# Creating a Forestry for the 21st Century

## The Science of Ecosystem Management

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# 2

# Forest Stand Structure, Composition, and Function

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Over the last 100 years, steep increases in human populations and the development of global market economies have rapidly changed the values of forests and increased societal conflicts over their use. The cutting and widespread exploitation and management of forests for fiber production, agriculture, and development have changed the face of many forest landscapes across the globe (Nelson et al. 1987, Ellenberg 1978, Perlin 1989). Forest lands have been converted to agricultural uses and human developments in large areas of the world (Perlin 1989). In other areas, unsound forestry practices have resulted in poor or delayed tree regeneration. Where forests have been exploited for fiber production, economically driven forestry practices have shifted the composition and structure of forests toward younger stands dominated by commercially valuable tree species, or shifted the composition toward other species that may have lower economic value than the previous dominant species (Graham et al. 1963, Seymour and Hunter 1992).

In some landscapes, such as in parts of the northeastern United States, the amount and age of the forest is increasing following declines resulting from logging in the 19th century (Foster 1993). The net effect globally, however, appears to be a decline in the amount of older forests or forests that have not been strongly influenced by modern agricultural and industrial human cultures. For example, worldwide the amount of primary forest is estimated to be 16 percent of its preindustrial amount (Postel and Ryan 1991). In the Pacific Northwest, where forest-use conflicts are especially severe, the amount of old-growth forest has declined over 50 percent in the last 60 years (Bolsinger and Wadell 1993). What remains has become highly fragmented in the last 20 years (Spies et al. 1994). The decline in older forest, or loss of primary forest, such as in the tropics and parts of the temperate zone, has lead to conflicts between segments of societies that value forest land for forest products and other land uses and those that value forests for biological diversity, ecosystem productivity and quality, and aesthetic and spiritual values (Aplet et al. 1993). These concerns have arisen not just from changes in the amount of old forest. For example, the quality of many forests has changed because of fire control, grazing, introduced forest pathogens and species, and effects of roads and agriculture on water quality. However, the loss of old forests has become symbolic of changes and losses in forest biodiversity resulting from human activities.

The kind and rate of human-induced changes in forests are superimposed on and interact with changes that result from natural processes, including disturbance, dispersal, establishment, competition, herbivory, and environmental change. The ability of society to understand, manage, and sustain the diversity of values associated with forests depends in part on our ability to understand ecological changes that forests undergo over time in natural, seminatural, or unmanaged stands and landscapes and understand the ecology of changes associated with direct and indirect human activity.

The primary objective of this chapter is to provide an ecological basis for this understanding by reviewing ecological changes associated with natural processes of disturbance and succession from young to old forests. Secondarily, the chapter will examine some of the variability in late-successional forests and contrast plantation forests with natural or wild stands. I assume that society's goals for forest ecosystem diversity include ecosystems dominated by old trees and associated structures. The way to achieve this goal is a subject of considerable debate. Options range from reserve-based approaches in which land managers seek to maintain at stand or landscape levels old forest ecosystems without direct human manipulations, to objectives that call for direct intervention to "restore" older forests at stand or landscape scales, to strategies that call for providing both wood fiber and at least some components of old-forest ecosystems. The ability of managers to meet any of these objectives will depend in part on how well they understand the ecology and dynamics of forest change in stands and landscapes.

## Forest Stands and Ecosystems

Stands and ecosystems are the fundamental units of forest management and ecosystem science, respectively. With the advent of forest ecosystem management, attention needs to be paid to reconciling these two disciplinary building blocks. The definitions and spatial boundaries of stands and ecosystems are typically determined for specific purposes of management and science. A stand typically has been defined as a unit of trees that is relatively homogeneous in age, structure, composition, and physical environment (Smith 1962, Oliver and Larson 1990). The characteristics used to delineate stands often refer to the tree layer since this traditionally has been the focus of forest management and is relatively easily mapped using aerial photographs. Soil and topographic features also frequently are used to delineate stands, especially if they have a strong effect on stand productivity or harvesting operations. Specific stand definitions, sizes, and shapes will vary depending on management intensity and objectives and the spatial heterogeneity of the vegetation, soil, and topography.

Ecosystems, in contrast to forest stands, typically have been more conceptual than real physical entities (Kimmins 1987). Whittaker (1962) defined an ecosystem as "the functional system comprising a community of interacting organisms—plants, animals, and saprobes—and the environment that affects them and is affected by them." Since ecosystems are open systems, defined by functions, interactions, and flows, the spatial boundaries of ecosystems are not easily defined (Kimmins 1987). Typically they are delineated based on specific purposes and limitations of a study.

Relatively rapid changes in ecosystem structure and function can facilitate the definition of spatial boundaries. Many of these boundaries are defined by topography (e.g., watersheds and wetlands), by distinct changes in forest structure, or by vegetation patchiness (e.g., forest woodlots in an agricultural landscape or old-growth forest stands in intensively managed forests). Thus, although forest stands are components of forest ecosystems, forest ecosystems are not necessarily forest stands—unless those stands are defined in a way that includes organisms other than trees as well as environmental factors and functions. The boundaries of stands and ecosystems will not necessarily coincide unless the criteria used to identify the two units are very similar. This chapter focuses on the ecological attributes of forest stands and assumes that the stands are defined and delineated based on ecosystem criteria such as soil, topography, vegetation structure, and landscape pattern and position in addition to management considerations.

## Modern Concepts of Forest Succession

Popular and scientific views of forest succession have changed over the last century. Early concepts emphasized relatively predictable cycles of plant communities, behaving almost like organisms, that developed toward climax communities whose characteristics were controlled by the regional climate (Clements 1916). This view was modified as it became clear that the species comprising communities frequently behave individualistically and that local site factors give rise to a diversity of climaxes in a region. The concept of climax, a relatively stable community condition toward which succession proceeds, lost much of its value as ecologists began to describe climax vegetation as "varying continuously across a continuously varying landscape" (Whittaker 1953). Ecosystem-level concepts of succession that arose in the 1960s and 1970s emphasized theoretical generalities of ecosystem change in terms of information theory (e.g., species diversity measures) and flows of energy and matter. However, these ecosystem perspectives were in many ways another expression of climax, equilibrium concepts (Glenn-Lewin and van der Maarel 1992).

More recently, ecologists conceptualize succession as a nonequilibrium spatial process (dynamic mosaic of Watt 1947) that is the outcome of disturbance and population processes such as birth, death, dispersal, and growth under changing environmental conditions (Peet and Christensen 1980, Glenn-Lewin and van der Maarel 1992). Thus the theoretical concept of succession has moved away from simple generalizations toward more complex constructs. Site-specific predictions about vegetation dynamics cannot be made from broad general theory; rather, they require a more complex scientific framework and specific information about disturbance, environment, propagule availability, and species biology (Pickett et al. 1994).

The maturation of ecological thinking about succession and the increased involvement of ecologists in conservation and management issues has moved ecology toward site-specific, mechanistic approaches. Such approaches are similar to those used by forest scientists and silviculturists who typically have not been concerned with generating broad general theories, but rather with developing the ability to make site-specific predictions for growing stands for forestry applications.

The empirical studies and approaches of applied forest ecologists provide a rich source of information about growing commercially valuable species under relatively short rotations; this will be useful to ecologists seeking to develop and test new theoretical frameworks. However, while applied forest scientists have been focused on developing information relevant to the dominant forestry objectives (primarily timber production), they have not kept up with advances in ecology (Oliver and Larson 1990). The emergence of a broader set of objectives related to ecosystems and biodiversity, such as the maintenance of old-growth ecosystems, and new fields, such as landscape ecology and conservation biology, have caught most applied forest ecology professionals by surprise. Consequently, information is lacking about how to implement forest management practices that will meet new broader ecological objectives while providing for the more traditional objectives of wood fiber production.

## General Models of Forest Development

While stand development is complex and diverse—a function of initial disturbance, environmental patterns, species mix, and intermediate disturbances—some general patterns of development appear across a wide range of forest types and locations (Oliver and Larson 1990). Several authors have proposed general models of natural stand development following major disturbances. Four major phases of forest development are typically identified: (1) establishment, (2) thinning, (3) transition, and (4) shifting mosaic (Bormann and Likens 1979, Oliver 1981, Oliver and Larson 1990, Peet 1981, Peet and Christensen 1987, Spies and Franklin 1995). These phases are idealized states of relatively homogeneous areas of forests called stands. They range from a fraction of a hectare to thousands of hectares in size, depending on forest structure, composition, and the objectives of stand classification and mapping.

### Establishment Phase

This first phase following a major disturbance, which is also termed "stand initiation" (Oliver and Larson 1990), is characterized by establishment of new individuals, release of surviving seedlings and saplings, and vegetative reproduction of injured plants from belowground structures (Figure 2.1). It is marked by relatively rapid changes in species dominance, environment, structure, and levels of competition and high mortality among small individuals. Initially this phase is characterized by an abundance of sites free from competition of established plants. Consequently, many species can establish during this period, including nonnative species (Halpern 1989) and hybrids (Spies and Barnes 1982). At the same time, many individuals of the original understory that survived the disturbance but lost aboveground parts may resprout and begin to reoccupy their previous aboveground spaces. Consequently, a stand or patch can achieve high species diversity for a time with the mixture of new and old individuals. Establishment of trees may begin immediately following the disturbance or be delayed for short to long periods depending on the availability of seed sources and competition from shrubs and herbs. The processes of tree invasion may be highly patchy depending on microsite availability, seed and seedling mortality from competition, climatic factors, or herbivory and disease (Veblen 1992). Patches of trees may eventually initiate in places and grow together in a spatial process of nucleation and coalescence. Horizontal patchiness may be very high, composed of a mosaic of patches of trees, shrubs, herbs, dead wood, and bare ground. Vertical heterogeneity, while high at fine scales and increasing at larger scales with the growth of shrubs and trees, is still low overall because of the short stature of the vegetation. As shrub and tree canopies grow together, shade-intolerant herbaceous and shrub species are typically lost from the site—although they may persist for varying lengths of time in gaps that do not close and in the soil seed bank.

**Figure 2.1** Establishment stage following fire in *Pinus sylvestris* forests in northern Sweden. (Photo: Thomas Spies)

Although this stage lacks live tree structure, standing and down dead trees can be prevalent during this phase depending on the previous stand's composition and structure and the type of disturbance (Harmon et al. 1986, Spies et al. 1988). Dead wood is prevalent following death from blowdown, insects, disease, drought, standing water, and fire (Figure 2.2). Dead wood may be completely absent in the establishment phase following avalanches, high-en-

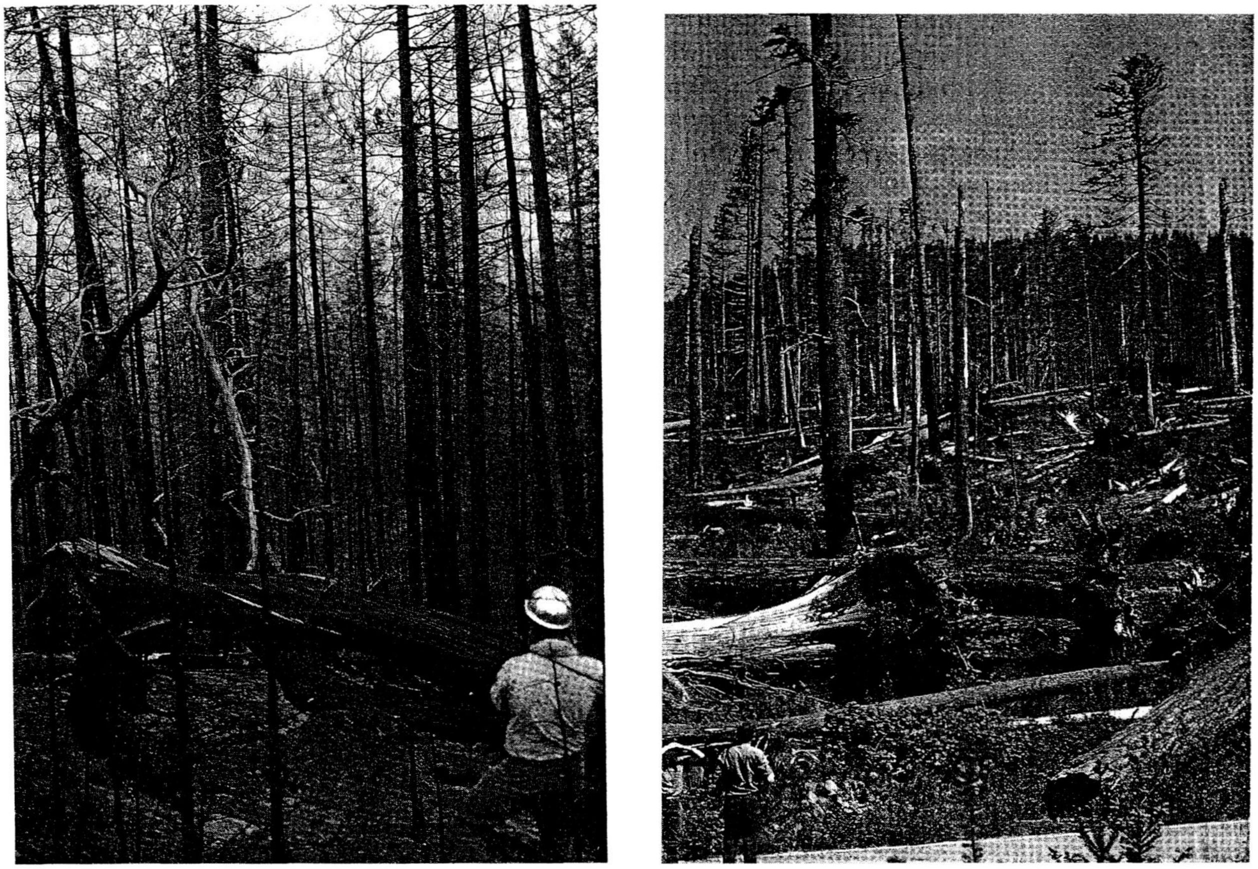
(a) (b)

**Figure 2.2** (a) Carryover of coarse woody debris following fire in old-growth mixed-conifer forest in southwestern Oregon. (b) Carryover of coarse woody debris following blowdown in old-growth forests on the Mount Hood National Forest in Oregon. (Photos: Thomas Spies)

ergy floods, and fires in stands with small trees or low biomass of live trees (Figure 2.3).

### Thinning

The next phase, which is also termed the stem exclusion phase (Oliver and Larson 1990), is characterized by the closing together of tree canopies. This results in steep declines in understory establishment and growth, increases in mortality of many understory plants, and the onset of mortality in the tree layer associated with competition for light and water. Understory vegetation may become sparse or absent in many areas beneath the dense tree canopy (Figure 2.4). Species diversity typically declines relative to the establishment phase due to loss of shade-intolerant species (Schoonmaker and Mckee 1988, Halpern 1989, Elliot and Swank 1994). Populations of shade-tolerant forest species that were eliminated by the disturbance or the unsuitable environment of the establishment phase may not recolonize during this phase because of loss of seed sources, slow dispersal rates, or competitive barriers to establishment. The degree to which understories decline or disappear depends on the density and species of the overstory trees, spatial heterogeneity of the site, and tree regeneration. Where the tree layer is dominated by shade-intolerant species, enough light typically penetrates to the understory to maintain many shrub and herb species. In addition, site conditions and regen-

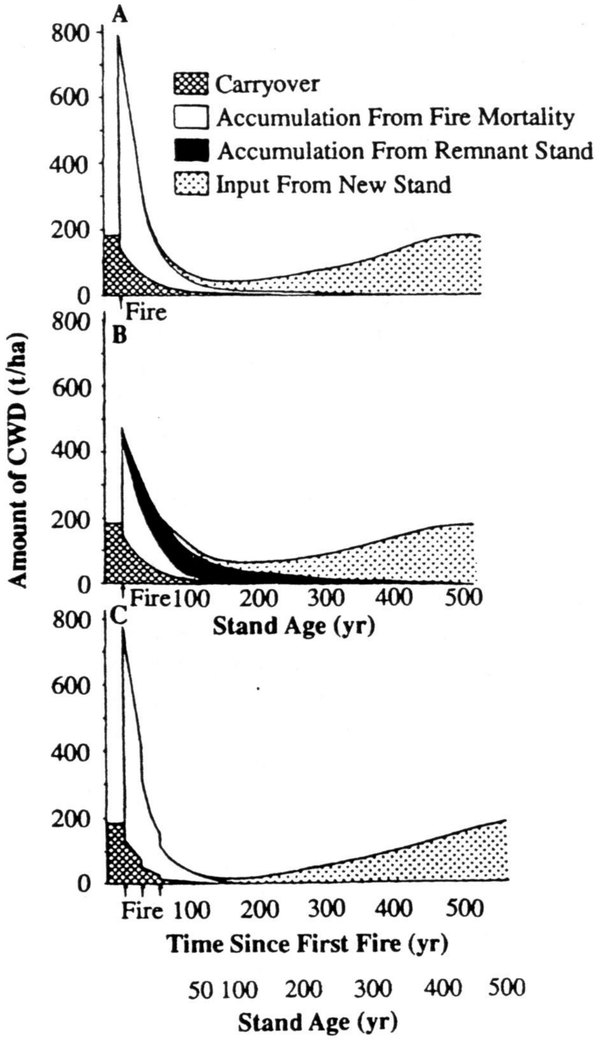

**Figure 2.3** Alternative models of the dynamics of coarse woody debris in stands with different disturbance histories (from Spies et al. 1988).

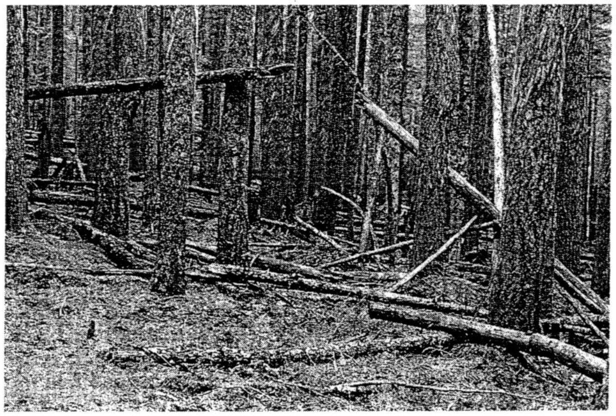

**Figure 2.4** Dense Douglas-fir stand in stem exclusion stage illustrating sparsely developed ground layer of vegetation. (Photo: Thomas Spies)

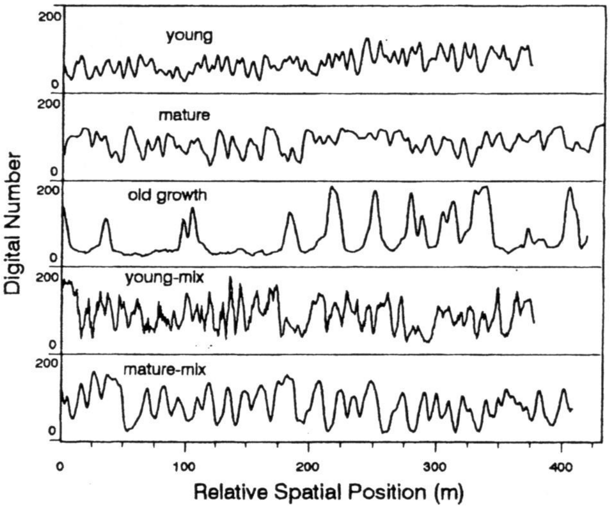

**Figure 2.5** Spatial variability in canopy brightness (digital number) recorded along transects by video camera above five conifer stands of different ages in Oregon. Areas of high brightness are tree crowns and areas of low brightness are gaps in the upper canopy (from Cohen et al. 1990).

eration may provide relatively large canopy openings or gaps that allow understory vegetation to survive and grow in many places in stands (Bradshaw and Spies 1992) (Figure 2.5). Thus, the understory "exclusion" process of this phase may not occur in many stands dominated by shade-intolerants or may be very short-lived as tree canopies rapidly differentiate and open up. Yet, on some very low productivity sites, stands may stagnate in this phase, creating a dense, slowly changing stand of relatively small trees with sparse understory (Oliver and Larson 1990). Typically, however, the number of canopy trees declines during this phase as mortality occurs from competition, diseases, and other disturbances.

Vertical heterogeneity in the vegetation increases rapidly as the height of the forest increases. Canopy

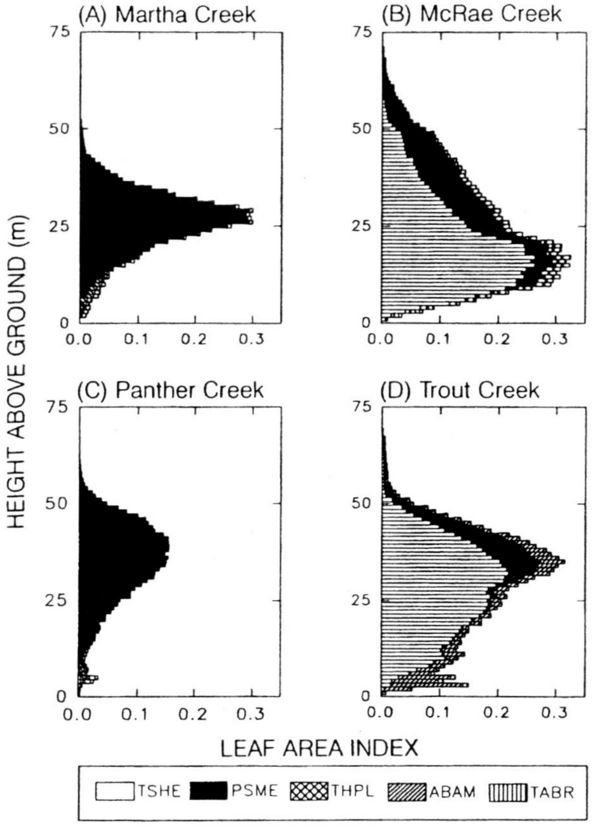

**Figure 2.6** Vertical distribution of leaf area index in two mature stands (A and C) and two old-growth stands (B and D) in Oregon and Washington: TSHE, Tsuga heterophylla; PSME, Pseudotsuga Menziesii; THPL, Thuja plicata; ABAM, Abies amabilis; TABR, Taxus brevifolia (from Easter and Spies 1994).

growth often creates two relatively distinctive vegetation layers: an uppermost layer of canopy trees and a sparse layer of dying and surviving shrubs and herbs (Figure 2.6). The canopy tree layer is composed of dense, rapidly growing tree crowns with high foliage-to-branch-biomass ratios. Not much light penetrates to mid and lower portions of the crowns. In dense stands, lower-side branches in tree crowns die in the low-light environment.

Amounts of wood debris will be variable during this phase. Large well-decayed standing dead and fallen trees may still be present from the preceding stand if it contained many large decay-resistant trees that were not removed or destroyed by disturbance. Canopy trees of the new cohort that die during this thinning phase do not contribute much to the accumulated mass of dead wood because they are relatively small and decay rapidly without decay-resistant heart wood.

### Transition

Stand development following the first two phases is less understood (Oliver and Larson 1990) and has been classified in different ways. Two major phases can be recognized: a transition phase and a steady-state or shifting gap phase (Peet 1992, Spies and Franklin 1995). Of these, the transition phase may be the most variable and least understood. It is marked by a variety of gradual changes in population, stand structure, and vegetation processes that can last from less than 100 to over 1,000 years depending on the forest type and disturbance history. The original cohort of trees slowly breaks up, tree establishment and release of suppressed understory trees increases, and a new cohort of trees gradually grows into the canopy gaps. Tree size, live biomass, and diversity of tree sizes and canopy layers typically peak, while dead wood biomass may decline to a low point before increasing.

Because of the diversity and gradual nature of changes during this stage, it has been subdivided in several different ways. Oliver and Larson (1990) identify an understory reinitiation phase that coincides with the beginning of the transition phase. It is characterized by the appearance and growth of new trees and other plants in the understory. This understory reinitiation phase ends when these newer cohorts of trees begin to reach the overstory. At this point a transition old-growth stage begins. It is characterized by canopies containing trees that established in the understory reinitiation phase and relics from the original establishment phase (Oliver and Larson 1990). When these relic trees finally die, the stand enters a "true old-growth stage" in which all of the live trees in the stand originated from smaller-scale gap disturbances resulting from "autogenic" factors such as pathogens, insects, and wind.

Recent studies and observations of long-lived Douglas-fir forests in the Pacific Northwest suggest that the transition phase may be divided into four subphases based on changes in structure and processes: (1) understory release, (2) maturation, (3) early transition, and (4) old-growth and late-transition old-growth phases (Spies et al. 1988, Spies and Franklin 1991, Spies and Franklin 1995).

In the understory release subphase, existing individuals of shrubs, herbs, and some trees that survived through the thinning phase, either because of their tolerance of low light levels or because of their persistence in microsites with higher light levels, grow and expand from existing roots and rhizomes. This occurs as light levels increase as a result of the numerous small gaps forming in the canopy with the death of weak and suppressed trees. Stands during this subphase may appear as single-storied stands of trees with well-developed shrub and herb layers. In some cases, such as in the salmonberry/alder/conifer stands in coastal Oregon, these well-developed understory layers may inhibit the establishment of new trees from seed.

The maturation subphase begins as overstory trees become more widely spaced, dominant individual trees approach their maximum size, gaps that form from tree death grow larger and more persistent, trees that have established from seed in the previous stage move above the shrub layers, and more tree seedling establishment occurs (Figure 2.7). Dead woody biomass in the stand may be at a low point during this phase because dead wood from the previous stand has lost most of its mass and new inputs of large new trees are just beginning (Spies et al. 1988).

The early transition old-growth phase begins as trees that established during the understory release and maturation stages dominate the upper canopy layers (Figure 2.8). Trees that established during the first establishment phase may still dominate the uppermost layer—such as in old-growth Douglas-fir–western hemlock stands where large Douglas-firs occupy a scattered layer of emergent trees above western hemlock and other shade-tolerants. The presence of remnant trees and new cohorts of trees beneath them and in gaps creates a multilayered foliage canopy that is distinctive of many old-growth types. This phase is also characterized by the buildup of relatively large amounts of dead woody debris as trees from the original cohort die and dead biomass accumulates more rapidly than it is lost from decay processes (Spies et al. 1988). This phase typically requires 100 to over 500 years to develop (Oliver and Larson 1990) for forest types in North America.

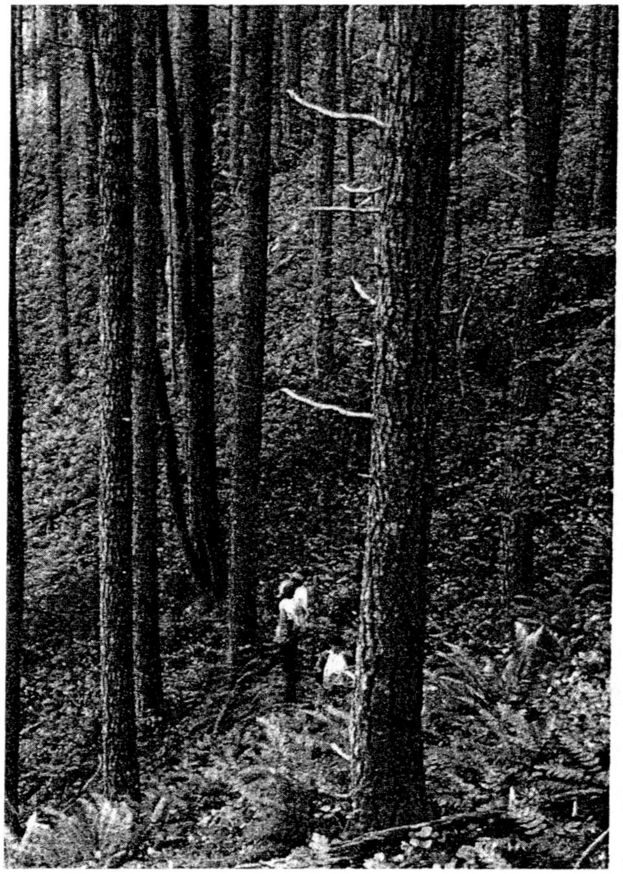

**Figure 2.7** Mature Douglas-fir forest about 130 years old on the Willamette National Forest in Oregon. (Photo: Jerry Franklin)

A late transition old-growth subphase, which may occur following the early transition old-growth phase, is distinguished by the absence of live remnant trees from the establishment phase and the continued presence of dead wood from trees that originated during this phase. This phase may be marked by a lower live biomass relative to the early transition old-growth phase, but with a relatively high mass of dead wood. A late transition old-growth phase is probably most distinctive in forest types with long-lived trees and decay-resistant wood or in climates that result in slow decay. It may last centuries depending on the decay rates of large wood and the frequency of disturbance.

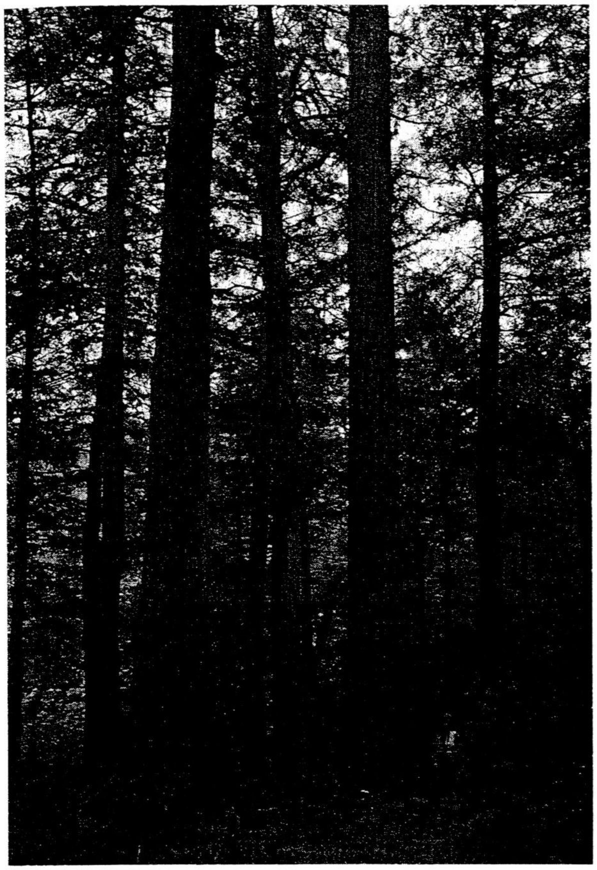

**Figure 2.8** Transition-phase eastern white pine and eastern hemlock old-growth forest in the Upper Peninsula of Michigan. (Photo: Thomas Spies)

### Shifting Mosaic

The last phase that is recognized in most classifications of stand development has been termed the "steady state phase" (Peet and Christensen 1987), "true old growth" (Oliver and Larson 1990), "shifting mosaic" (Borman and Likens 1979) or "shifting gap" (Spies and Franklin 1995). Despite the variety of terms, all authors agree that this last stage is characterized by a shifting pattern of relatively small patchy disturbances (death of individual canopy trees or groups of trees forming gaps of various sizes and shapes) which provide resources for new establishment of trees in the understory and increased height growth of individuals in lower and mid-canopy positions. By aggregating these small disturbances and vegetative responses to a larger spatial area such as a stand, the net changes in forest composition and structure typically appear very small or nonexistent.

This aggregate behavior of small patch dynamics has been frequently described as a steady state or equilibrium. The term "climax" has also been used to characterize a condition similar to this in which vegetation composition and structure are considered stable. However, the term "climax" has fallen out of favor among forest ecologists. It has been used in many different ways (Oliver and Larson 1990), often to mean a simplistic and unrealistic end point of succession that lacks disturbance and is stable. The current view of the last stage of forest development recognizes the occurrence and role of small disturbances and the presence of instability resulting from larger disturbances and climate change. This last phase typically requires many hundreds to over a 1,000 years to develop in a stand that originated following a large, severe disturbance—due to longevity of the trees that form the original cohort and the decay resistance of their wood. Consequently, this phase is uncommon in many current landscapes where logging and natural disturbances occur more frequently than the typical life span of the major tree species.

Structural and compositional differences between this phase and the transition phase are typically small (Spies and Franklin 1991). Variation in live and dead tree size or diversity of size classes may be lower if large seral dominants were present in the previous phase. Composition may shift toward shade-tolerant plants that can regenerate in relatively small canopy gaps. However, where early phases of stand development are already dominated by shade intolerants, composition may not change (Oliver and Larson 1990). As such, the composition of tree regeneration becomes more similar to that of the mature overstory trees (McCune and Allen 1985).

## Variability of Developmental Stages in Space and Time

The four major phases of forest development described above are idealized, and although understanding these stages is often helpful, there is considerable variability in a population of real stands that blurs boundaries (Spies and Franklin 1991). Variation in disturbance history and site productivity, for example, result in stands being composites of two or more phases. In some cases, multiple disturbances may leave patches of several different previous stands, creating a variety of phases mixed within a stand horizontally or vertically or both. Consequently, actual site-specific management practices should be based on actual conditions within stands rather than on broad classes of stand development. The classes may be useful, however, in broad landscape-level planning and mapping.

The temporal pattern of stand developmental stages may also be quite complex—controlled by disturbance regimes and composition of propagules available at critical periods during stand development. Stand dynamics over time in complex landscapes can result in multiple pathways of development (Cattelino et al. 1979) for a given site or landscape (Figure 2.9). Over long periods, these trajectories might assume the patterns of chaotic systems with "strange attractors" (Gleick 1987). In the modern scientific view, with its emphasis on nonequilibrium dynamics, the strange attractors may represent something close to a climax state—a condition toward which stands may move statistically, but not attain for very long (Figure 2.10). In a landscape with a variety of environments, several strange attractors may occur, and under climate change these points may vary over time.

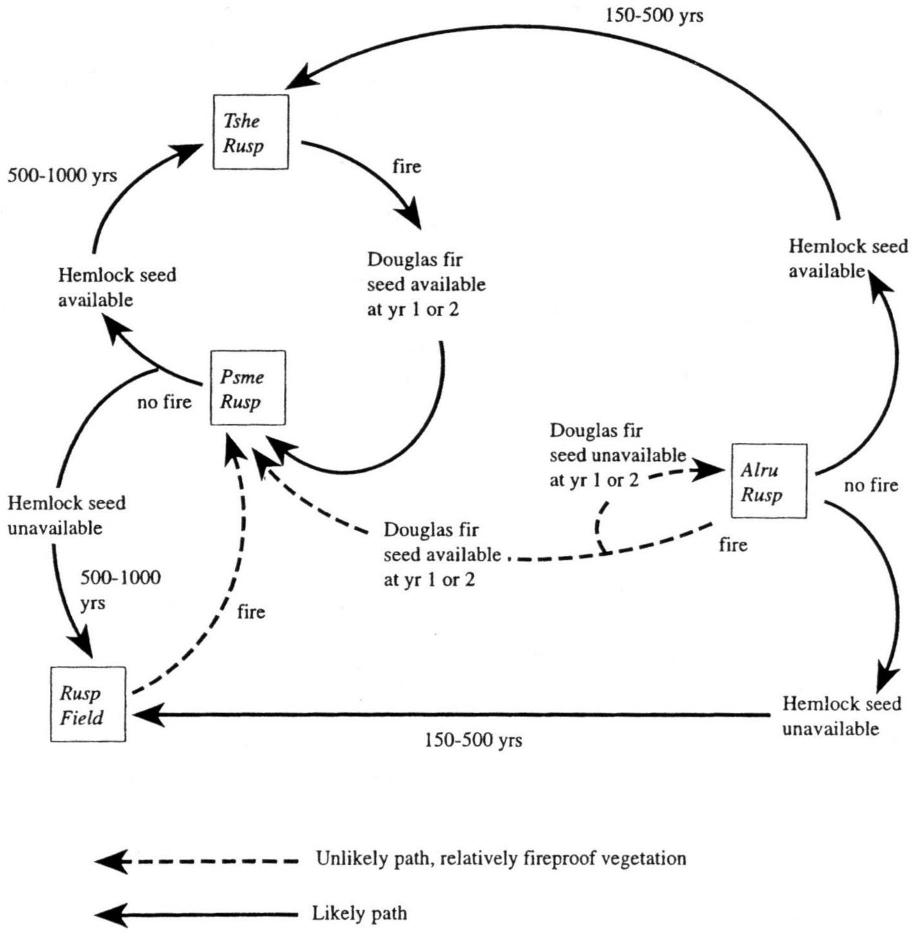

**Figure 2.9** Multiple pathways of forest development in the Coast Range of Oregon. Tshe: Tsuga heterophylla; Rusp: Rubus spectabilis; Alru: Alnus rubra; Psme: Pseudotsuga menziesii (from Hemstrom and Logan 1986).

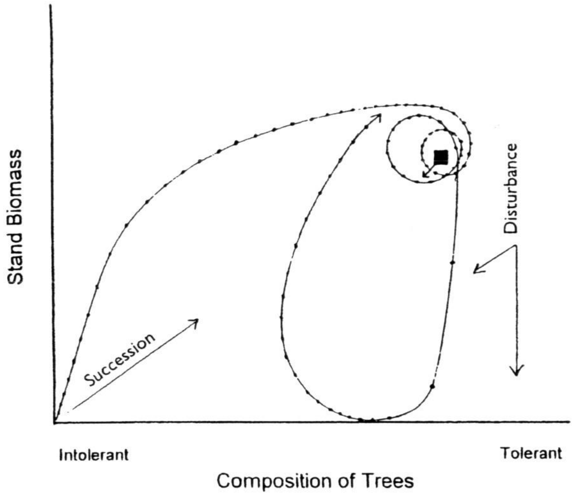

**Figure 2.10** Theoretical phase-state diagram for forest succession. Intervals between points indicate equal time intervals.

## Environmental and Ecosystem Characteristics of Stands

We know much less about the structure and composition of nontree biological communities and ecosystem functions than we do about the tree layer. The general models of stand development described above are based largely on the population dynamics and structure of tree layers. The degree to which this framework translates to other components of ecosystems is not well documented, although we have learned much in the last 15 to 20 years. Where organisms and ecosystem functions are strongly linked to the structure and dynamics of the live and dead tree components of the ecosystem, stand development can be a major driver of ecosystem change over space and time. On the other hand, the patterns of some ecosystem components and functions may be more strongly determined by the physical environment, competition, or accidents of migration and mortality than by stand characteristics.

Despite the relatively poor documentation of the role of stand structure and development in biological diversity and ecosystem function, we have a good conceptual model of stand structure linkages between trees and other biological and ecological characteristics (Peet 1992, Franklin and Spies 1991, Perry 1994).

### Resources and Microclimate

After the death of many trees in an area, a variety of changes occur in the microclimate and resources of stands. Above- and belowground resource availability is characteristically high in the establishment phase. The loss of the canopy layer typically results in more extreme environmental conditions across the patch, such as in temperature, radiation, and soil moisture (Chen et al. 1992). The role of microsites and fine-scale heterogeneity becomes important in modifying the overall climate of the site and creating "safe sites" for the establishment of species that are more sensitive to temperature and moisture extremes and high radiation.

As tree canopies close, available light and moisture near the ground become low. Nutrient availability may be low as well. Microclimates of the understory probably have higher relative humidity and a smaller range of temperatures compared to the extremes of the open establishment phase. However, they may not be as buffered relative to later stages when canopy heights, protective phytomass, and number of foliage layers are greater.

During the transition phase, as tree mortality occurs in the overstory and height and crown growth slow, available light increases in the understory, and belowground resources such as moisture and nutrients may increase as well (Oliver and Larson 1990, Easter and Spies 1994). In later stages of the transition phase, the invasion of the understory and midstory layers by new cohorts of trees results in patchy variation in resource availability from very low levels beneath understory trees to relatively high levels in canopy openings. Canopy gaps may increase in size (Spies et al. 1990, Bradshaw and Spies 1992) between the mature phase and the early transition old-growth phase, although large gaps may also be found in earlier phases. Microclimate variation beneath gaps and canopies can be high, and variation within gaps can control the survival of establishing tree species (Gray and Spies, in press). Surface soil moisture might be lower in the understory release and mature phase compared with the later stages of the transition phase. This is probably due to moisture uptake by well-developed shrub and herb layers in these early phases.

Environmental characteristics of the shifting mosaic phase are poorly known and may differ little from the latter stages of transition. Resources such as available light and moisture are distributed in a spatially heterogeneous manner with high levels in gaps (small areas of the establishment phase) and low levels beneath canopies in small areas of thinning and transition phases (Canham et al. 1990). This mosaic of resources selects for plants and animals that are adapted to relatively small variations in resources and habitat over time, such as organisms with low mobility and greater competitive ability (Bazzaz 1991, Tilman et al. 1994).

### Composition

The high resource availability during the establishment phase allows many understory shrub and herbaceous species that were formerly suppressed by the shade of the tree layer to grow rapidly and increase in biomass and productivity. Flower and fruit production typically increases for many shrubs and herbs. High vegetative productivity, phytomass, and flower and fruit production near the ground increase herbivory and foraging by invertebrates and vertebrates. Many large ungulate species that are adapted to living in forest landscapes find important sources of energy in this phase—particularly where they can venture into it from the protective cover of nearby closed or semiclosed canopy forests (Thomas 1979). Herbivory from invertebrates may also be high during this time (Schowalter 1989). Numerous bird and mammal species forage in stands of this phase of development (Brown 1985).

Vertebrate use of stands during the thinning stage is generally thought to be low relative to earlier and later stages. If understories are sparse, not much cover or food will be available. Dense tree canopies may be used by those species, such as Kirkland's warbler, that find cover and food there (Probst 1987). Canopy epiphytes are less common in younger stands (Spies 1991, McCune 1993).

Vertebrate and invertebrate species may become relatively abundant during the transition phase of forest development in some forest types. For example in Douglas-fir– western hemlock stands in the Pacific Northwest, several species of vertebrates are more abundant in the mature and old-growth phases than in earlier forest development phases (Ruggiero et al. 1991 ). These species include groups that use relatively large dead trees, deep or multilayered canopies, and deep forest floor layers and organic matter–rich soils. Changes in invertebrate communities may also occur during the transition phase, including an increase in the relative abundance of arthropod predators (Schowalter 1989). There is some indication that some species of fungi, lichens, and bryophytes are also more abundant in old-growth forests compared with earlier phases, although quantitative studies are limited (FEMAT 1993).

Little is known about general differences in vertebrate and invertebrate species between the transition phase and the shifting mosaic phase. Differences in animal communities might be expected if vegetative structure and composition of the shifting mosaic phase differ from the transition phase. For example, if large live and standing-dead Douglas-firs drop out of a stand over a long period of time and are replaced by western hemlocks, which have different canopy architectures and snag decay rates, then differences in species that use canopies and standing dead wood might be expected.

### Ecosystem Functions

Following a major disturbance, overall ecosystem biomass and net primary productivity (NPP) are low but increasing rapidly (Peet 1992) (Figure 2.11). During early stages when mineral soil layers are exposed, sediment losses from erosion may be relatively high on steep slopes with high rainfall or where soil particles are fine and winds are high. As vegetation covers the soil surface, these outputs decline rapidly. Soil water and nutrient outputs typically increase during this period and remain relatively high until roots recolonize the belowground environment and leaf area regenerates toward previous levels. On steep slopes that are prone to mass movements because of unstable soils and high precipitation, the loss of the treeroot network may result in mass movements (Swanson and Dyrness 1975).

During the thinning phase, NPP and the rate of carbon sequestration may be very high. However, live biomass, total live and dead biomass, and storage of

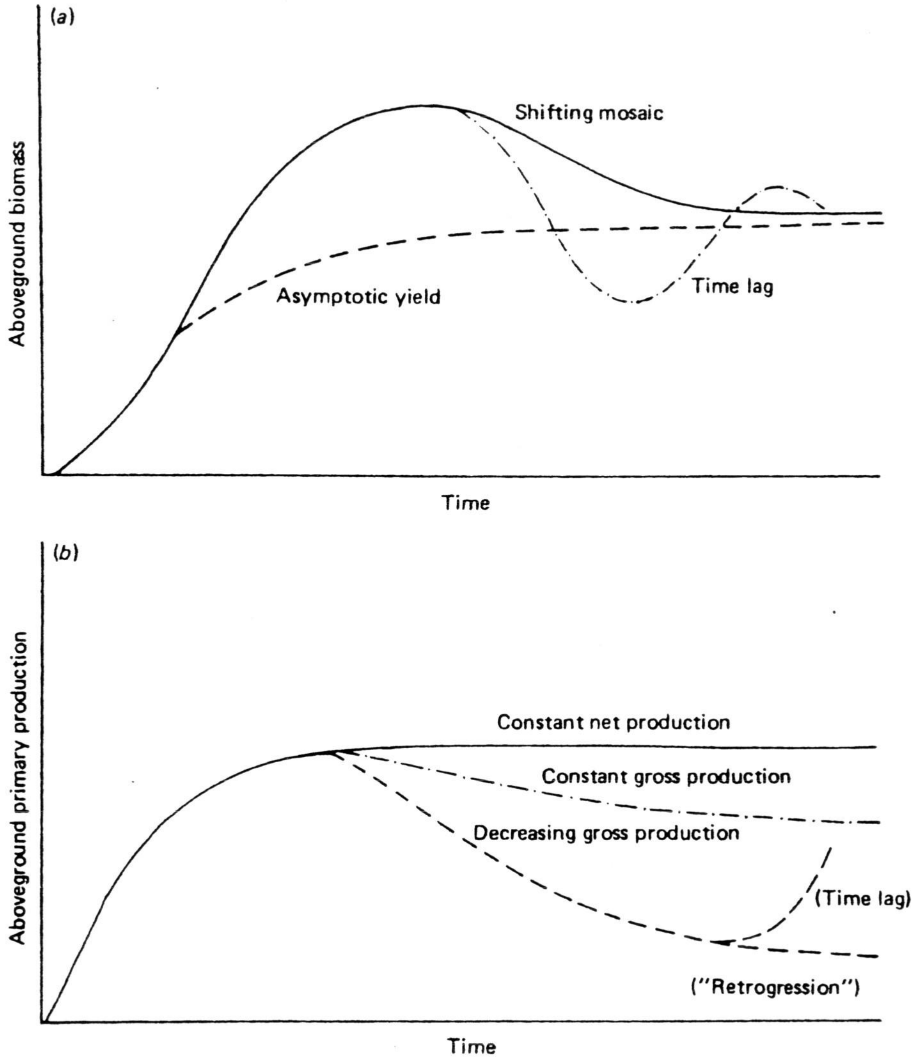

**Figure 2.11** Idealized changes in biomass and net plant yield in relation to time. Curves represent different conceptual models reflecting variability in processes and environment (from Peet 1992 modified from Peet 1981).

carbon are not yet close to their maximum (Harmon et al. 1990). Nutrient losses from stands in this phase are expected to be low because of the rapidly aggrading biomass and near full occupancy of sites by trees (Vitousek and Reiners 1975, Vitousek 1977). Leaf area is thought to peak during this stage (Perry 1994), although few field studies have been made. Herbivory and mortality from pathogens are common in suppressed, weakened trees and may spread to more dominant trees through root grafts. Moreover, dense stands with relatively narrow-diameter tall trees may be more susceptible to breakage from wind and ice.

Live biomass typically peaks during the early part of the transition phase and then may level off or decline as mortality breaks up the dominant canopy of trees and slowly replaces them with tree species with smaller stature (Peet 1981). Carbon storage in live and dead components may also peak during the transition phase (Harmon et al. 1990). Nutrient retention is thought to decline as stands develop from the thinning phase into the transition and shifting mosaic phase (Vitousek 1977) where gaps are more persistent and available nutrients may be exported from the ecosystem following gap disturbances. However, nutrient retention in early transition old-growth Douglas-fir–western hemlock stands appears to be high (Sollins et al. 1980), and sediment outputs from watersheds dominated by transition phase forests appear to be low (Swanson et al. 1982). Tall, deep canopies of transition old growth may intercept more moisture from clouds than the establishment phase (Harr 1982), which lacks deep, well-developed canopies.

Live stand biomass may be lower in the shifting mosaic phase than the transition phase as the proportion of gaps or areas of the establishment phase increases in the stand (Peet 1992, Shugart 1984). Biomass may also be lower if species composition shifts toward lower-stature shade-tolerant species such as occurs in the shift from Douglas-fir to western hemlock. Theoretically, net primary productivity is close to zero because mortality and growth are roughly equal. Nutrient retention is hypothesized to be relatively low during the shifting mosaic phase because biomass and nutrient stores are near equilibrium and therefore inputs roughly equal outputs (Vitousek and Reiners 1975).

Biomass and productivity do not always increase with stand development. In boreal ecosystems, increasing accumulations of organic matter in the forest floor and soil can lead to shallower permafrost and declines in soil productivity and biomass in the latter stages of stand development (Kimmins 1987). In these ecosystems, site productivity typically declines with stand age and is enhanced through disturbances that remove or mix the surface organic matter (Spies et al. 1991).

## Time as a Factor in Forest Compositional Development

The general model of stand development described above views stand development from the perspective of changes in structure, composition, and ecosystem processes associated with tree population dynamics. In this perspective, stands are a dynamic structural template or filter that allows some species to establish and grow while preventing or inhibiting others. Thus, changing structural and environmental templates can result in a changing species composition (Spies 1991, McCune 1993). For many species, however, especially plant species, the most important factor associated with their establishment and growth may simply be the amount of time since the last disturbance that removed the species from the site (Matlack 1994). Populations of these species are typically limited in landscapes and stands more by dispersal than particular stand structures. For example, some understory and epiphytic plant species with limited dispersal capabilities may move across landscapes at rates measured in meters per year (Mesler and Lu 1983). Where disturbance has removed these species from a stand, many decades or centuries may be required for enough propagules to land and successfully establish new populations (Duffy and Meier 1992, Peterkin and Game 1984). While some of these species may be limited by or favored by particular stand structures (such as nurse logs for tree seedlings or particular branch characteristics for epiphytes), many simply may be favored by particular combinations of light, moisture, and nutrients that occur through a variety of structural-environmental pathways. For example, shady moist microsites with high levels of soil organic matter, common in old-growth forests, may be found in very young stands. Similarly, open, relatively exposed areas may be found within the mosaic of vegetation of the shifting gap phase. Some species may function independently of stand development, but may be responding to the same factor as stand development—time.

## Perspectives on Old Growth

Recently, considerable attention has been focused on the ecology, conservation, and management of old-growth forests. Old growth has been described variably in terms of stand structures (Franklin et al. 1981), stand development processes (Oliver and Larson 1990), and a combination of perspectives, including genetic, population, ecosystem, and landscape levels (Spies and Franklin 1995) as well as aesthetic and timber management perspectives. The variety of old-growth definitions is symptomatic of the complexity of forest stand development and the diversity of scientific and societal views of forests. In this chapter, I use the most encompassing simple definition: an ecosystem distinguished by the presence of populations of old trees that is not necessarily in a late-successional condition or free from evidence of human activity. In this definition, "a population of old trees" means the presence of at least several trees that are close to their maximum age for the particular site and climatic conditions and exhibit characteristics of old trees, such as crown and bole senescence, relatively slow growth, and relatively large size for site, species, and climate.

Using this age-based definition, old growth occurs in the last two major phases of stand development (transition and shifting gap). The onset of old growth during the transition phase depends on the species and site conditions; it can occur in as short a span as 50 years or after 500 or more years in forest types of North America. More-detailed, structure-based definitions for specific forest types have been based on tree size, tree composition, amount and size of dead trees, and vertical and horizontal heterogeneity (Old-Growth Definition Task Group). Process-based definitions (Oliver and Larson 1990) have been based on population dynamics of tree cohorts. Both perspectives have advantages and disadvantages. Structure-based definitions are particularly useful for inventory, wildlife habitat, recreation, and timber management. In these situations it is essential to have objectives described in terms of relatively easily measured objects such as the size and species of live trees and dead wood, and vegetation distribution. However, structure-based definitions do not provide information on the processes that created the structures; the same structure may be achieved through different developmental pathways. Furthermore, because of variation across forest types and landscapes, it is difficult to extrapolate structural definitions from one forest type to another without detailed sampling. In most areas of the world, detailed knowledge of old-growth conditions does not exist due to the lack of older forests. In addition, the old growth that does exist in a landscape may have developed from a particular disturbance history under a climate that no longer exists.

Process-based definitions have the appeal of focusing on the way forests develop rather than the way they appear at particular stages. This perspective is valuable in cases where old forest conditions do not currently exist and the objective is to have them in the future. It is also valuable in situations in which management is directed toward maintaining old growth across a landscape as a whole, including maintaining processes within current old-growth stands and insuring that future ones will develop. Process-based definitions also provide a stronger conceptual link with the idea that vegetation is a dynamic entity. On the other hand, it is difficult to incorporate processes into inventory or management based on habitat-suitability models. A particular process, such as the population dynamics of canopy trees or gap-phase reproduction, can lead to very different structures and ecological and management conditions across a diverse forest environment.

## Implications for Forest Management

Forest management is determined by particular human objectives for stands and landscapes. Where these objectives are determined by short-term economic considerations—as they frequently are—the range of stand conditions and silvicultural practices is limited at stand and landscape scales (Davis and Johnson 1987). This has often lead to development of increasingly intensive plantation management practices. Such practices tend to limit the diversity of stand development phases and greatly shorten the time between logging disturbances relative to the potential range of natural structures and disturbance regimes. In many cases, stand development is stopped by clearcut logging somewhere near the end of the thinning phase when tree growth rates begin to level off (Oliver and Larson 1990). In addition, the establishment phase may be shortened by planting trees at high densities and controlling or removing competing vegetation to maximize resources capture by commercial tree species. Precommercial and commercial thinnings also may be applied to control species composition and tree size and obtain intermediate forest products. This type of intensive forest management will tend to produce stands that are structurally and compositionally homogeneous. However, some degree of heterogeneity often develops through patchy mortality of planted seedlings and unwanted and unexpected physical and biotic disturbances such as wind, insects, and disease. Nevertheless, stands that result from intensive timber management are not representative of the full potential range of stand development and variability of a landscape. Moreover, they may not even be close to conditions that occurred prior to forest-use practices of modern industrial economies, especially where plantations of introduced species are used. The implications of differences between intensive forest plantations and more natural stands only can be assessed in terms of a particular forest ecosystem, the management objectives for that ecosystem, and the context of the larger landscape.

Where areas are managed primarily for wood fiber production, differences between managed stands and their wilder predecessors may not be of interest. However, if basic ecosystem processes that maintain long-term site and ecosystem productivity (such as soil organic matter development and disease and insect dynamics) are altered through site-level or landscape-level changes in stand structure and composition, then intensive forest plantation practices may not lead to desirable outcomes even in terms of wood fiber production.

In situations where forest management objectives include maintenance of a broader array of ecological and human values, current intensive forest plantation practices will not meet those objectives. Species, processes, and values associated with the transition and shifting gap phases of stand development will be inhibited or absent within stands managed to maximize wood fiber production. Species and processes associated with the establishment phase may occupy sites for shorter periods of time before canopy closure, although the frequency of this phase of forest development will be greater with short rotations.

This does not necessarily mean that intensive forest management practices are incompatible with multiple forest objectives at a landscape scale. Maintenance of species and ecosystems associated with early and later forest developmental phases can only be assessed over large areas such as landscapes, subregions, and regions. All species are adapted to disturbance and environmental heterogeneity, and all have evolved life history traits that increase population survival in dynamic landscapes. However, some are better adapted than others. Hence the maintenance of many species and processes associated with later phases of forest development is probably a nonlinear function of the amount and distribution of that habitat across the landscape. This means that populations of some species require landscapes that have relatively large proportions or absolute areas of later developmental phases. For example, long-term maintenance of northern spotted owl populations in the Pacific Northwest is expected to require many large forest areas at least 20,000 ha in size that are dominated by multistoried old-growth Douglas-fir–western hemlock forests (Thomas et al. 1990). The overall landscape that spotted owls and other species live in will contain early successional stages and intensively managed stands as well as areas of human development. In landscapes where the maintenance of many forest values is the objective, the challenge to management is to determine the mix and pattern of various stand conditions and disturbance regimes that will meet the diversity of objectives.

It may be possible to modify silvicultural practices at the stand level to meet multiple objectives at landscape and larger scales. For example, thinning in young plantations may decrease the time required to develop large trees and multiple-canopy forests for late-phase species such as the spotted owl. This practice may produce suitable owl habitat in shorter time frames as well as produce some economic benefits from thinnings and mid-rotations instead of very long rotations. It may not, however, produce desired amounts of dead wood or heavy-limbed tree crowns. In addition, for species that are limited by dispersal rather than by particular habitat structures, accelerating the rate of stand development may not help if logging disturbances are too frequent and severe to allow populations of those species to reestablish between major disturbances. These species may benefit from practices such as tree and patch retention designed to reduce mortality through maintenance of refugia. Similarly, allowing for areas of low-severity disturbances within a stand at the time of logging and lengthening rotations are compatible with slow recolonization rates. For some dispersal-limited species, it may be possible to actively move propagules around the landscape. However, this may be practical for only a few species such as some of the canopy lichens.

Given our imperfect knowledge of forest stand structure and function and poor understanding of forest management effects on biodiversity and long-term ecosystem function, it is uncertain how well we can sustain ecosystem values while providing commodity resources. Prudence calls for an adaptive ecosystematic approach that spreads environmental risks across management strategies ranging from reserves to restoration to intensive plantations. The challenge to management is to find the mix of stand and landscape practices that meet biological and social objectives.

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