gap scale these processes actually promote alpha (within community) diversity rather than excluding species.

The shift from the stand-level to within-stand patch or gap scale in structural development processes is an important aspect of forest development, especially for stands originating following a catastrophic disturbance. Initially, such stands are typically dominated by processes that operate relatively uniformly over the entire stand. Gap-level disturbances subsequently generate more and more within-stand spatial heterogeneity. In contrast, most structural development is at the gap-level in stands subject to chronic disturbances, such as light- to moderate-intensity wildfire or windthrow. Consequently, forests with catastrophic and chronic disturbance regimes tend to develop similar gap- or patch-level structural complexity over time—stands which incorporate all stand development processes simultaneously!

Finally, processes that generate stand spatial heterogeneity occur throughout a sere although not all are recognized as gap generation. Areas with little

or no tree regeneration are often present in stands as a result of severe environmental conditions, competing vegetation, or other factors. Gaps are created and enlarged by patch-level mortality in young forest stands due to root rots (e.g. laminated root rot, *Phellinus wierii* [Murr.] Gilbn.).

3. Developmental stages in natural forest series

Classifications of stand structural developmental stages are arbitrary. First, development is clearly continuous rather than a series of discreet stages. Second, many processes, such as those that create spatial heterogeneity, operate throughout the life of the stand. Third, individual stands may skip particular developmental stages. Nevertheless, there is heuristic value in recognizing a series of developmental stages that are commonly encountered and in which specific stand structural conditions and developmental processes predominate.

We recognize eight such exemplary developmental stages in stand development (Table 3). Disturbance and legacy creation, cohort establishment, canopy closure, biomass accumulation/competitive exclusion, maturation, vertical diversification, horizontal diversification, and pioneer cohort loss. These stages build on earlier classifications (e.g. Spies and Franklin, 1996; Carey et al., 1996) and numerous studies of structure and developmental processes within natural stands. Structural conditions and dominant developmental processes are illustrated with a Douglas-fir dominated sere growing within the *Tsuga heterophylla* (Raf.) Sarg. and lower *Abies amabilis* (Dougl.) Forbes Zones of the Pacific Northwest (Franklin and Dyrness, 1988). Our developmental stages are contrasted with other classifications in Table 3.

3.1. Disturbance/legacy creation stage

Stand development begins with a disturbance that provides conditions for establishment of a new dominant tree cohort. Natural disturbances rarely eliminate all structural elements from the preceding stand, however, even in the case of extreme or multiple disturbances (Fig. 2a) (e.g. Franklin et al., 1995, 2000; Foster et al., 1997). Many living organisms often survive including sexually mature trees or tree

Table 3
Comparison of stand development stages under several classification schemes

Typical stand age (years)	Classification				
	This article	Oliver and Larson (1990)	Spies and Franklin (1996)	Carey and Curtis (1996)	Bormann and Likens (1979)
0	Disturbance and legacy creation				
20	Cohort establishment	Stand initiation	Establishment phase	Ecosystem initiative	Reorganization phase
30	Canopy closure	Stem exclusion	Thinning phase	Competitive exclusion	Aggradation phase
80	Biomass accumulation/ competitive exclusion	Understory re-initiation		Understory re-initiation	
150	Maturation	Old-growth	Mature phase	Botanically diverse	Transition phase
300	Vertical diversification		Transition phase (early)	Niche diversification	Steady-state
800	Horizontal diversification		Transition phase (late)	Old-growth	
1200	Pioneer cohort loss		Shifting-gap phase		

regeneration or both. Trees are killed by natural disturbances but most disturbances consume or remove only a portion of the killed trees or, in some cases (wind storm) none of the organic matter. The dead remnants are typically snags (standing dead trees) and logs on the forest floor. Persisting living and dead structures are described as biological legacies (Franklin et al., 2000; Franklin and MacMahon, 2000).

Quantity and types of biological legacies differ greatly among disturbances leading, in turn, to widely varying starting points for stand structural development (Table 4). Wildfire converts large living trees to standing dead and downed while consuming varying quantities of organic material (Fig. 2b) from relatively small amounts (although this may be nutrient-rich

foliage) to more substantial quantities, such as branches, portions of boles and soil organic layers. The largest trees are most likely to survive and small trees (seedlings and saplings) are most likely to succumb to wildfire. Many natural Douglas-fir stands established following wildfire incorporate large old trees, as well as snags and logs, from the previous stand (Fig. 2c).

Catastrophic windthrow converts overstory trees to logs and debris on the forest floor although some overstory trees may survive either as intact or damaged individuals (Fig. 2d) (Cooper-Ellis et al., 1999; Foster et al., 1997). No organic matter is consumed although some material transfer may occur by the wind and uprooting. If advanced tree regeneration



Fig. 2. Contrasts in biological legacies in areas subject to different kinds of disturbances: (a) short snags and logs in the central portion of devastated zone created by the 1980 eruption of Mount St. Helens (Washington); (b) abundant snags and logs following catastrophic fire in Yosemite National Park (California); (c) surviving legacies of old-growth trees incorporated into young Douglas-fir stand developed following the 1902 Yacholt Burn (southern Washington cascade range); (d) abundant logs, short snags, rootwads, and an abundant understory of shrubs and advanced tree regeneration, following a catastrophic blowdown in old-growth Douglas-fir forest (Mount Hood National Forest, Oregon) (photos by J.F. Franklin).

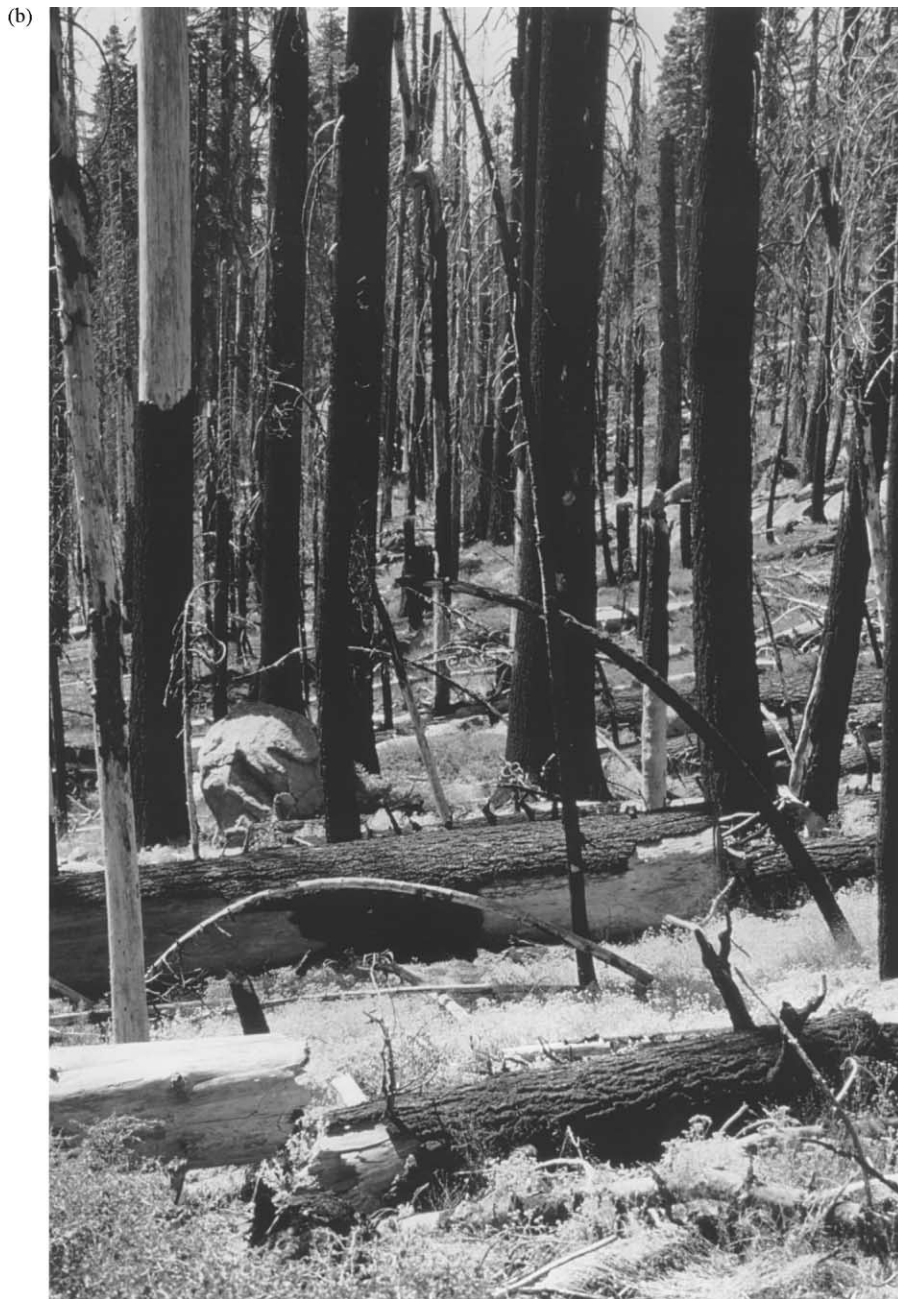


Fig. 2. (Continued).

is present the new tree cohort is already in place and released; advance regeneration is most likely composed of shade-tolerant species that establish themselves in shaded understories. Dense advance

regeneration may result in very dense new stands, such as the western hemlock stands developed following the 1921 windstorm on the western Olympic Peninsula (Henderson et al., 1989).

(c)



Fig. 2. (Continued).

Post-disturbance conditions following clearcutting differ greatly with those following most natural disturbances in terms of the types, levels, and patterns of structural legacies (Table 4) (Fig. 3). Traditional clearcutting leaves no legacy of overstory trees or even coarse woody debris, when intensive slash disposal practices, such as broadcast burning, are utilized.

Remnant trees have important influences on stand development. Remnant tree density affects the spatial patterning of colonizing tree seedlings (Goslin, 1997). High densities of remnant trees can reduce growth rates in younger cohorts (Zenner et al., 1998). Remnant tree densities influence development rates of horizontal complexity in either positive or negative ways (Zenner, 2000). In mature stands with limited seed sources, remnant shade-tolerant conifers can aid re-establishment of these species by increasing seed availability (Keeton, 2000).

To summarize, disturbances vary in type, intensity, size, frequency, and homogeneity resulting in widely

contrasting starting points for stand development. These contrasts include marked differences in structural legacies as well as rate, composition, and density of tree regeneration. Significant structural legacies are the rule rather than the exception with most natural disturbances. At the landscape level areas of undisturbed forest are often skipped leaving habitat islands with diverse structural legacies and unique environmental conditions (Foster et al., 1998; Keeton, 2000).

3.2. Cohort establishment stage

A new generation of trees is established during cohort establishment. This stage varies widely in duration and in stocking levels that are eventually achieved. Regeneration can be limited by a lack of seed source either due to distance from seed trees or infrequent seed years or both. Seed limitations can occur following intense wildfires of moderate to large size although single large, intense wildfires have

(d)



Fig. 2. (Continued).

promptly regenerated (Hofmann, 1917; Gray and Franklin, 1997). Regeneration can also be delayed by severe environmental conditions (drought) and competing vegetation that result in high mortality of germinants and seedlings. Repeated wildfire typically

accentuates most of these problems. Stand establishment is typically most rapid when it forms from surviving advance regeneration allowing the interpretation that, in this case, cohort establishment actually preceded disturbance and legacy creation!

Table 4

Biological legacies associated with different type of intense disturbances in many temperate and boreal forest regions

Biological legacy	Different types of intense disturbances		
	Wildfire	Windstorm	Clearcut
Large living trees	Few	Few	None
Snags	Abundant	Common	None
Down logs	Common	Abundant	Few
Intact tree regeneration layer	Patchy	Yes	Variable ^a
Undisturbed forest floor	Patchy	Patchy	Variable ^a

^a May be some present depending upon time and method of harvest and site prep slash disposal practices.

Regeneration density achieved during cohort establishment varies widely. Many stands and portions of stands established after wildfires, especially multiple fires, have stocking below levels of “normal” stands. Such stands undergo gradual canopy closure and escape a significant period of density-dependent mortality. In contrast, stands that achieve normal to

very high stocking in relatively short-periods of time undergo intense self-thinning processes.

3.3. Canopy closure stage

Trees re-establish site dominance during canopy closure. This stage may be brief in many stands and



Fig. 3. Traditional clearcutting leaves little or no above-ground structural legacy in contrast to most natural disturbances (H.J. Andrews Experimental Forest, Willamette National Forest, Oregon) (photo by J.F. Franklin).

could be viewed as a transition between cohort establishment and biomass accumulation/competitive exclusion. However, it is the most dramatic developmental episode in rate and degree of change in stand conditions, excepting only the initiating disturbance.

The major process is forest canopy closure through development of overlap among individual tree canopies. Major environmental changes in the understory include greatly reduced light levels, moderated temperature regimes, increased relative humidity, and near-exclusion of wind. Significant shifts occur in both the composition and function of the forest ecosystem. Some species of shrubs, herbs, and lichens are suppressed or eliminated while others, such as saprophytes and invertebrate detritivores, may increase.

The rate of canopy closure depends upon density of the tree regeneration and site productivity. When tree regeneration establishes slowly or at low densities, tree canopy closure may require several decades, as appears to be the case with many existing old-growth Douglas-fir stands (Tappeiner et al., 1997) although not all of them (Winter, 2000). For a given density of tree regeneration, canopy closure is most rapid on more productive sites; some low productivity forest sites never achieve canopy closure.

3.4. Biomass accumulation/competitive exclusion stage

The biomass accumulation/competitive exclusion stage is an extended period of young stand development in which the tree cohort totally dominates the site (Fig. 4). In Douglas-fir serotines it commonly extends from canopy closure until 80–100 years of age (Table 3). This stage is characterized by rapid growth and biomass accumulation, competitive exclusion of many organisms, and, in many cases, intense competition among the tree cohort. It has been labeled the stem exclusion (Oliver, 1981) and thinning (Spies and Franklin, 1996) stage but many natural young stands display little evidence of thinning mortality, perhaps because of low initial stand densities. The most universal characteristics of this developmental stage are, therefore, rapid biomass accumulation (explicitly recognized by Bormann and Likens, 1979) and competitive exclusion of many organisms. Hence, our choice of nomenclature.

In this stage dominant stand development processes are: (1) development of woody biomass; (2) competitive exclusion of many organisms; (3) density-dependent tree mortality or self-thinning; (4) natural pruning of lower tree branches; and (5) crown-class

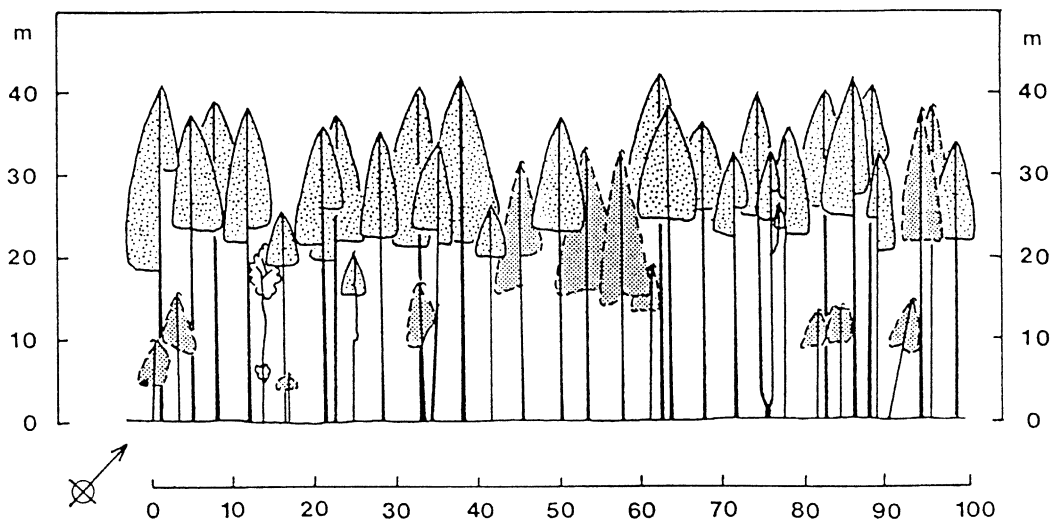


Fig. 4. Biomass accumulation/competitive exclusion stage of Douglas-fir stand development; 55-year-old stand near Humptulips River, Olympic Peninsula, Washington (redrawn by R. Van Pelt from Kuiper, 1994).

differentiation. Rapid biomass accumulation from growth in both tree diameter and height is characteristic in this exponential growth phase so prized by production foresters.

Competitive exclusion of species and competitive thinning amongst the tree cohort began with canopy closure and intensifies during this stage. Species diversity of many groups of organisms, such as vertebrates (Harris, 1984), declines because of shading that suppresses or eliminates light-dependent understory plants and reduces food for herbivores. Species favored by shaded, humid, litter-rich environments, such as many saprophytes and detritivores, flourish.

Intense intra-tree competition occurs in dense stands resulting in significant density-dependent mortality, primarily of trees at the low end of stand diameter distributions. This competition eases gradually as stands approach maturity. The thinning process is more common and intense in plantations and other

intensively managed stands where uniform tree size and high stand densities are aggressively created than it is in natural stands that are often understocked by traditional forest management standards.

Natural pruning of shaded branch systems during this developmental stage rapidly lowers live crown ratios. Foliage becomes concentrated high on the boles and light penetration is limited although total stand leaf areas are substantially below levels later achieved. Douglas-fir stands during biomass accumulation typically have leaf area indices of 5–7 while older stands on identical sites have indices of 9–11 or more. Some lower branch systems may persist and later participate in re-establishment of the lower canopy.

3.5. Maturation stage

The pioneer cohort of trees attains maximum height and crown spread (mature) during the maturation stage (Fig. 5). Other distinctive features include: (1) mass of

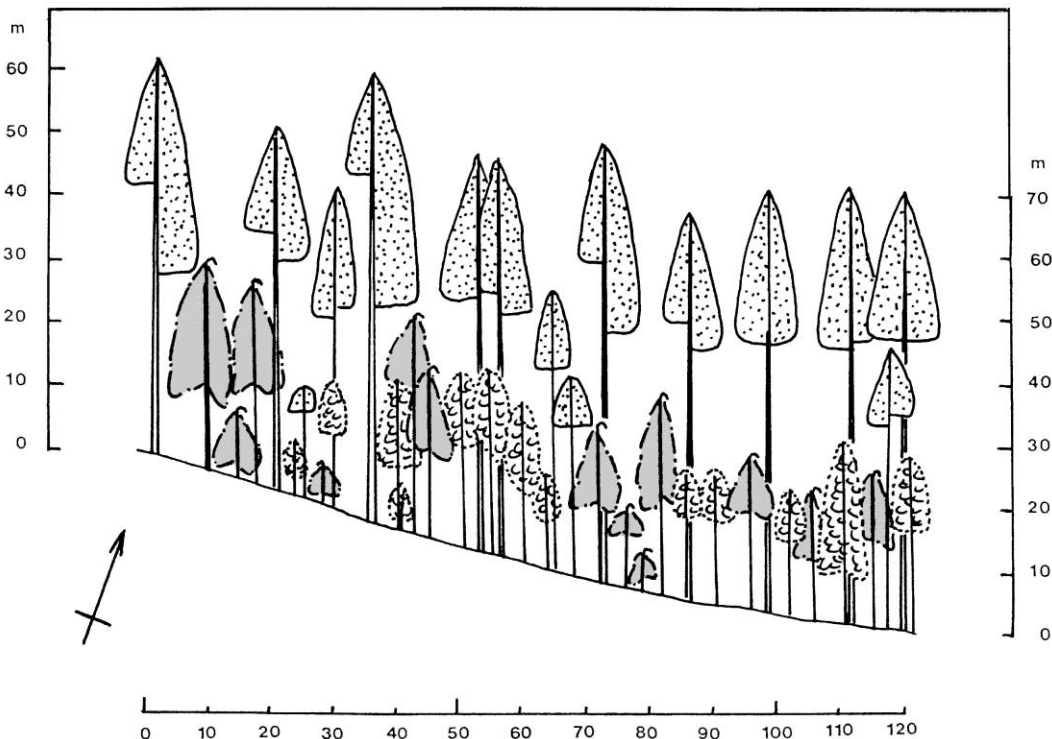


Fig. 5. Maturation stage of Douglas-fir stand development with Douglas-fir trees approaching their maximum heights and crown spread and shade-tolerant associates becoming established; 177-year-old stand on Hugo Peak in Pack Forest near Mount Rainier, Washington (redrawn by R. Van Pelt from Kuiper, 1994).

coarse woody debris at minimal levels during the sere; (2) re-establishment of the understory community including shade-tolerant trees; (3) a shift from density-dependent to density-independent causes of overstory tree mortality; and (4) development of decadence in overstory trees. The maturation stage typically begins at 80–100 years and may persist for 100–150 years in naturally-regenerated Douglas-fir stands.

While biomass levels approach an asymptote after the biomass accumulation stage, individual trees undergo additional growth in height, crown spread, and diameter. Douglas-fir trees at 100 years have typically achieved only 60–65% of their eventual height; they complete most of its growth in height and crown spread during the maturation stage.

Mass of coarse woody debris typically reaches its low for the sere during the maturation stage (Maser et al., 1988; Spies et al., 1988). The initiating disturbance generated a massive input of woody debris but after a century much of the mass has been decomposed and new inputs of coarse woody debris have been limited to small trees. Substantial volumes of coarse woody debris may still be apparent but most of it is of low density except where logs of decay-resistant species, such as Douglas-fir, American chestnut, and species of the family Cupressaceae (*Castanea dentata* (R.S. Marsh) Borkh.) are present.

The understory community is re-established as the thinning canopy of overstory dominants allows more light to reach the forest floor during maturation. Of course, in low density stands understory communities have persisted throughout preceding stages and increased light results primarily in expansion of existing herbaceous and shrubby components.

Significant establishment of shade-tolerant tree species in the understory typically begins during the maturation stage but the process is highly variable in speed and uniformity. Many mature natural Douglas-fir stands on sites suited to western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and western redcedar (*Thuja plicata* Donn.) lack significant shade-tolerant regeneration after a century or more of development (Acker et al., 1998). Availability of seed sources, such as mature and remnant old-growth trees, presence of suitable seed beds, competition with herbaceous shrubs, stand density, and environmental conditions all affect this process (Schrader, 1998; Keeton, 2000).

Causes of overstory tree mortality shift from competitive to non-competitive during the maturation stage. Density-dependent mortality has been dominant up to this point. During maturation insects (e.g. bark beetles), diseases (e.g. root rots), and wind become much more important causes of mortality. Such agents along with ice and snow storms typically do cause some tree mortality earlier in succession but these causes are secondary to competition among trees. The shift from competitive to non-competitive mortality causes also represents a stand-level change from uniform to spatially-aggregated patterns of mortality.

Sub-lethal damage to trees from various biological and environmental agents accelerates development of a greater diversity of individual tree conditions during maturation and increases niche diversification (Carey et al., 1996, 1999). Examples of such damage include broken and multiple tops, top and bole decay, and brooming.

3.6. Vertical diversification stage

Significant development of late-successional or old-growth forest attributes particularly the re-establishment of canopy continuity between the ground and upper tree crowns occurs during vertical diversification (Fig. 6). Increased decadence in overstory trees, accelerated generation of coarse woody debris, and re-establishment of foliose lichen communities are also characteristic. This developmental stage often occurs at 200–350 years in Douglas-fir stands although development of shade-tolerant co-dominants can be slow.

Two processes contribute to re-establishment of a continuous canopy between ground and dominant tree crowns in Douglas-fir forests. First, shade-tolerant species, such as western hemlock, western redcedar and Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) grow into intermediate and co-dominant canopy positions. Second, Douglas-fir trees re-establish lower crowns, primarily by developing epicormic branch systems. Of course, this latter process is limited to tree species capable of generating epicormic branch systems at advanced ages. These two processes combine to produce a continuous canopy from ground to canopy top (Parker, 1997; Parker and Brown, 2000), a feature sometimes incorrectly described as “multiple canopy layers”. Both processes are stimulated by

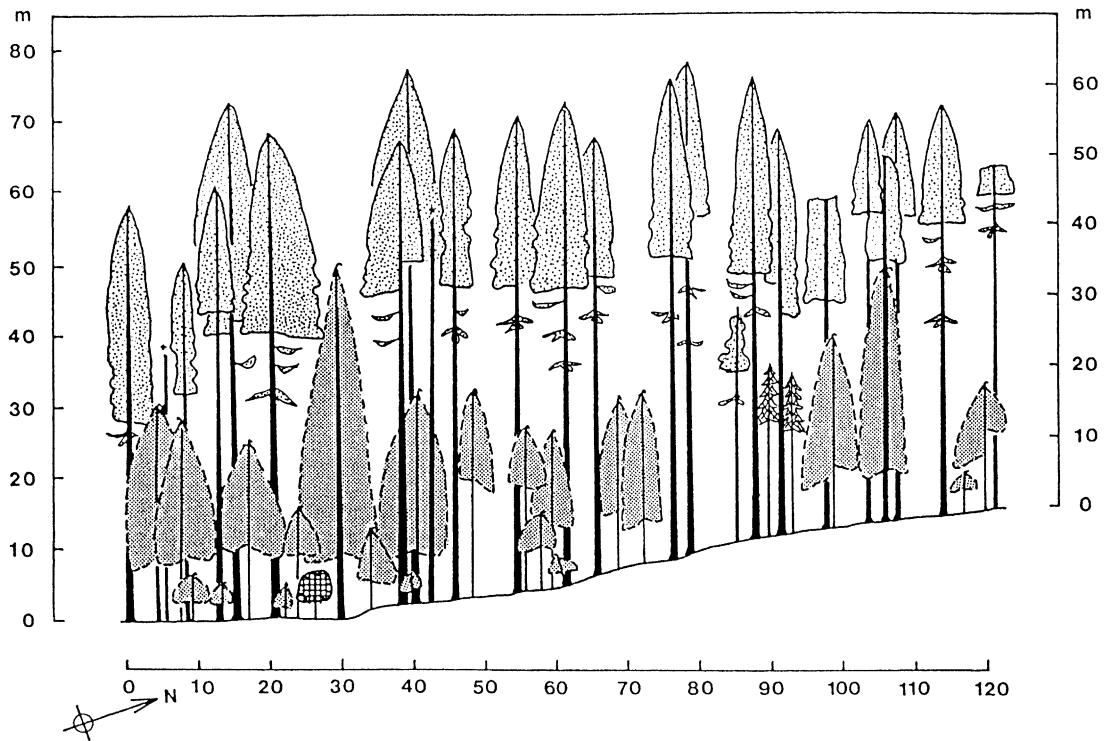


Fig. 6. A continuous vertical canopy profile develops during the vertical diversification stage of Douglas-fir stand development with associated shade-tolerant western hemlock moving into a co-dominant position in the canopy; 250-year-old stand near Ohannapecosh Campground, Mount Rainier National Park (redrawn by R. Van Pelt from Kuiper, 1994).

increased light due to thinning of overstory Douglas-firs by mortality.

Sub-lethal damage to trees and mortality continues to generate structural complexity and diversify niches. During vertical diversification stands large numbers of snags and logs are generated through mortality of larger trees; masses of coarse woody debris approach levels typical of old-growth stands. Density-independent mortality dominates and much of this mortality is aggregated resulting in initiation or expansion of gaps. Density-dependent mortality is occurring primarily among dense cohorts of shade-tolerant saplings and poles that established in canopy gaps and that are now evident as heavily-shaded patches. Development of decadence in living trees continues through top breakage, wood rots, scarring, and, in susceptible species, such as western hemlock, mistletoe infections.

Significant coverage and biomass of bryophytes and foliose lichens typically develops during the vertical diversification stage (McCune, 1993). Many of the

foliose lichens are cyanolichens that fix atmospheric nitrogen. Presence of these epiphytic communities requires development of larger branch systems (Clement and Shaw, 1999). The large branches also are critical habitat for many vertebrates, such as nesting habitat for the endangered marbled murrelet (*Brachyramphus marmoratus* Gmelin.) in the Pacific Northwest.

3.7. Horizontal diversification stage

The stand evolves into multiple structural units during the horizontal diversification stage, primarily as a result of gap creation and expansion (Fig. 7a and b). Although processes that produce horizontal spatial heterogeneity have been active throughout stand development, gap development is a dominant process at this stage. Generally this stage begins after at least 300 years in Douglas-fir seres but it may occur earlier on highly productive sites.

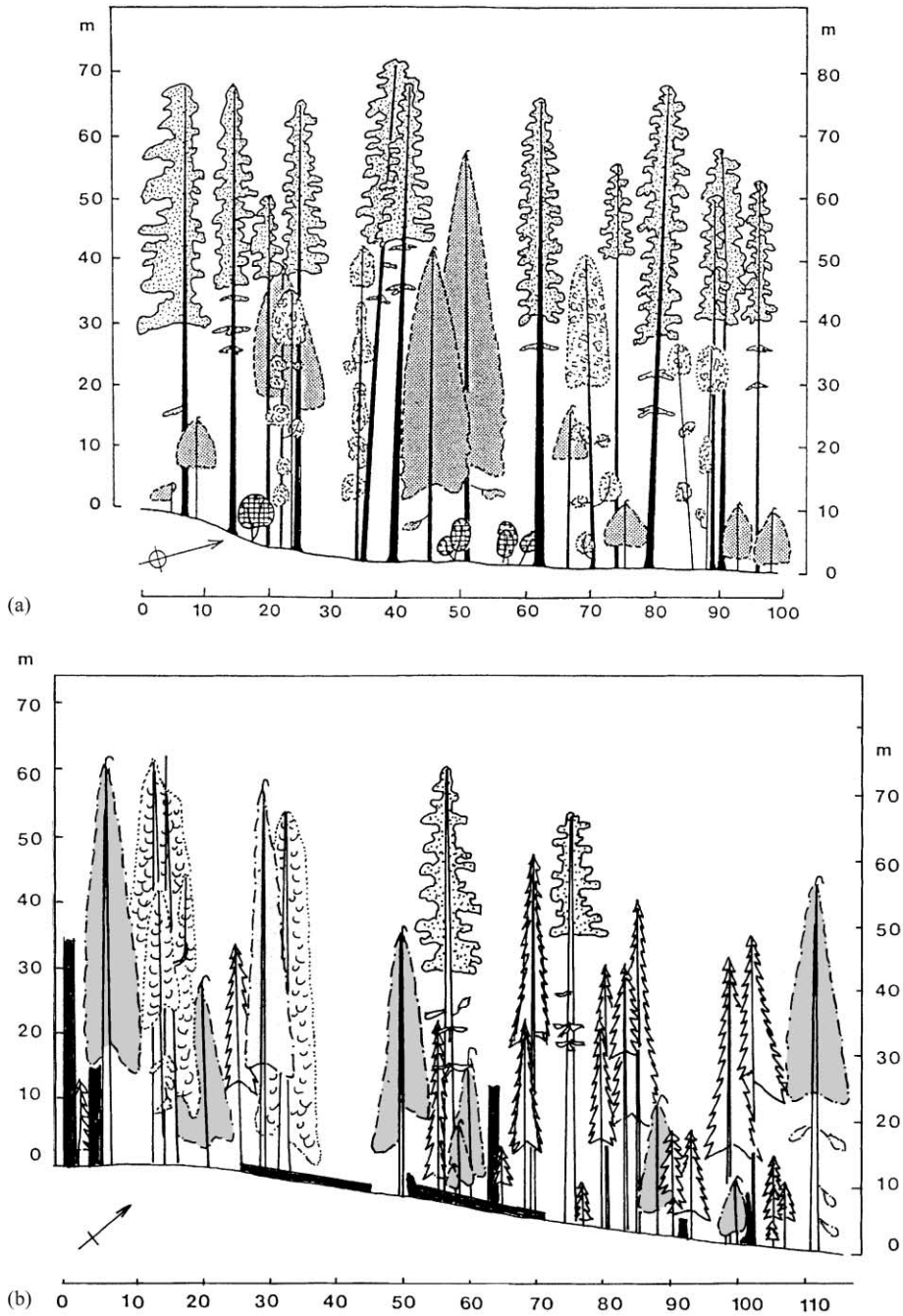


Fig. 7. Stands evolve into multiple structural units during the horizontal diversification stage, primarily as a result of gap-creating and gap-filling processes: (a) modest levels of horizontal complexity in a 450-year-old Douglas-fir western hemlock stand on the H.J. Andrews Experimental Forest, Willamette National Forest, Oregon; (b) high levels of horizontal complexity in a 1000-year-old stand along Chinook Creek, Mount Rainier National Park, Washington (both diagrams redrawn by R. Van Pelt from Kuiper, 1994).

Dominant processes during this stage contribute to development of high levels of horizontal variability: creation of gaps through spatially-aggregated mortality and creation of heavily-shaded areas where dense patches of shade-tolerant species have reached the mid- or upper-canopy. The light environment of the mid- and lower-canopy is controlled primarily by shade-tolerant species at this stage and not by the remaining emergent Douglas-fir trees (Thomas and Winner, 2001; Van Pelt and Franklin, 2000). Patterns of foliage distribution are distinctive and predictable at this stage of development with high variability at the mid-canopy level and low variability in the upper and lower canopies (Parker, 1997; Parker and Brown, 2000).

Gaps result from agents that create contagious tree mortality, such as wind and many diseases and insects. In Douglas-fir forests such diseases include laminated root rot and velvet top fungus (*Phaeolus schweinitzii* [Fr.] Pat.); important insects include Douglas-fir bark beetle (*Dendroctonus pseudotsugae* Hopkins). Some gaps initiate earlier in stand development but expand during horizontal diversification; this circumstance varies with forest type, however, as gaps fill rapidly in some forest types and slowly in others. Gaps generate much spatial variability in environmental conditions within the stand. This is because some resources, such as moisture, nutrients, and coarse woody debris are coincident with the gap area while other resources, such as light and heat are spatially displaced in temperate forests because of sun angles at mid to high latitudes (Van Pelt and Franklin, 1999).

Other processes during horizontal diversification are continued development of decadence in overstory trees and reductions in density of the Douglas-fir cohort.

3.8. Pioneer cohort loss stage

This developmental stage occurs when shade-intolerant species are present in the sere but the gaps present in older stands are too small for their successful regeneration. This is typical for Douglas-fir in coastal regions of the Pacific Northwest although, surprisingly, the species does sometimes regenerate in gaps where wind and pathogens create large openings. Examples of pioneer cohorts that can be lost in other temperate forests are tulip poplar

(*Liriodendron tulipifera* L.) in eastern North America and mountain ash (*Eucalyptus regnans* F. Muell) in southeastern Australia.

The loss of emergent dominants from the stand can be consequential for ecosystem processes and diversity if the tree species provide distinctive conditions, such as unique structures preferred or required by some other species, or unique chemical compounds.

The structural influence of a large pioneer species extends for several centuries beyond the death of the last individual because of the large snags and logs that are generated. This is particularly true when the wood is highly decay-resistant, as in the case of Douglas-fir.

Loss of dominant living Douglas-firs probably occurs between 800 and 1300 years depending upon site conditions. Individual Douglas-firs persist in 1000-year-old stands on cool, moist sites in the Washington cascades (Franklin et al., 1988). Douglas-fir persistence until stand age 1275 was predicted in another stand based on current rates of mortality (Franklin and DeBell, 1988; DeBell and Franklin, 1987). However, Douglas-fir can drop out of stands as early as 800 years on more productive sites.

3.9. Structural endpoint of stand development

The preceding stages are characteristic of a sere initiated by a catastrophic disturbance and composed of a mixture of pioneer shade-intolerant and associated shade-intolerant species. The sere culminates in a stand that is horizontally and vertically diverse with many kinds of individual structures and a high level of niche diversity. Strong spatial patterning is typical of such stands but this has only recently been recognized (Freeman and Ford, 2001).

A structurally diverse endpoint also characterizes natural forests occurring in regions of chronic low- to moderate-intensity disturbances (e.g. many pine forests). Spatial heterogeneity is often more obvious in chronically-disturbed forest types than it is in the denser forest subject to catastrophic disturbances. Many western ponderosa pine forests (*Pinus ponderosa* Dougl.) (Fig. 8b), the mixed-conifer forests of the Sierra Nevada (Franklin and Fites-Kaufmann, 1996) (Fig. 8a), and the southeastern longleaf pine (*Pinus palustris* Mill.) forests exemplify the spatially-complex forest structures developed under regimes of frequent wildfire. Chronic wind disturbance can result

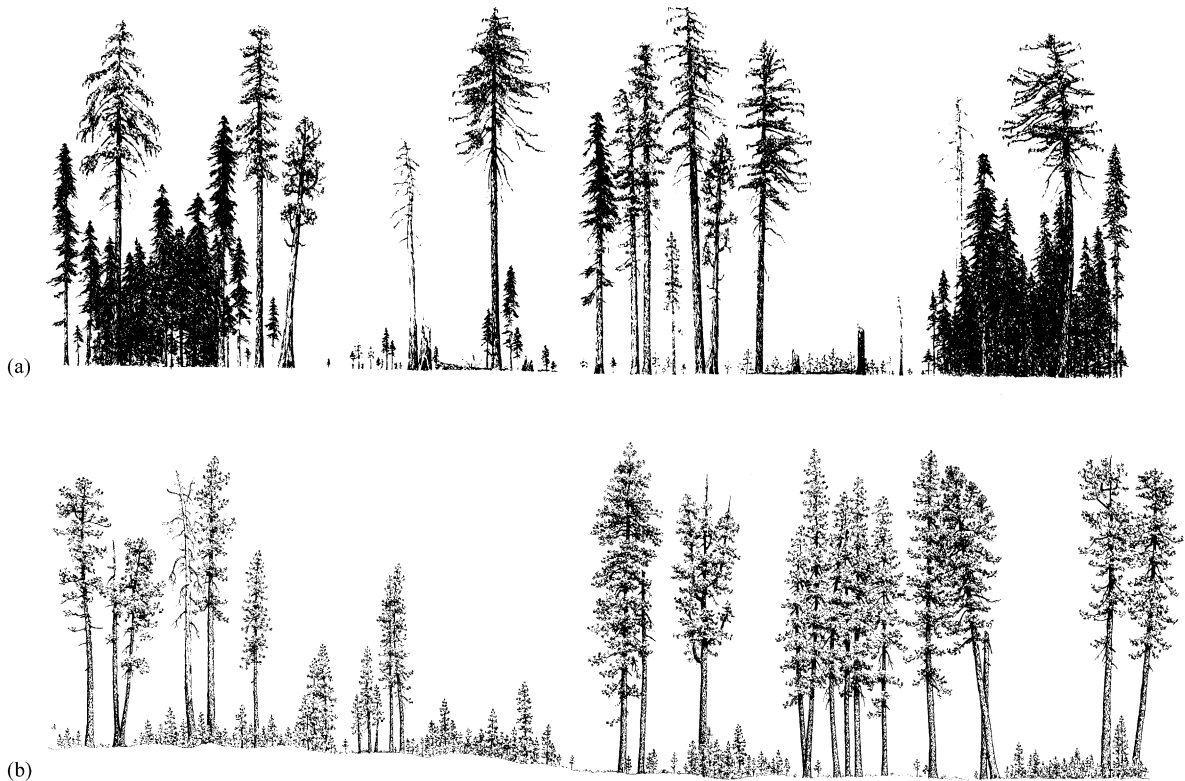


Fig. 8. Old-growth forest structure in two forest regions characterized by low- to moderate-intensity disturbances showing the mosaic of structural patches that collectively form the functional old-growth stand: (a) 200 m \times 20 m profile of old-growth stand characteristic of the Sierra mixed-conifer type (Aspen Valley, Yosemite National Park, California); (b) 15 m \times 150 m transect of old-growth pure ponderosa pine stand (Bluejay Springs Research Natural Area, Winema National Forest, Oregon) (drawings by R. Van Pelt).

in similar stand-structure, as illustrated by lenga (*Nothofagus pumilio* Poepp. et Endl. Krasser) forests in Tierra del Fuego (Rebertus et al., 1997).

Forests subject to frequent, light to moderate disturbances develop a mosaic of structural units that collectively constitute the stand (Fig. 8a and b). The entire array of structural processes and stages from disturbance, legacy creation, and cohort establishment to groves of large-diameter trees are present but spatially segregated within the stand. Foresters often view each structural unit as a stand, based on the classical definition of a stand as a group of trees relatively homogenous in structure and composition. However, ecologically it is more useful to view the functional late-successional stand in such environments as a mosaic of structural units (Franklin and Fites-Kaufmann, 1996). Altering the definition of a stand to include multiple structural units does pose

new challenges, such as defining minimum stand sizes and boundaries between stands; quantitative approaches to such definitions are being developed, however.

4. Some silvicultural implications of disturbances and structural development of natural stands

The diversity of structures, importance of spatial pattern, richness of developmental processes, long time periods essential, and especially, the complex contribution of disturbances to stand development processes typically receive little attention in traditional silviculture. Many textbooks and silvicultural prescriptions focus primarily on live trees. Management goals have been to minimize variability in tree size and condition and create spatially homogenous, fully stocked stands. These traditional regimes are not

based upon models of natural stand disturbance and development, as they are currently understood. Where the goal is intensive management of exotic plantations of *Pinus* or *Eucalyptus* spp. for production of wood fiber the disparity between traditional management regimes and natural models may not be a problem. In such cases ecological concerns are confined to the autecology of crop tree species, management-relevant peculiarities of the local environment, and measures to sustain site productivity.

However, silviculturists managing forests for a mixture of ecological and economic goals need a comprehensive understanding of natural stand development, including the role of natural disturbances. Silviculture based on modern models of natural stand development are being increasingly adopted on both public (Tuchmann et al., 1996) and private forestlands, such as the former MacMillan–Bloedel

(now Weyerhaeuser Corporation) timberlands in coastal British Columbia. Generic approaches include: (1) structural retention at the time of harvest (Franklin et al., 1997); (2) use of longer rotations (Curtis, 1997); and (3) active creation of structural complexity including structures and spatial heterogeneity, in managed stands (Carey et al., 1996, 1999; Carey and Curtis, 1996; Carey, 2000).

Biological legacies are central to development of silvicultural systems that emulate natural models. Creating and leaving biological legacies maintains critical structural elements as components of managed stands thereby sustaining many organisms and ecological processes dependent upon these structures (Franklin et al., 1997, 2000). Structural retention silviculture is modeled on the legacy concept and is one approach and sometimes the only feasible option for maintaining large-diameter snags, logs, and



Fig. 9. Fire creates small natural openings in Sierra mixed-conifer forests that provide opportunities for abundant regeneration of ponderosa pine; group selection can be used to emulate this natural disturbance regime (Aspen Valley, Yosemite National Park, California) (photo by J.F. Franklin).

old decadent trees as a part of managed stands. Silvicultural prescriptions can be tailored to specific management goals by identifying the types, numbers and spatial distribution of necessary structures. Specific management actions can create missing structures, such as by killing living trees to create snags. Where there are issues with worker safety and survival of structures, reservation of small islands of vegetation around these structures (aggregates) can be used. Silvicultural planning can even utilize multiple rotations to create structures of sizes and conditions that cannot be created in a single rotation.

It may be easiest to model silvicultural practices on natural disturbance regimes in forest types and regions that are (or were) characterized by frequent low- to moderate-intensity disturbance regimes. In such areas disturbances created and maintained a fine-scale mosaic of structural patches. Harvesting by group selection can produce stands that closely approximate those generated by the natural disturbance regime, such as the structural mosaics characteristic of lenga forests in Tierra del Fuego (Rebertus et al., 1997) or many pine forests in western North America (Franklin and Fites-Kaufmann, 1996) (Fig. 8a and b). Harvest patch sizes under group selection should approximate those in the natural stand. Silviculturalists tend to prescribe larger patches than those characteristic of the natural mosaic for such reasons as increased growth of the regenerated stand (Knight, 1997), overall ease of application, and even short-term profits. The structural match between harvesting by group selection and natural stands can be improved further by retaining some individual structures within the harvested patches (Fig. 9) and permanently reserving some patches in the stand from logging.

Shelterwood harvesting of forest types characterized by fine-scale mosaics ultimately produces stand-structures that contrast with those of the natural stands. The shelterwood system is designed to spatially homogenize the treated forest, creating an even-aged stand, rather than maintaining a high level of spatial heterogeneity in a natural multi- or uneven-aged stand.

Designing silvicultural systems based upon natural disturbance models is much more challenging for forest types characterized by large-scale catastrophic disturbances. Traditional clearcutting has little in common with most natural catastrophic disturbances except for creating a light environment suitable for

regeneration of a shade-intolerant tree species (Fig. 3). Similarly, plantations created on clearcut sites are much simpler than young stands developed after natural disturbances.

Structural retention at the time of forest harvest is clearly essential in modeling silviculture on catastrophic disturbance regimes (Franklin et al., 1997) (Fig. 10a and b). Structural legacies sustain species and processes that provide young natural stands with functional and compositional diversity characteristic of more successional advanced forests (see, e.g. Ruggiero et al., 1991). The major challenge in writing the silvicultural prescriptions is determining the kinds, numbers, and spatial patterns of retained structures

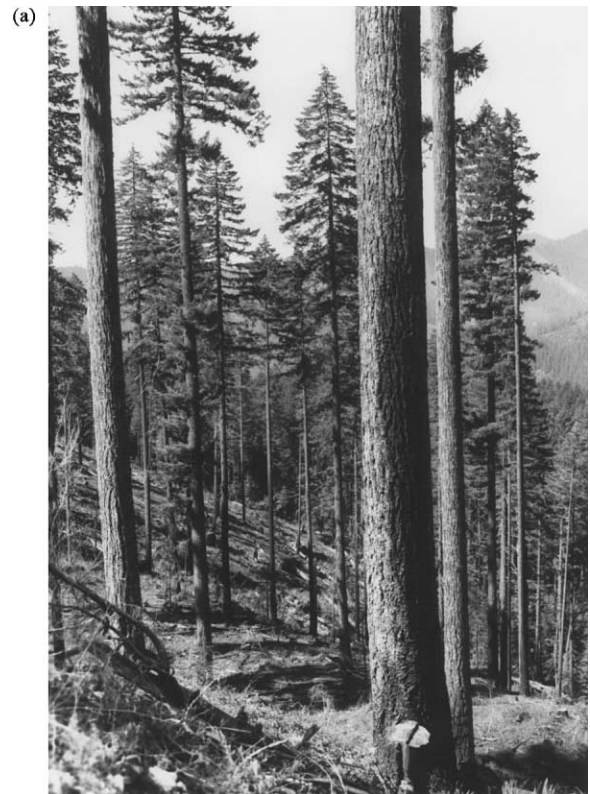


Fig. 10. Harvesting practices in the Pacific coast coniferous forests can use structural retention to provide conditions more comparable to natural disturbance events: (a) dispersed retention of 15% of the stand basal area in dominant Douglas-fir trees in a 150-year-old stand on the H.J. Andrews Experimental Forest, Willamette National Forest, Oregon; (b) aggregated retention of 15% of a 25 ha stand in the form of strips and blocks on Plum Creek Timber Company lands near Cougar, Washington (photos by J.F. Franklin).

(b)



Fig. 10. (Continued).

required to achieve defined management objectives. Difficult issues include trade-offs among environmental and economic objectives and operational and safety issues.

Rotation lengths (Curtis, 1997) and active management of stands to create specific structures and structural patterns (Carey et al., 1996; Carey and Curtis, 1996) are also essential elements of silvicultural systems that purport to incorporate processes and structures characteristic of natural stands.

5. Conclusions

It is clear from recent research that structural development of natural forest stands is more complex than foresters have traditionally believed. Some general conclusions are that:

- there are many relevant structural features in addition to live trees;
- there are numerous developmental processes contributing to stand development and many of these operate throughout the seres;
- disturbances and the biological legacies from preceding ecosystems are significant aspects of stand development that have been largely ignored;
- spatial patterns of structures (horizontal and vertical) are significant aspects of forest stands that have not been fully appreciated;
- structural development involving ecologically significant processes and structures may continue for many centuries in forests of long-lived species;
- sequences of forest development (seres) almost always end in structurally diverse forests, regardless of whether the dominant disturbance regimes are catastrophic or chronic.

Traditional even-aged harvest practices (clearcut, seed tree, and shelterwood) are not based upon natural models of disturbance and stand development, as they

are currently understood. On many public and private forests, managers have begun to provide for structural complexity by retaining structural elements of preceding stands and modifying management regimes in established stands. More of this is expected as management goals expand to fully incorporate biological diversity and a broad range of ecological processes.

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