20

THE DIVERSITY AND MAINTENANCE OF OLD-GROWTH FORESTS

Thomas A. Spies

USDA Forest Service
Pacific Northwest Research Station
Corvallis, Oregon
U.S.A.

Jerry F. Franklin

College of Forest Resources
University of Washington
Seattle, Washington
U.S.A.

The contribution of old-growth forests to biological diversity has only become widely recognized in the last 10 years (Franklin et al. 1981), despite an interest in the ecology of virgin or "wild" forests which has existed among naturalists and ecologists for at least 130 years (Thoreau 1864). On a global scale, the area of old-growth forests has probably steeply declined over the last 2,000 years, although no estimates of past or current amounts of old growth are available. The area of "primary" forest or original forest cover, of which old-growth forests would make up a large part, is estimated to be only 24% of its pre-settled-agriculture amount, and in the United States excluding Alaska, less than 5% of its presettlement amount (Postel and Ryan 1991). In most areas of the world, where old-growth forests are totally gone or exist as fragments in highly altered landscapes, the ecological values of old growth are poorly known. Scientific knowledge of the ecological characteristics of old-growth forests is probably best developed for forests of the Pacific Northwest (Franklin et al. 1981; Ruggiero et al. 1991), and scientific interest in the ecology and conservation and management of old growth is increasing in many parts of the world (Mayer et al. 1987; Kaufmann et al. 1992; Esseen et al. 1992; Botkin and Talbot 1992; Peterkin 1993). In regions lacking old-growth forests, efforts are being made to restore this type of ecosystem (Henderson and Hedrick 1991), typically with very limited information to develop the specific objectives of restoration. Maintenance or restoration of old growth requires a good understanding of forest dynamics and the diversity and ecological roles of all successional stages including old growth. In most

biomes, adequate information about the ecological characteristics of old growth does not exist, especially information about how old growth is distinguished from other forest conditions and how it varies across landscapes and vegetation types.

Understanding the ecology of old growth and maintaining its distinctive biological diversity requires a hierarchical perspective. Biological hierarchies have been expressed in different ways (Rowe 1961; MacMahon et al. 1978; Noss 1990) and we use the framework comprised of genes, species and populations, ecosystems, and landscapes (Noss 1990). Placing old growth in a biological hierarchy provides a more unified concept of old growth and demonstrates how human manipulations at one biological level can affect old-growth values at other levels. Our objectives in this paper are to: (1) review the ecological perspectives on old growth at genetic and physiological, population and species, ecosystem, landscape levels; (2) characterize some of the diversity in types of old growth; and (3) discuss options for the maintenance and restoration of old growth.

PERSPECTIVES AND DEFINITIONS

The term "old growth" has many definitions. To some it is synonymous with "virgin" or "primary" forest, i.e., forests that have never been cut or lack evidence of human activities. To others, old growth is the same as "climax" or "late successional" forests where stand composition is relatively stable. To others, old growth represents an "ancient forest" of very old trees which has spiritual, cultural, and/or ecosystem values. In this paper we begin with a very simple and broad definition of old growth as an ecosystem distinguished by old trees not necessarily (1) in a late successional condition and (2) free of evidence of human activity. Within this broad definition we recognize more restrictive definitions that we hope will encompass most of the ecological perspectives on old growth.

Concepts and definitions of old growth have become more refined in recent years with scientific discoveries and changing societal values. In North America old growth was traditionally defined from a timber production viewpoint as a stand of trees beyond a certain age, or rate of growth. Before old forests became a subject of detailed scientific inquiry, there was little interest in precise definitions or in knowing the amount or distribution of old growth. Since the mid-1970s, old growth has taken on more scientific and political significance, and generic and specific definitions or standards have been developed (Old-Growth Task Group 1986; USDA Forest Service 1989) primarily as tools for inventory and mapping. The specific definitions are typically based on minimum levels of structural features such as large or old live and dead trees, features that can be relatively easily measured in extensive ground-based inventories or in some cases with remote sensing (Cohen and Spies 1992). These precise definitions should be distinguished from general characterizations of old growth which provide the ecological basis of the rather arbitrary inventory standards.

Although inventory of old growth requires common and relatively precise definitions, ecological and management characterizations of old growth will be diverse and hierarchical, a reflection of the complexity of ecosystems and diversity of scientific and societal values. Although the concept of old growth has been too narrowly focused in the past on the age and structure of the trees as a timber crop, the nature of old growth at

genetic, species, population, ecosystem, and landscape levels is strongly controlled by life histories of cohorts of trees, and tree population phenomena. Landscape and ecosystem characteristics, such as disturbance regimes and the physical environment, however, constrain the population, species, and genetic patterns of old growth.

GENETIC AND PHYSIOLOGICAL PERSPECTIVES

The genetic characteristics of old-growth forests have received relatively little attention because most forest genetics research has been oriented toward genetic traits associated with young trees growing in forest plantations and because of the difficulties of studying genetic characteristics that might take centuries to be expressed. From a genetic perspective, a population of old trees in a forest represents a genetic pool that is the product of a long period of intense competition and selection. However, the oldest or most dominant trees in a forest are not necessarily the most genetically superior for a particular trait, because survivorship can be more related to "accidents" of history and site variation than genetically superior traits which increase reproductive success (Oliver and Larson 1990).

The selective pressures shaping the gene pools of trees vary with the growth stage of the individuals and the population (Namkoong and Conkle 1976). In the establishment stage of forest development, genetic patterns can be strongly affected by microenvironmental heterogeneity (Campbell 1979). Following canopy closure, which signifies the beginning of the thinning stage of stand development, cohort competition for resources, weather, and other macro-site factors appear to affect survivorship and control genetic patterns (Namkoong and Conkle 1976). Genetic patterns created by selective pressures in early stages of stand development might still be evident in old-growth populations (Campbell 1979). Consequently, the genetic structure within a population of old-growth trees is the sum of selection forces acting over centuries. Cohorts of old individuals might be genetically distinct from nearby populations of younger trees (Tiegerstedt et al. 1982), if the regeneration is a product of inbreeding. Selection and competition which occur as the population matures, resulting in the death of inbred individuals, are important processes that reduce inbreeding depression in natural populations. The existence of trees in a landscape that have survived into mature and old-growth stages probably help keep the larger population in the landscape well adapted and genetically healthy. However, genetic structure among tree age cohorts might not differ if levels of individual-tree heterozygosity and outcrossing are high (Neale 1985).

The forces of natural selection are hypothesized to decline following the onset of reproduction for many organisms (Olshansky et al. 1993). However, for many tree species that regenerate infrequently, natural selection pressures probably continue into mature and even old ages. As trees age and stand density decreases, mortality results more from "extrinsic" factors such as fire, wind, insects, and diseases than "intrinsic" factors associated within-stand competition for resources (Oliver and Larson 1990). Consequently, any natural selection during the old-growth stage is probably associated with the ability of the individual to withstand disturbance (e.g., thick bark and decay-resistant wood), regenerate dead or damaged parts (e.g., release of dormant buds below damaged stems), or allocate resources to seed production when highly stressed.

The process of senescence or aging in trees is characterized by increases in physiological stresses resulting from the effects of large size on food and water supply to meristems and the accumulation of defects and injuries from the sources mentioned above. These damages accrue, either rapidly or slowly, to a point at which the tree no longer has enough vital structures to regenerate the dead parts and the tree dies. This is a general pattern of degeneration that is found in all organisms, particularly the large, complex ones with sufficient redundancy of vital structures (Gavrilov and Gavrilova 1993) to allow for a period of decline. In large, long-lived species with decay resistant wood, such as Sequoia and Douglas-fir, this period of senescence, or the old-growth stage, can be centuries long. Given that many disturbances, such as fire, which damage or kill canopy trees, can also create opportunities for regeneration, some natural selection probably occurs for the ability to survive these events by growing large, disturbance-resistant structures and surviving disturbances, at least long enough to produce seeds that could colonize the open habitats created by the disturbance. At extreme ages, however, old individuals have little influence on population gene pools (Pianka 1978) because of their low reproductive value relative to more numerous and vigorous younger age classes of trees.

SPECIES AND POPULATION PERSPECTIVES

It is widely recognized that life history characteristics of the tree species play a major role in determining rates and patterns of change during forest succession and stand development (Noble and Slayter 1977). The rate at which old growth develops, the structure and composition of old growth, and the relative stability of old growth will differ as a function of the age of reproduction, shade tolerance, size at maturity, longevity, and reproductive systems of the tree species of a landscape or region. For example, short-lived tree species such as aspen (*Populus* spp.) can reach maturity and old age in 50 years and be completely gone from a site in 150 years, whereas Douglas-fir can take 150 to 250 years to reach maturity and live for another 700 years. Because of their light requirements, neither species can regenerate in small openings left by the death of individual trees, and typically require relatively large and intense disturbances to regenerate.

The dynamics of aggregates of conspecific tree species is a population-level phenomena, with the population characteristics determined by the life history characteristics of the tree species. A general theoretical model of forest dynamics following major disturbances such a large intense fires or clearcutting has been developed and refined by several investigators (Bormann and Likens 1979; Oliver 1981; Peet and Christensen 1987; Mueller-Dombois 1987). In this model, forest development is driven by population process of trees and can be broken into several stages: establishment, thinning, transition, and steady state (Peet and Christensen 1987). These stages are distinguished by growth rates of dominants, mortality rates and causes, origin of the tree cohorts, and importance of small canopy openings to tree regeneration.

Only Oliver (1981) has used the term "old growth" in a forest classification scheme. In his scheme old growth corresponds to the transition and steady-state stages. More recently, Oliver and Larson (1990) have termed these stages "transition old growth" and

"true old growth". In the transition stage, the canopy is dominated by large individuals of the cohort that established following the major disturbance. However, new tree establishment of the same or different species is occurring within the stand and those individuals are growing into intermediate and dominant canopy positions. In the steady-state stage, most or all of the individuals in the initial cohort have died, gap dynamics control growth in the understory and the pattern of canopy tree replacement, and the forest can be viewed as a shifting mosaic of all the stages of stand development.

The general model of forest stand dynamics described above lacks some important details of forest dynamics. Recent research in the Pacific Northwest has indicated that stand dynamics between the end of the thinning stage and the end of the transition stage can be quite protracted and characterized by considerable change (Spies and Franklin 1991) which is obscured by recognizing only thinning and transition stages. In addition, the general model has only focused on the population dynamics of live trees, ignoring the dynamics of dead trees. Dead trees play many important ecological roles (Harmon et al. 1986) in a forest and we propose that the general model of forest dynamics must encompass tree population dynamics over the entire existence of a tree as a biological and ecological structure. Based on these perspectives of forest dynamics, we modify the general model of forest dynamics, with the recognition that it represents an idealized continuum of change.

Establishment Phase

After disturbance new individuals and species establish for some period of time. Dead tree accumulations are typically high and originate in the predisturbance stand and are now declining. The accumulations of dead trees may be relatively low if the predisturbance stand had low numbers or small sizes of live trees.

Thinning Phase

Once canopy closure as occurred, additional establishment might stop or become rare, and the understory might become relatively free of vegetation ("Stem exclusion stage" of Oliver 1981). Mortality resulting from competition among canopy trees eventually leads to increases in understory light levels which allows establishment or growth of surviving individuals of shade tolerant trees, shrubs, and herbs ("Understory reinitiation stage" of Oliver 1981). Accumulations of dead trees are beginning to originate in the post-disturbance stand from thinning mortality although the small stems are typically not persistent. Considerable accumulations of well-decayed dead trees might still occur if carry-over from previous stand was high and decay rates are low.

Mature Phase

During this phase some of the first live structural characteristics of old growth appear, such as relatively large, live trees and local areas of multiple canopy layers. Growth rates of the dominant trees (either single or multiple species) have slowed and trees

begin to approach their maximum height and crown width. Canopy gaps that form from the death of dominant trees do not close from lateral growth of surrounding canopy trees. However, gaps are typically smaller and shade tolerant saplings are less restricted to gaps than in the later phases (Spies et al. 1990). Shade tolerant associates might be regenerating throughout the understory and a few may have reached intermediate canopy levels. Mortality occurs less from inter-tree competition and more from other factors, such as disease or windthrow. The mass of dead wood is typically at a low point and most of the dead wood originating in the pre-disturbance stand is gone (Spies et al. 1988).

Transition Phase

This phase is characterized by a transition from a forest dominated by live and dead trees that established following the initial large disturbance to a forest dominated by live and dead trees that established in the understory and gaps of the developing forest. This phase can be subdivided into early and late stages. In the early stage the canopy is still dominated by a relatively dense stand of large old trees from the cohort that established following the major disturbance. The crowns of the old trees have become large, relatively open and frequently flat-topped with large limbs. Trees that regenerated in the understory have typically increased in density and filled-in the intermediate canopy levels. The numbers and mass of dead trees is building in response to mortality of the large dominants and codominants. In the latter stage of this phase, all or nearly all of the live individuals that made up the original cohort have died. However, the population of dead, relatively large tree boles (standing or fallen or both) from this cohort is close to its maximum density and biomass.

Shifting-Gap Phase

During this stage the live and dead structures of the original tree cohort are gone, and the establishment and growth of the population of live and dead trees results from gap-phase dynamics. The biomass of dead trees has declined from its high levels in the previous phase. Tree death might be less synchronous in space and time than in previous phases and the wood of late successional tree species might decay more rapidly so dead wood amounts might be lower. The forest can be viewed as a relatively fine-grained shifting mosaic of all stages of stand development. Slow changes in forest composition and structure can still occur as a consequence of climatic change or changes in mortality rates or establishment rates among tree species.

The general model of forest stand dynamics described above applies primarily to post-disturbance conditions following catastrophic disturbance, in which all or most of the original stand is killed by the disturbance. Analyses of large disturbances, however, frequently reveal that areas of low to moderate disturbance severity occur where portions of the original stand survive (Zackrisson 1977; Morrison and Swanson 1990; Foster and Boose 1992). In cases of patchy disturbances, the forest can behave as combinations of the above stages occurring the same time and space with varying degrees of interaction between cohorts. For example, a new establishment phase can occur beneath the surviving canopy. The new cohort can proceed through various stages while the surviving cohort

becomes a remnant population which might disappear slowly or rapidly, leaving a patch of forest in a regeneration, thinning or transition stage. Consequently many stands or landscapes following "major" natural disturbances are composed of an overlapping mosaic of tree population patches of different phases. These mosaics retain some of the characteristics of the previous old-growth stages, such as large live or dead trees, and might return more rapidly to the more complex structure of the transition and shifting gap phases than in the case where the disturbance kills or removes all the trees. In the case of the shifting-gap phase of old growth, in which the tree size structure appears to be a result of fine-grained small gap disturbances, analysis of forest age structure and dynamics frequently reveals that these stands have had a history of larger disturbances that is partially obscured by the patchiness of the larger disturbances, differential growth rates of even-aged groups of species, and/or an overlay of smaller disturbances (Foster 1988).

Not all of the latter stages described above occur in a given forest type and some might be very ephemeral. For example, the shifting-gap phase rarely occurs in forest types such as Douglas-fir because it can take 800 to 1000 years for the original tree cohort to die out and another several hundred years for the tree boles to decay. Stand-replacing fires typically occur before this time (Franklin and Hemstrom 1981; Spies et al. 1988). The transition phases can be very short, e.g., a few decades, in some forest types such as *Populus* and *Alnus* where the tree dominants are short-lived and have high decay rates.

ECOSYSTEM PERSPECTIVES

At the ecosystem level we consider the composition, structure, and function of the biological and physical components of old growth. The development of old-growth plant and animal communities relative to younger stand developmental stages is not well known for most groups of organisms. Tree composition of old-growth or late successional forests have been documented for many temperate forests ecosystems (Nichols 191;3, Cline and Spurr 1942; Jones 1945; Habeck 1968; Muller 1982; Peterkin and Jones 1987; Foster 1988). Far less is know about the compositional uniqueness of old-growth forests for other life forms such as non-tree vegetation, vertebrates, and soil and canopy invertebrates (Anon. 1993; Romme et al. 1992). Recent studies in the Pacific Northwest indicate that most vertebrate and plant species do not show differences in abundance between closed canopy forest developmental stages (Ruggiero et al. 1991). However, in the survey, at least 49 plant (including hypogenous fungi and epiphytic lichens) and animal species did occur more frequently in old growth (transition phase) relative to earlier forest stages (thinning and mature phases). Differences in plant communities between old-growth and younger stages or secondary forests have also been observed in other forest types (Peterkin and Game 1984; Whitney and Foster 1988; Romme et al. 1992; Duffy and Meier 1992). Community differences in invertebrates have also been observed (Heliovaara and Vaisanen 1984; Schowalter 1989).

Although old growth might contain plant and animal specialists, it is typically not the stage of highest species richness during stand development. The establishment stage has the highest diversity for plants and mammals (Brown 1985; Schoonmaker and McKee

1988; Spies 1991). Species richness typically declines in the thinning stage and increases again to intermediate levels in the later stages.

The distinctiveness of the plant and animal communities of old-growth forest can be related to changes in resource levels and the spatial patterns of their availability, habitats and structures, and the poor colonizing ability of many old-growth forest species. For plants, the most dramatic resource change involves light levels and patterns in the understory. Light levels under closed canopies of late successional forests can be as little as 2% of full sunlight (Canham et al. 1990). Consequently, many shade intolerant species do not occur or are rare in old-growth forest stands where the canopy is composed of shade tolerant species. Where canopy openings occur, light levels can be high enough to enable shade intolerant plants to exist within the mosaic of old-growth vegetation. In the darkest areas within these forests, mycotrophic plants that lack chlorophyll might find suitable habitat.

Changes in food resources and habitat conditions drive development of old-growth animal communities. Because understories of forests are low light environments, vegetative and fruit production is typically lower than in more open environments. In old growth, the presence of canopy openings can result in higher forage production and quality relative to younger forests with dense continuous canopies (Alaback 1982; Hanley 1984). The presence of large standing dead and fallen trees and multiple layers of vegetation in old-growth stages provides nesting and roosting sites and hiding and thermal cover for many species. Although, large dead trees are not unique to old growth they are far more common relative to earlier developmental stages (Spies et al. 1988). The presence of relatively tall deep canopies provides for vertical niche differentiation and gradient of microclimate from exposed high, radiation environments at the top of the canopy to buffered environments near the forest floor.

Some of the differences observed between old-growth forests and younger forests might result from the slow rate of dispersal and colonization of suitable sites of many forest organisms, such as herbs which might be dispersed by ants or splashes from raindrops. Consequently, for many organisms old-growth forests are ecosystems which simply have had a longer time to accrue forest species than younger forests (Peterkin and Game 1984; Matlack in press). This suggests that accelerating stand development through silvicultural means will not be able to shorten the long time periods required for the development of some components of these old ecosystems.

The maturation, transition, and shifting gap phases of stand development appear to differ in some ecosystem characteristics from the thinning and establishment stages of natural forests and plantations. Relative to younger stages, these later stages of forest development can have more buffering of microclimates (Chen et al. 1993), greater production of food for some consumer organism groups (Ure and Maser 1982; Huff et al. 1992), higher storage of carbon (Harmon et al. 1990), greater inputs of precipitation (Harr 1982) and higher populations of arthropod predators and organisms beneficial to other ecosystems or successional stages (Schowalter 1989). Soil erosional potential is low in transitional old-growth stands (Swanson et al. 1982). Epiphytic nitrogen-fixing lichens, which can be more abundant in old growth (Lesica et al. 1991), can be sources of nitrogen for the ecosystem (Sollins et al. 1980). Ecosystem biomass typically peaks in the transition phase old-growth development and stays relatively high. In some

ecosystem types, such as Douglas-fir-western hemlock, live biomass might decline as the original tree canopy breaks-up and is replaced by a forest of smaller stature (T. Spies, J. Franklin, and Spycher unpubl. data). While net primary productivity might be close to zero in the later stages of forest development, gross primary productivity can be relatively high (Grier and Logan 1977).

Nutrient retention varies through stand development. Highest outputs of nutrients from watersheds occur in the establishment phase and in the shifting-gap phases when net biomass increments are low (Vitousek and Reiners 1975). During the thinning and maturation stages when net biomass increments are high, nutrient outputs are low (Cole et al. 1967). During the transition old-growth phase, nutrient outputs also appear to be low (Sollins et al. 1980), but net biomass accumulation is also low (Grier and Logan 1977). The reason for the retention of nutrients during this phase, despite the low net biomass accumulation, may be net accumulation of detrital components (Sollins et al. 1980; Spies et al. 1988) as the original cohort of trees dies.

LANDSCAPE PERSPECTIVES

The general model of forest dynamics described above has been applied primarily to "stands," i.e., relatively homogeneous patches of vegetation whose areas are typically determined by management considerations (Daniel et al. 1979). In practice, stands usually range from 10s to 100s of ha in size. Although the "shifting-gap" phase of old growth describes a stand mosaic, it is typically applied to a fine-grained, "homogeneous," repeating pattern of different vegetation phases generated by the death of single or small groups of trees.

Old growth cannot be characterized entirely at a single spatial scale, e.g. a stand typical of most forestry cutting units. Vegetation patterns, disturbances and ecological processes occur at both finer and coarser scales (Vitousek and Reiners 1975). In addition, homogeneity is scale-dependent—what appears heterogeneous over small areas might appear homogeneous over large areas. For example, a small watershed can be composed of two very different "stands" based on vegetation structure and development, but over a larger area those two stands can be part of a "homogenous" repeating mosaic of vegetation phases.

In a landscape perspective, old growth is characterized across multiple spatial scales including landscapes (Forman and Godron 1986) and "regional landscapes" (Noss 1983) which are heterogeneous mosaics of interacting ecosystems ranging from 10^1 to 10^7 km^2 in area. Rather than emphasizing homogeneity, as the stand concept does, a landscape perspective emphasizes spatial patterns and heterogeneity. The principles of landscape ecology are not restricted to mosaics of large extent (Forman and Godron 1986), however. Forest mosaics covering small areas (<100 ha) are also composed of interacting ecosystems and can be viewed as "landscapes."

Old growth can be viewed as an element of a larger mosaic of vegetation phases and as the entire dynamic mosaic itself (Mueller-Dombois 1987; Vankat et al. 1991). The first view emphasizes influences of the surrounding forest matrix on the old-growth patches and interactions and movements between the old-growth parts of the mosaic.

For example, microclimate and forest structure of edges of old-growth stands bordering clear cuts might be altered for more than 200 meters into the interior of the stand (Chen et al. 1993).

In the second landscape perspective, the ecological character and function of the entire mosaic is emphasized. Mosaic characteristics, such as kind and proportion of patch types, their sizes, spatial pattern, and stability, affect the behavior of the landscape. In fine-grained mosaics, e.g., shifting-gap old growth, where contacts between patches are frequent because of the high edge to patch area ratio, the taller and more massive older patches can exhibit considerable control over the microclimate, resources, habitat, and function of the younger patches in the mosaic. In coarser-grained mosaics which occur over larger spatial extents, older and younger patches are larger and contacts between patch types are less frequent as a proportion of the mosaic area than in fine-grained mosaics. Consequently, edge effects among stages might have less ecological influence on the dynamics and function of the entire mosaic. However, interactions among patches still occur through processes that operate over greater distances such as dispersal of wide-ranging organisms, disturbance initiation and propagation, and flows of water and materials. In landscapes where old growth exists as patches in a matrix of younger or more homogeneous stand conditions, outbreaks of insects, which originate and spread in a relatively uniform matrix, can threaten the stability of the old-growth islands (Lynch and Swetnam 1984).

The spatial and ecological characteristics of old-growth mosaics will vary as a function of the landscape disturbance regimes including disturbance size, frequency, and intensity. We describe below a classification of old-growth types based on species life history traits and landscape dynamics which might be useful in conserving and managing a broad range of old-growth types.

A LANDSCAPE CLASSIFICATION OF OLD GROWTH

The diversity of old-growth types and ecological perspectives can be organized into a frame-work based on landscape disturbance regimes and species life history characteristics and (Table 20.1). A first division in the classification is based on disturbance patch size which will control the species that can regenerate and the size of area needed to maintain the landscape dynamics. Shade intolerants are restricted to coarse-grained mosaics where light and other resources are typically higher in disturbance patches. Shade tolerants, on the other hand, can regenerate in large or small patches, but tend to be less common in larger patches where they are frequently outcompeted by faster growing intolerants or stressed by environmental extremes.

Examples of coarse-grained old-growth forests include, aspen, lodgepole pine, and Douglas-fir. Examples of fine-grained old-growth forests include those dominated by shade tolerants such as hemlock, beech and maple, and *Picea* and *Abies* spp. Most tree species or groups have the potential to occur as coarse-grained old growth, whereas, the set of species that can occur as fine-grained old growth will be limited to those tolerant of resources levels in small disturbance patches. Waves of old growth can occur as successive populations or communities mature in the same area. Eventually, as small

disturbances occur, the coarse-grained old growth will become fine-grained until a major disturbance intervenes.

A further division of old-growth forests can be made along a gradient of tree or patch longevity (Table 20.1), determined by the interplay between environment, physiology, and genetics. The longevity of a patch of trees has both ecological and management implications. The longer a patch persists the greater its influence will be on the soil characteristics, such as build-up of litter layers and chemical and climatic influences on soil development. Patch conditions that persist a long period of time can also provide more stable habitat and be more likely to be found, and used by less mobile organisms.

Examples of short-lived old-growth forests include coarse-grained types, such as aspen and lodgepole pine, and fine grained types, such as balsam fir or grand fir. In these forest types, old-growth conditions can begin in as little as 50 years and the original tree population can die out in less than 100 years. Consequently, old-growth conditions might persist at the patch level for 50 years or less. Intermediate to long-lived trees such as Douglas-fir, eastern white pine and ponderosa pine can dominate a patch for 400 to 1,000 years.

A third division of old-growth forests can be made on the basis of the type of disturbance that regenerates the canopy trees and/or kill the canopy trees. Disturbances that remove the understory vegetation and litter layers will create very different regeneration environments than those that do not disturb the lower strata of the forests. Old-growth forests in which fire is a frequent component typically have less down woody debris than old-growth forests in which fire is infrequent. Old-growth forests and landscapes, such as Ponderosa pine, which are subjected to frequent low intensity fires, experience a shifting mosaic of safe-sites and canopy openings. Fire helps to clear away competing vegetation and reduce coarse and fine litter for pine establishment (Moir and Dieterich 1988). In the absence of fire, fire-sensitive species such as *Abies* spp. become established and eventually replace the pine.

Table 20.1. Classification of old-growth forest types based on landscape structure and dynamics and tree longevity.

I. Coarse-grained forest mosaics (disturbances >> 0.1 ha)

    A. Short-lived trees (maximum age < 250 years)

        Examples: aspen. red alder. jack pine. black cherry, pin cherry, black spruce

    B. Intermediate to long-lived trees (maximum age >250)

        Examples: Douglas-fir, ponderosa pine. white pine. tulip poplar, longleaf pine

II. Fine-grained forest mosaics (disturbances << 0.1 ha)

    A. Short-lived trees (maximum age < 250)

        Examples: balsam fir, white fir, black spruce

    B. Intermediate to long-lived trees (maximum age > 250)

        1. Fire-frequent forests

           Examples: ponderosa pine. longleaf pine. Douglas-fir

        2. Fire-infrequent forests

           Examples: western hemlock. sugar maple

ACTIVE MANAGEMENT FOR OLD GROWTH AT THE PATCH LEVEL

The maintenance and management of old-growth forests requires consideration of both patch (stand) and landscape (mosaic) level perspectives of old growth. Maintenance of old-growth patches requires that disturbances be infrequent enough that old, relatively large live and dead trees can develop. The time it takes for a single patch to develop old-growth characteristics depends upon the life span of the trees, density of the trees, and productivity of the environment.

Several patch-level approaches are available to retaining or accelerating the development of old-growth characteristics, such as multiple tree sizes, relatively large diameter trunks and crowns, and large dead trees (Nyberg et al. 1987; Spies et al. 1991). The first approach is to use silvicultural systems that do not remove all the structural elements of old growth at the time of cutting. Retaining live and dead trees on cutting units. which imitates natural disturbances more than clearcutting, can help to accelerate the redevelopment of transition and shifting gap stages of old-growth ecosystems. A second cohort of trees then becomes established, either artificially or naturally, beneath the surviving canopy. This approach, which is called green tree retention (Franklin 1989), or irregular shelterwood (Smith 1962), leaves the stand in a higher state of structural diversity so that it will take less time to reach the later stages of stand development than using clearcutting. This silvicultural approach is now being implemented in many areas of the Pacific Northwest and some parts of Sweden, where 5 to 40 trees per ha are left from the previous stand.

Selection systems (Smith 1962) that remove single or small groups of trees can also be used to maintain characteristics of shifting-gap old-growth types on some sites. However, selection management can be difficult to apply in practice (Oliver and Larson 1990), and is not a suitable imitation of natural landscape disturbance regimes for all types of old growth.

Where forest stands have already been regenerated through even-aged methods such as clearcutting, and relatively dense young plantations exist, thinning can be applied to make more resources available to the remaining trees and allow them to attain large dimensions sooner than if the thinning process occurs more slowly. Thinnings would be applied in a patchy manner to provide for horizontal and vertical heterogeneity. Several thinnings can be applied during the lifetime of the stand. However, when trees are relatively large. it is important that thinning be applied in a way that retains or allows development of large standing dead and fallen trees.

MANAGEMENT OF OLD GROWTH AT THE LANDSCAPE LEVEL

Old-growth conservation requires a dynamic landscape perspective. The maintenance of old growth within large areas is dependent the rate, size, pattern, and intensity of disturbances. If the frequency of disturbance is too high, some types of old growth, such as Douglas-fir or ponderosa pine. will not develop in a landscape and if the frequency of disturbance is too low, other types. such as aspen, will be lost from landscapes. If

disturbances are too small, then shade intolerant types of old growth, such as alder or long-leaf pine, will not occur.

The minimum dynamic area of land (Pickett and Thompson 1978) required to maintain a mosaic containing old growth will vary with the disturbance regime of the landscape and the size of patch needed to regenerate the old-growth species. Size of the area will be a function of the number of patches needed to represent compositional and structural diversity of a landscape and the degree of desired degree of stability in the proportions of the different patch types (Shugart 1984). For example, if 100 patches are needed to maintain a quasi-equilibrium, then an area of 10 ha is needed, without considering edge effects, for a fine-grained old-growth type characterized by 0.1-ha disturbance patches, . Whereas, a quasi-equilibrium of 100 patches of coarse-grained old growth characterized by 1,000-ha fire disturbance patches, would require 100,000 ha. Edge effects (Chen et al. 1993; Matlack in press) and the needs of wide-ranging old-growth associated organisms would also affect the area of landscape needed to maintain old-growth conditions.

Old growth is sensitive to the frequency of disturbance in a landscape. In the case of Douglas-fir, a long-lived species, the old phases can persist in landscapes for 500 to 1,000 years. Consequently, many areas of the mosaic must remain free of severe disturbances for 200 to over 500 years, the typical period of development for the ·transitional old-growth phase of this species (Spies and Franklin 1991). The frequency of disturbance to maintain an old-growth aspen landscape, by contrast, would have to be 50 to 100 years depending the productivity of the landscape.

IMPLICATIONS TO CONSERVATION OF OLD GROWTH

The diversity of old-growth types means that conservation, management, and restoration strategies must be tailored to the particular type of old growth. Patch level and landscape level plans and management practices that work for one type might not work well for another. For example, growth types maintained by frequent burning, such as ponderosa pine, will require prescribed burning or thinning every decade to maintain their structure and function (Moir and Dieterich 1988).

The feasibility and opportunities for conservation and management of old growth will vary according to type, remaining amounts, and land ownership patterns. In the Pacific Northwest, where old growth has been rapidly declining but some relatively large areas remain on National Forest lands, old-growth conservation strategies have focused on reserving large existing old-growth areas and maintaining connectivity between them for wide-ranging species such as the Northern Spotted Owl (Thomas et al. 1990; Johnson et al. 1991; Anon. 1993). In these conservation plans, the old-growth reserves are large and numerous enough, that regional amounts of old-growth Douglas-fir will probably be stable for many decades despite the large fires characteristic of this region.

Many forest regions do not currently have large areas of remaining old growth or large, uniform land ownership patterns to facilitate implementation of idealized conservation networks. Where landscapes and ownerships patterns currently allow only

small old-growth areas (<100 ha), it only will be feasible to grow and maintain fine-grained old-growth types. However, even fine-grained types are subject to infrequent coarse-scale disturbances, so their long-term stability is doubtful. If prescribed fire is not allowed or used, then fire-frequent old-growth types cannot be maintained with any size of landscape. If timber rotations are too short, then long-lived old-growth types will not develop. Conversely, where timber rotations are long or natural disturbances are suppressed, then short-lived old-growth types such as aspen will not be common. Biodiversity planning and management will necessarily involve evaluating tradeoffs between different old-growth types.

Although old-growth types have disappeared from most landscapes or are not feasible to maintain or restore over large areas, it is still possible to sustain some elements of biological diversity associated with old growth. This can be accomplished in several ways.

Maintaining Current Areas of Old Growth

In landscapes where old growth is limited, maintaining existing areas of old growth will typically be the best strategy to providing old-growth habitat in the short term (Harris 1984; Thomas et al. 1990; Johnson et al. 1991). This is particularly true of long-lived old-growth types, which are both relatively stable and take long periods to develop. Silvicultural manipulations to existing stands will only degrade the quality of the old growth, and manipulations to young stands to accelerate development of old-growth conditions will not provide for short-term habitat needs.

Providing for Continued Presence of Old Growth

Long-term strategies for old-growth conservation require identifying areas that will provide future old-growth patches and landscapes. This is required from the stand-point of losses of old growth that are deterministic (forest succession) and stochastic (e.g., wild disturbances). Where short-lived old-growth types are desired, the need to plan disturbances, such as cutting or prescribed burning, will be relatively immediate.

Facilitating Dispersal Among Old-Growth Areas

In most forested landscapes, human needs for wood products or other land-uses, will limit the areas available to develop multi-aged forest mosaics. Old-growth areas will probably be fragments of once-larger expanses and some old-growth species may have difficulty maintaining population levels in isolated fragments. Smaller areas of old growth may still be able to support species specializing in old-growth habitats if the ability of those species to move among old-growth areas is not seriously impaired.

Dispersal can be maintained or facilitated through several means: (1) maintain short distances between old-growth reserves or habitat areas; (2) create a general landscape matrix for the reserves in which habitat conditions favor dispersal and reduce the probability of mortality (Thomas et al. 1990); (3) identify landscape areas of old-growth

or similar habitat to serve as corridors and "stepping stones" between old-growth areas (Harris 1984). The relative values of these approaches have received relatively little research attention and should be a high priority for research.

Providing Old-Growth Habitat Elements in Managed Forests

Plantation forestry has traditionally attempted to create relatively uniform, short-rotation forests. This type of managed forest lacks many of the characteristics of old-growth patches and landscapes. Silvicultural practices (Franklin 1989; Spies et al 1991), such as long-rotations, green tree retention, and selection forestry, might be able to maintain old-growth structures and their associated species and functions in managed forest landscapes.

Accelerating the Development of Old-Growth Characteristics

Even where timber objectives are not a concern, silviculture could be used to speed the development of old-growth structures or change the direction of forest succession toward desired old-growth conditions. This might be desirable for landscapes currently lacking old-growth conditions and will require centuries before they develop. For example, many young forest plantations were planted at high densities, which will greatly slow the onset of old-growth structures. Thinning and underplanting in such stands can help to reduce the time for old growth development. In other cases, cutting or prescribed fire could be used to reset the landscape to allow development of coarser-grained or fire-frequent old-growth types.

CONCLUSIONS

Old-growth forests contribute to biological diversity at many levels of the biological hierarchy, from genes to landscapes. Old-growth ecosystems are as diverse as the species and landscapes that mold them. On a given area many stages of forest development will occur over time including several different types and stages of old growth. The types differ in their stability, composition, and stand and landscape structure. All types of old growth share the common element of an aging population or community of trees. The presence of an aging population of trees, the environments created by these trees and the long time-spans following intense disturbances leads to the development of an ecosystem which is distinctive in its composition, structure, and function.

Old growth cannot be maintained without a patch dynamics (landscape) perspective. The rates and sizes of disturbances will determine potential types of old growth in an area. Sustaining elements of biological diversity associated with old growth can be facilitated by: (1) maintaining current areas of old growth; (2) providing areas for replacement of old growth lost to disturbances; (3) facilitating organism dispersal among old-growth areas in landscapes; (4) providing old-growth habitat elements in managed forests; and (5) using manipulations to reduce the time needed to develop old-growth characteristics.

LITERATURE CITED

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeastern Alaska. *Ecology* 63:1932-1948.

Anonymous. 1993. Forest Ecosystem Management: An Ecological, Economic, and Social Assessment. Report of the Forest Ecosystem Management Assessment Team. USDA Forest Service. Government Printing Office 1993-793-071.

Bormann, F. H., and G. E. Likens. 1979. *Pattern and Process in a Forested Ecosystem*. Springer-Verlag, New York.

Botkin D. B., and L. M. Talbot. 1992. Biological diversity and forests. In *Managing the World's Forests. Looking for Balance Between Conservation and Development*, ed. N. P. Sharma, pp. 47-74. Kendall/Hunt Publishing Co., Dubuque, Ia.

Brown, E. R., ed. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. USDA Forest Service, Pacific Northwest Region, Portland, Ore.

Campbell, R. K. 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. *Ecology* 60(5):1036-1050.

Canham, C. D., J. S. Denslow, J. S. Platt, W. J. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20:620-631.

Chen, J., J. F. Franklin, and T. A. Spies. 1993. An empirical model for predicting diurnal air-temperature gradients from edge into old-growth Douglas-fir forest. *Ecol. Modeling* 67:179-198.

Cline, A. C., and S. H. Spurr. 1942. The virgin upland forest of central New England. A study of old growth stands in the Pisgah mountain section of southwestern New Hampshire. *Harvard Forest Bull.* 21.

Cohen, W. B., and T. A. Spies. 1992. Estimating structural attributes of Douglas-fir/western hemlock forest stands from landsat and spot imagery. *Remote Sens. Environ.* 41:1-17.

Cole, D. W., S. P. Gessel, and S. F. Dice. 1967. Distribution and cycling of nitrogen, phosphorus, potassium, and calcium in a second-growth Douglas-fir ecosystem. In *Primary Production and Mineral Cycling in Natural Ecosystems*, ed. H. E. Young, pp. 197-223. University of Maine Press, Orono, Me.

Daniel. T. W., J. A. Helms. and F. S. Baker. 1979. *Principles of Silviculture*. 2nd ed. McGraw-Hill, New York.

Duffy, D. C., and A. J. Meier. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conserv. Biol.* 6:196-201.

Esseen. P. A., B. Ehnstrom, L. Ericson, and K. Sjoberg. 1992. Boreal forests-the focal habitats of Fennoscania. In *Ecological Principles of Nature Conservation. Applications in Temperate and Boreal Environments*, ed. L. Hansson, pp. 252-325. Elsevier, London.

Foster. D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, U.S.A. *J. Ecol.* 80:79-98.

Foster. D. R., and E. M. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *J. Ecol.* 80:79-98.

Forman. R. T. T., and M. Godron. 1986. *Landscape Ecology*. John Wiley and Sons, New York.

Franklin, J. F. 1989. Toward a new forestry. *Am. For.* (November/December):37-44.

Franklin, J. F., and M. A. Hemstrom. 1981. Aspects of succession in coniferous forests of the Pacific Northwest. In *Forest Succession: Concepts and Applications*, eds. D. C. West, H. H. Shugart, and D. B. Botkin, pp. 212-219. Springer-Verlag, New York.

Franklin, J. F., K. Cromack, Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. Gen. Tech. Rep. PNW-118, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Ore.

Gavrilov, L. A., and N. S. Gavrilova. 1993. Fruit fly aging and mortality. *Science* 260:1565.

Grier, C. C., and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* 47(4):373-400.

Habeck, J. R. 1968. Forest succession in the Glacier Peak cedar-hemlock forests. *Ecology* 41:872-880.

Hanley, T. A. 1984. Relationships between Sitka black-tailed deer and their habitat. USDA Forest Service. Gen. Tech. Rep. PNW 168.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. In *Advances in Ecological Research*, Vol. 15, eds. A. MacFadyen and E. D. Ford, pp. 133-302. Academic Press, Orlando, Fla.

Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247:699-702.

Harr, R. D. 1982. Fog drip in the Bull Run municipal watershed, Oregon. *Water Resources Research* 18:785-789.

Harris, L. D. 1984. *The Fragmented Forest*. University of Chicago Press, Chicago, Ill.

Heliovaara, K., and R. Vaisanen. 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. *Acta Forestalia Fennica* 189:5-29.

Henderson, D., and L. D. Hedrick, eds. 1991. Restoration of old growth forests in the Interior Highlands of Arkansas and Oklahoma. Ouachita National Forest and Winrock International Institute for Agriculture Development, Ark.

Huff, M. H., D. A. Manuwal, and J. A. Putera. 1992. Winter bird communities in the southern Washington Cascade Range. In *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*, tech. coords. L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, pp. 207-220, Gen. Tech. Rep. PNW-GTR-285, USDA Forest Service, Portland, Ore.

Johnson, K. N., J. F. Franklin, J. W. Thomas, and J. Gordon. 1991. Alternatives for management of late-successional forests of the Pacific Northwest. Report to the Agriculture Committee and the Merchant Marine and Fisheries Committee of the U.S. House of Representatives. Washington, D.C.

Jones, E. W. 1945. The structure and reproduction of the virgin forest of the north temperate zone. *New Phytol.* 44:130-148.

Kaufmann, M. R., W. H. Moir, and W. W. Covington. 1992. Old-growth forests: what do we know about their ecology and management in the southwestern and Rocky Mountain regions. In *Old-growth Forests in the Southwest and Rocky Mountain Regions, Proceedings of a Workshop*, tech. coords. M. R. Kaufmann, W. H. Moir, and R. L. Bassett, pp. 1-11. USDA Forest Service GTR RM-213, Fort Collins, Colo.

Lesica, P., B. McCune, S. V. Cooper, and W. S. Hong. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Can. J. Bot.* 69:1745-1755.

Lynch, A. M., and T. W. Swetnam. 1992. Old-growth mixed-conifer and western spruce budworm in the southern Rocky Mountains. In *Old-growth Forests in the Southwest and Rocky Mountain Regions, Proceedings of a Workshop*, tech. coords. M. R. Kaufmann, W. H. Moir, and R. L. Bassett, pp. 81-99. USDA Forest Service GTR RM-213, Fort Collins, Colo.

MacMahon, J. A., D. L. Phillips, J. V. Robinson, and D. J. Schimpf. 1978. Levels of biological organization: an organism-centered approach. *BioScience* 28:700-704.

Matlack, G. R. In Press. Plant species mobility determines the composition of the understory in a fragmented forest landscape in eastern North America. *Ecology*.

Mayer, H., K. Zurigl, W. Schrempf, and G. Schlager. 1987. Urwaldreste, Naturwaldreservate und schutzenswerte Naturwalder in Osterterreich (Old-growth remnants, natural forest reserves

and natural forests of protection-value in Austria). Institut fur Waldbau, Universitat fur Bodenkultur, Wien.

Moir, W. H., and J. H. Dieterich. 1988. Old-growth ponderosa pine from succession in pine-bunchgrass forests in Arizona and New Mexico. *Natural Areas J.* 8:17-24.

Morrison, P. H., and F. J. Swanson. 1990. Fire history in two forest ecosystems of the central western Cascade Range, Oregon. Gen. Tech. Rep. PNW-GTR-254 USDA Forest Service, Pacific Northwest Research Station, Portland, Ore.

Mueller-Dombois, D. 1987. Natural dieback in forests. *BioScience* 37:575-583.

Muller, R. N. 1982. Vegetation patterns in the mixed mesophytic forests of eastern Kentucky. *Ecology* 63:1901-1917.

Namkoong, G., and M. T. Conkle. 1976. Time trends in genetic control of height growth in ponderosa pine. *For. Sci.* 22:2-12.

Neale, D. B. 1985. Genetic implications of shelterwood regeneration of Douglas-fir in southwestern Oregon. *For. Sci.* 31:995-1005.

Nichols, G. E. 1913. The vegetation of Connecticut. II. Virgin forests. *Torreya* 13:199-215.

Noble, I. R., and R. O. Slayter. 1977. Post-fire succession of plants in Mediterranean ecosystems. In *Proc. Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems,* eds. H. A. Mooney and C. E. Conrad, pp. 27-63. USDA Forest Service. Gen. Tech. Rept. WO-3, Washington, D.C.

Noss, R. F. 1983. A regional landscape approach to maintain diversity. *BioScience* 33:700-706.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.* 4:355-364.

Nyberg, J. B., A. S. Harestad, and F. L. Bunnel. 1987. "Old growth" by design: managing young forests for old-growth wildlife. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 52:70-81.

Old-Growth Definition Task Group. 1986. Interim definitions for old-growth Douglas-fir and mixed-conifer forests in the Pacific Northwest and California. Research Note PNW-447. USDA Forest Service, Pacific Northwest Research Station, Portland, Ore.

Oliver, C. D. 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.* 3:153-168.

Oliver, C. D., and B. C. Larson. 1990. *Forest Stand Dynamics.* McGraw-Hill, New York.

Olshansky, S. J., B. A. Carnes, and C. K. Cassel. 1993. Fruit fly aging and mortality. *Science* 260:1565-1566.

Peet, R. K., and N. L. Christensen. 1987. Competition and tree death. *BioScience* 37:586-595.

Peterkin, G. F. 1993. *Woodland Conservation and Management.* 2nd. ed. Chapman and Hall, London.

Peterkin, G. F., and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *J. Ecol.* 72: 155-182.

Peterkin, G. F., and E. W. Jones. 1987. Forty years of change in Lady Park Wood: the old growth stands. *J. Ecol.* 75:477-512.

Pianka, E. R. 1978. *Evolutionary Ecology.* 2nd ed. Harper and Row, New York.

Pickett, S. T. A., and J. N. Thompson. 1978. Patch dynamics and the design of nature preserves. *Biol. Conserv.* 13:27-37.

Postel, S., and J. C. Ryan. 1991. Reforming Forestry. In *State of the World, 1991,* ed. L. R. Brown, pp. 74-92. W. W. Norton, New York.

Romme, W. H., D. W. Jamieson, J. S. Redders, G. Bigsby, J. P. Lindsey, D. Kendall, R. Cowen, T. Kreykes, A. W. Spencer, and J. C. Ortega. 1992. Old-growth forests of the San Juan National Forest in southwestern Colorado. In *Old-growth Forests in the Southwest and Rocky Mountain Regions. Proceedings of a Workshop,* tech. coords. M. R. Kaufmann, W. H. Moir, and R. L. Bassett, pp. 154-165. USDA Forest Service GTR RM-213, Fort Collins, Colo.

Rowe, J. S. 1961. The level-of-integration concept and ecology. *Ecology* 42:420-427.

Ruggiero, L. F., L. C. Jones, and K. B. Aubry. 1991. Plant and animal habitat associations in

Douglas-fir forests of the Pacific Northwest: An Overview. In *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*, tech. coords. L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, pp. 447-462. Gen. Tech. Rep. PNW-GTR-285, USDA Forest Service, Portland, Ore.

Schoonmaker, P., and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *For. Sci.* 34(4):960-979.

Schowalter, T. D. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. *Can. J. For. Res.* 19:318-322.

Shugart, H. H. 1984. *A Theory of Forest Dynamics*. Springer-Verlag, New York.

Smith, D. M. 1962. *The Practice of Silviculture*. 7th ed. John Wiley and Sons, New York.

Sollins, P., C. C. Grier, F. M. McCorrison, K. Cromack, Jr., R. Fogel, and R. L. Fredriksen. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. *Ecol. Monogr.* 50(3):261-285.

Spies, T. A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Washington and Oregon. In *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*, tech. coords. L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, pp. 111-121. Gen. Tech. Rep. PNW-GTR-285, USDA Forest Service, Portland, Ore.

Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature and old-growth forests in Washington and Oregon. In *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*, tech. coords. L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. F. Huff, pp. 91-121. Gen. Tech. Rep. PNW-GTR-285, USDA Forest Service, Portland, Ore.

Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* 20:649-658.

Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69(6):1689-1702.

Spies, T. A., J. Tappeiner, J. Pojar, and D. Coates. 1991. Trends in ecosystem management at the stand level. *Trans. N. Am. Wildl. Nat. Res. Conf.* 56:628-639.

Swanson, F. J., R. L. Fredricksen, and F. M. McCorrison. 1982. Material transfer in a western Oregon forested watershed. In *Analysis of Coniferous Forest Ecosystems in the Western Unite States*, ed. R. L. Edmonds. US/IBP Synthesis Ser. 14. Hutchinson Ross Publishing Co., Stroudsburg, Pa.

Tiegerstedt, P. M. A., D. Rudin, T. Niemela, and J. Tammisola. 1982. Competition and neighbourouring effect in a naturally regenerating population of scots pine. *Silvae Fennica* 16:122-129.

Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the northern spotted owl. USDA Forest Service and USDI National Park Service, Portland, Ore.

Thoreau, H. D. 1864. *The Maine Woods*. Ticknor and Fields, Boston, Mass.

Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. *Can. J. Zool.* 60:3307-3315.

USDA Forest Service. 1989. Generic definition and description of old-growth forests. Report on file at PNW Research Station, Forestry Sciences Laboratory, Corvallis, Ore.

Vankat, J. L., J. Wu, and S. A. Fore. 1991. Old growth forests by design: Applying the concepts of landscape ecology. In *Restoration of old growth forests in the Interior Highlands of Arkansas and Oklahoma*, eds. D. Henderson and L. D. Hedrick, pp. 153-177. Ouachita National Forest and Winrock International Institute for Agriculture Development, Ark.

Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: A hypothesis. *BioScience* 25(6):376-381.

Whitney, G. G., and D. R. Foster. 1988. Overstorey composition and age as determinants of the understorey flora of woods of central New England. *J. Ecol.* 76:867-876.

Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. *Oikos* 29:22-32.