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DOUGLAS-FIR FORESTS

Managing for Timber and Mature-Forest Habitat

Millions of acres once dominated by mature and old-growth forests in western Oregon and Washington have been clearcut and are now dominated by young plantations. The point in stand development at which plantations might meet the needs of wildlife species associated with mature forests is unknown. Yet with rotations decreasing to 40 years in places and harvestable tree size declining (Sessions 1990), some plantations may not provide, prior to harvest, the structural and compositional features used by some mature-forest species. For example, designated conservation areas (DCAs) for northern spotted owls contain many acres of young plantations that may not provide suitable nesting or foraging habitat for 80 years or more (Thomas et al. 1990, US Department of the Interior 1992). Pressures to remove timber on remaining lands may be high in order to reduce the economic impact of spotted owl protection (Greber et al. 1990).

Alternative silvicultural systems should be tested to determine if timber extraction can be accomplished while meeting habitat needs of wildlife species associated with mature forests. This article describes a conceptual basis for silvicultural systems that integrates mature-forest wildlife habitat and timber objectives in managed Douglas-fir (*Pseudotsuga menziesii*) forests of western Oregon and Washington. Specifically, it describes the structural and compositional features of stands associated with abundance of mature-forest wildlife; the influence of natural disturbances and past

management practices; how silviculture may be used to more closely imitate the frequencies, sizes, shapes, intensities, and patterns of natural disturbances in these forests; and how silvicultural systems that provide these features can be developed and tested.

Historical Perspective

Most Pacific Northwest forest managers have regenerated stands by clearcutting during the past 50 years, although a form of selection cutting was tried earlier (Isaac 1956). In the 1930s, diameter-limit cutting (which removed about 35% of the volume in old-growth stands) produced mixed results in western Oregon and Washington Douglas-fir forests (Isaac 1956). Some stands sustained high damage to residual stems, especially to thin-barked species, and some had high levels of windfall after harvest (Munger 1950). Several stands exhibited decreased or stable growth rates following cutting (Munger 1950). For a number of reasons, including the failure of diameter-limit cutting to meet timber objectives and the risks of inadequate natural regeneration (Cleary et al. 1978), clearcutting and planting with Douglas-fir became the primary method of stand regeneration by the early 1940s.

Following passage of the National Forest Management Act of 1976 and pursuant regulations, land managers on national forests faced a new set of management objectives, including maintenance of biological diversity. Special treatments (such as retention of 1-2 trees or snags per acre) were designed to mitigate the loss of mature forest habitat (Neitro et al. 1985). In the more recent new forestry practices (Franklin 1989) trees, snags, and logs are retained during harvest with

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the intent of carrying these features through the next rotation. This and other alternatives to traditional plantation management need to be evaluated as to how effectively they will provide habitat for mature-forest wildlife.

Mature-Forest Habitat Characteristics

Species associated with mature stands seem to be associated with certain abiotic features—soils, topography, elevation—and biotic structures—large trees of several species; multilayered canopies; large snags and logs; and deep forest floor litter (Ruggiero et al. 1991). Although many species use these structures (Brown 1985), the abundance of some species has been found to be associated with them (Ruggiero et al. 1991), implying ecological dependency. No studies seem to have established cause and effect relationships; until these relationships can be quantified through experimentation, an objective of a stand-level silvicultural system should be to produce habitat structures associated with the abundance of vertebrates and a complementary, integrated design over the landscape.

Large trees. Douglas-fir larger than 40 inches dbh are associated with the presence of nesting marbled murrelets (Singer et al. 1991) and northern spotted owls (Forsman et al. 1984). Spotted owls usually nest in broken-topped snags and trees larger than 30 inches dbh (Carey 1985), although they can use platforms in smaller trees, especially in mixed-conifer forests. Large trees add to the vertical structure within a stand, and bird diversity is associated with vertical complexity in other forest types (MacArthur and MacArthur 1961). Douglas-firs larger than 40 inches dbh are more abundant in old-growth (more than 200 years, $\bar{x}=7.7/\text{acre}$) and mature (80–195 years, $\bar{x}=1.0/\text{acre}$) stands than in naturally regenerated young (40–79 years, $\bar{x}=0.2/\text{acre}$) stands (Spies and Franklin 1991). Many old-growth Douglas-fir stands in the Coast Range and Cascades of Oregon and Washington exhibit an inverse-J diameter distribution (US Department of the Interior 1992). This size-class distribution also contributes to the vertical distribution of foliage layers. Large trees can add large surfaces of deeply fissured or scaly bark that are used by bark-foraging birds (Peterson et al. 1989) and can support epiphytes eaten by northern flying squirrels (Maser et al. 1981).

Oregon white oaks (*Quercus garryana*) and bigleaf maples (*Acer macrophyllum*) larger than 20 inches dbh produce more natural cavities and large dead limbs (elevated snags) than conifers (Gumtow-Farrior 1991). Pacific madrone (*Arbutus menziesii*) also is cavity-prone (Raphael 1987). Hardwoods and shrubs provide forage, fruits, and foliar insects that are food resources for many vertebrates (Martin et al. 1951).

Large dead wood. About 100 species of vertebrates use snags and 150 use logs (Brown 1985), though use varies by size and decay class. Snags larger than 20 inches dbh are more abundant in old-growth ($\bar{x}=4.9/\text{acre}$) than in mature ($\bar{x}=2.5/\text{acre}$) or young ($\bar{x}=2.3/\text{acre}$) unmanaged stands (Spies and Franklin 1991). Although cavity-nesting birds use snags (Neitro et al. 1985, Nelson 1989, Marcot 1991), there is little quantitative information for other species, especially log-users. High proportions of clouded salamanders and Oregon slender salamanders were captured in or under bark on logs in Oregon forests (Bury and Corn 1988). The abundance of marsh shrews correlated positively with log densities in Oregon (Corn et al. 1988). Old-growth Douglas-fir forests typically have more than 13.8 tons/acre of dead and down logs (Franklin and Spies 1991).

Deep litter. Forest floor and below-ground conditions probably influence habitat quality for ground-foraging and burrowing species. Some terrestrial mammals and amphibians are primarily active below-ground during the summer. For instance, roughskin newts use logs and burrow systems of voles and shrews as summer daytime refugia. Other species use the burrow systems of mountain beaver (*Aplodontia rufa*) and pocket gophers (*Thomomys* spp.) (Maser et al. 1981), animals that also kill some conifer regeneration and may maintain small semipermanent openings in otherwise homogeneous stands. Litter depth was positively associated with the number of marsh shrews (Corn et al. 1988). The litter layer is deeper in old-growth ($\bar{x}=21$ mm) than in mature ($\bar{x}=14$ mm) or young ($\bar{x}=15$ mm) stands (Spies and Franklin 1991).

Species-Habitat Matrix Approach

Because each species has its own habitat requirements and hence responds differently to various silvicultural practices, managers need tools to predict these re-

sponses. In developing silvicultural systems for mature-forest species, an ideal first step is to determine the sizes and numbers per unit area of habitat structures needed to support self-sustaining populations of each species and then sum the structures over the species in the community—such as Neitro et al. (1985) did for cavity-nesters. Information on animal habitat associations may guide silvicultural prescriptions for some species that use mature and old-growth Douglas-fir forests of western Oregon and Washington for at least part of their life cycle (Brown 1985, Ruggiero et al. 1991). Unfortunately, quantitative relationships are lacking for many species. For instance, snags are used by bats and logs by shrewmoles, tailed frogs, and clouded salamanders; but data are insufficient to predict the needed snag and log density to support sustainable populations (Brown 1985). Information is unavailable to set habitat goals for species associated with forest floor litter and burrows.

An alternative is to provide habitat for indicator species and assume that meeting the needs of one or several species in a guild (a group of species that share similar resources) will meet the needs of all others in a guild. But Mannan et al. (1984) suggested that this may not be a valid assumption. Until data are available on optimal habitats for each species, new silvicultural approaches—based on natural disturbances, large conifers and hardwoods, dead wood, and litter—should be developed and tested. Incorporating key habitat features into silvicultural prescriptions can test hypotheses regarding the relationships between abundance of these features and abundance of the species they are predicted to support.

Natural Disturbance in Douglas-Fir Forests

Disturbances occur over a range of spatial scales, from coarse (thousands of acres) to fine (less than 1 tree height in width). Coarse- and fine-scale disturbances have affected the establishment, development, and at times destruction of unmanaged Douglas-fir forests. Data from stands sampled during the Old-Growth Habitat Relationships Program (Ruggiero et al. 1991) illustrate how disturbances influence the presence and abundance of habitat features (table 1). "Patch" describes a homogeneous unit of vegetation that is different from the ma-

Table 1. Comparison of natural disturbances and three silvicultural systems that consider both timber removal and mature-forest wildlife in Douglas-fir forests.

Disturbance characteristic	Natural disturbances		Managed stand		
	Coarse	Fine	Coarse		Fine
			Single-story	Few-storied	Many-storied
Generalized size					
Patch ¹ (acres)	>10	<0.5	>10	>10	0.5–2
Stand ² (acres)	>10	>10	>10	>10	>10
Stand-scale intensity					
Residual live trees	Low–moderate	High	Low	Moderate	High
Residual dead wood	Moderate–low	High	Low	Moderate	Moderate–high
Range of tree cover throughout cycle (%)	10–95	70–90	10–95	25–95	50–90
Frequency rate (% of stand disturbed/year)	0.5–1.0	0.1–0.8	1.3	0.4/1.5 ³	0.5–1.0
Return frequency to disturbed portions	100–500+	100–500+	75 ⁴	75/140 ³	100–200
Harvest entries/100 yrs			1–2	1–2	4–10

¹Area disturbed.

²The area that includes the patch.

³Overstory/understory.

⁴Some residuals may be left to develop a sparse emergent layer.

trix in which it occurs. Patches may occur at many scales: a canopy gap is a patch within a stand, and a stand is a patch within a landscape.

Coarse-scale disturbances. Except in coastal forests, fire was the most frequent and widespread coarse disturbance at scales up to 250,000 acres. The fire regime of the western Douglas-fir region is complex and includes varying frequencies, intensities, sizes, and patterns. Return frequencies for stand-replacement fires range from about 450 years at Mount Rainier National Park (Hemstrom and Franklin 1982) to 200 years in the central Oregon Cascades (Morrison and Swanson 1990). Smaller ground fires return more frequently—every 100–150 years (Stewart 1986, Morrison and Swanson 1990).

The first diagram in *figure 1A* shows the diameter distribution of a natural one-story, 100-year-old stand in the southern Oregon Cascades. A severe fire probably killed most trees in the previous stand, initiated establishment of Douglas-fir and western hemlock seedlings, and caused the hardwoods to sprout. This stand will probably develop old-growth structure at 150–250 years in the absence of management (Spies and Franklin 1988). Snags and logs probably increased following the fire, and will decrease until gap disturbances produce large dead wood late in stand development (Spies et al. 1988).

Lower-intensity fires usually killed trees in smaller patches (1–100 acres). For instance, the old-growth, few-storied stand in the Oregon Coast Range (the

first diagram in *figure 1B*) probably developed after such a fire, followed by new tree establishment in the burned patches. A stand of various tree sizes and large snags produced a multilayered canopy sooner than in the one-story scenario, perhaps in as little as 80–100 years; inputs of dead wood were more constant (Spies et al. 1988).

Wind may cause either coarse- or fine-scale disturbances. Areas of high wind, such as the Pacific Coast and the Columbia River Gorge, can produce large windfall after a small part of a stand is opened. Wind fetch along the windward edge of a stand increases as the stand progressively blows down (Ruth and Yoder 1953). Elsewhere, wind disturbance usually consists of single trees or small patches (less than 10 acres) of broken or blown-over trees. Rarely are all trees blown over, and large amounts of dead wood remain (Spies et al. 1988).

Fine-scale disturbances. The diameter distribution of a natural old-growth, many-storied stand in the southern Oregon Cascades (*fig. 1C*) was probably produced by fine-scale disturbances such as suppression mortality, root rots (*Phellinus* spp.), localized windthrow, and light ground fires. These disturbances led to the death of individual or small groups of trees, producing an inverse J-shaped distribution typical of an uneven-aged stand.

Gap formation rates are relatively low in old-growth Douglas-fir stands compared to other old-growth forest types (Runkle 1985). Canopy gaps are the sites of snag and log production and tree re-

generation in mature stands, particularly for shade-tolerant species that can be released by gap formation (*table 2*, Stewart 1986, Spies et al. 1990). Mortality rates for dominant trees more than 36 years old in a 500-year-old Douglas-fir/western hemlock stand were 0.75%/year, but mortality was balanced by recruitment of shade-tolerant species (Franklin and DeBell 1988). Gaps might be slow to fill, however, because more than 70% of old-growth canopy trees die without exposing bare mineral soil (Spies et al. 1990, Franklin and DeBell 1988), so existing shade-tolerant shrubs may dominate.

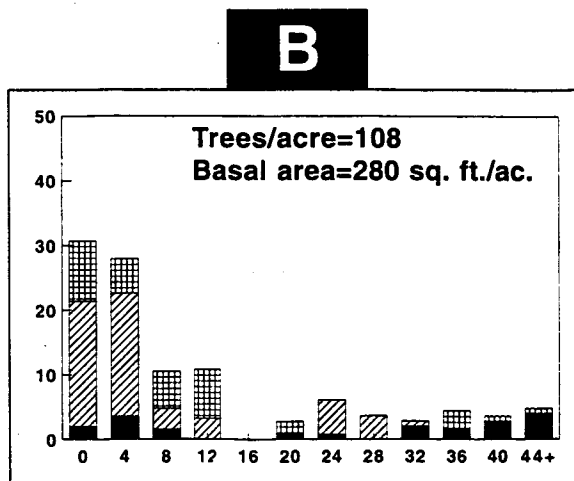
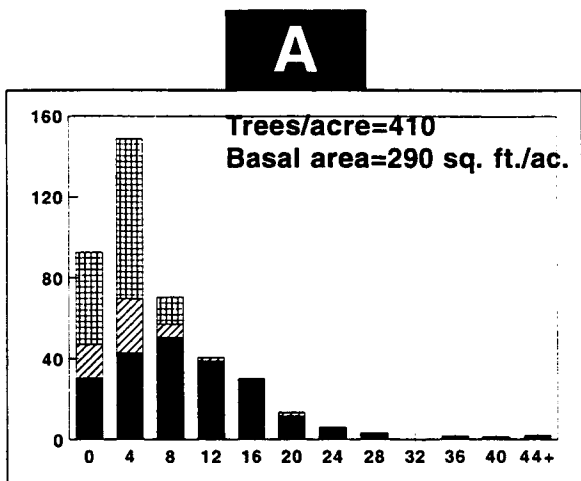
Prior to timber management, the disturbances described above shaped the structure and dynamics of the forests for several thousand years. The disturbances imposed by timber management deviate from natural disturbances to varying degrees (*fig. 2*), and these deviations might influence habitat quality for mature-forest wildlife. Estimating characteristics of natural disturbances can facilitate prediction of the development of stands that contain specific habitat structures.

Ecological Importance of Disturbance

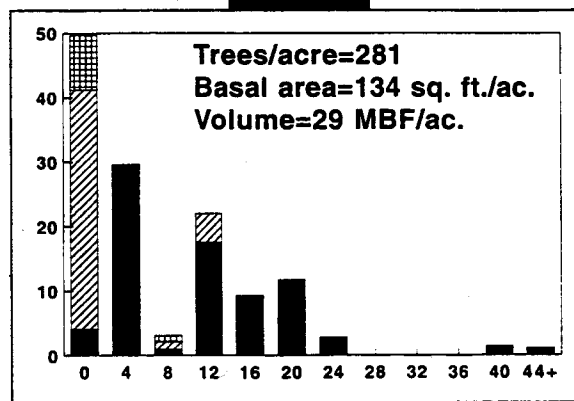
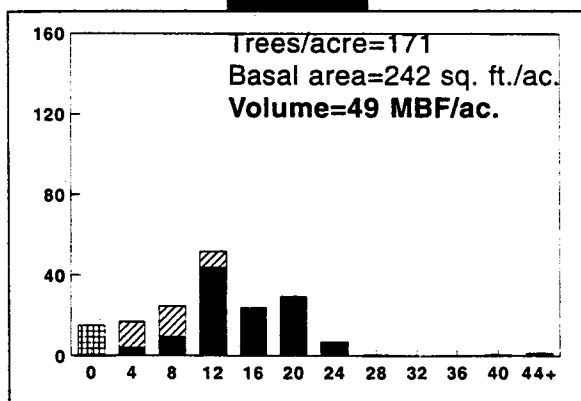
Size and shape. The abundance of some animal species is associated with patch size (Rosenberg and Raphael 1986). An organism may be displaced by disturbances larger than its home range (the area over which it secures resources), but it might not be displaced if the disturbance scale is sufficiently small relative to the home range. Similarly, mature-forest species may be more tolerant of frequent

MANAGED 70-YEAR STAND

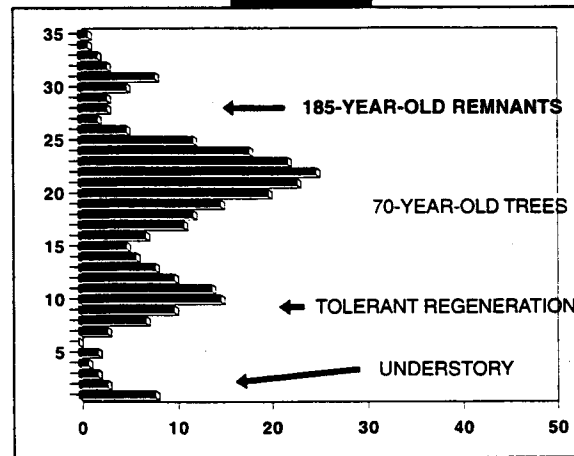
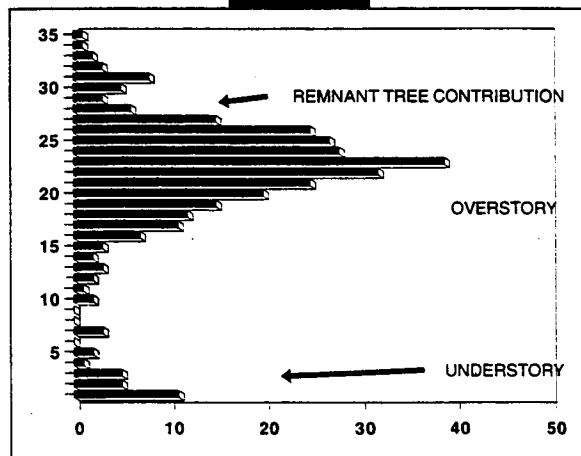
Natural stand
diameter distribution



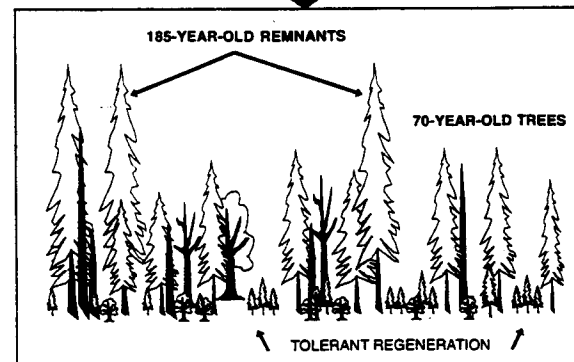
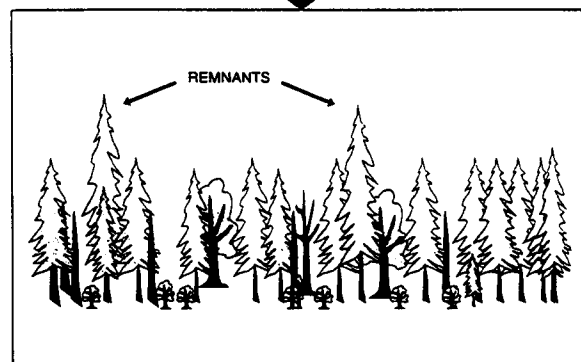
Diameter distribution



Foliage height profile



Schematic



C

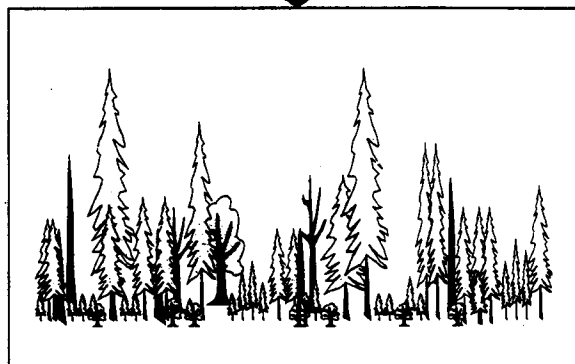
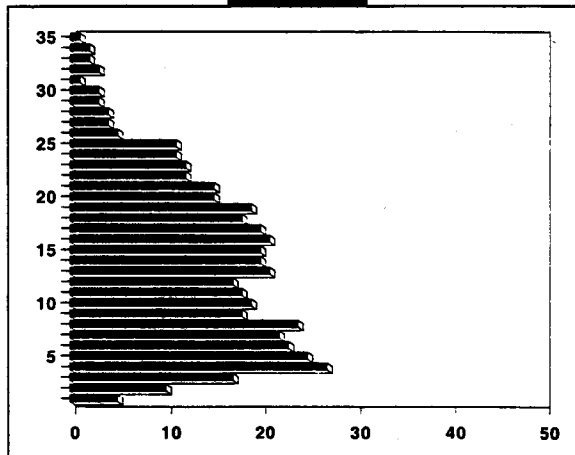
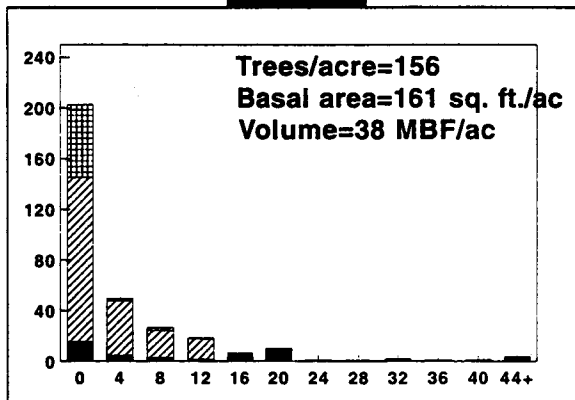
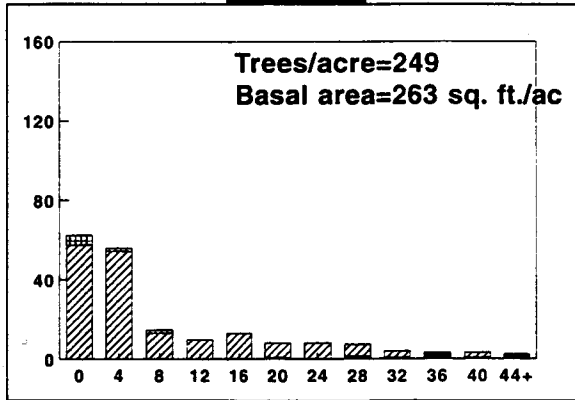





Figure 1. Characteristics for three desired future conditions: (A) a one-story, 100-year-old Douglas-fir stand with old-growth remnants; (B) a few-storied stand with 2-3 age class development typical following low-intensity fires; and (C) a many-storied stand dominated by small-size western hemlock and fir resulting from canopy-gap disturbance. The first row illustrates the diameter distributions for a natural stand. The lower three rows provide information on a managed 70-year-old stand. Vertical axis for diameter distributions indicates trees/acre and horizontal axis shows dbh class in inches. For foliage height profile, vertical axis is height in meters and horizontal axis shows percent cover.

KEY

-  Douglas-fir
-  Grand fir
-  Hardwoods

disturbances than those that occur once in many generations. It is likely that species selecting mature Douglas-fir forests have persisted in the region by (1) tolerating fine-scale disturbances that lead to enhanced stand complexity within their home ranges (fine-scale creation of snags, logs, or vertical structure); or, following coarse-scale disturbances, (2) recolonizing stands of sufficient size that regrow and contain residual trees and dead wood. Recolonization might occur over long periods of time following large disturbances, especially for species with low dispersal capability such as small mammals and amphibians (Harris 1984, p. 85). Refugia from coarse-scale disturbances, such as isolated patches of old forest, may have allowed some of these species to persist and recolonize following large disturbances such as fire or windthrow.

Shape. The shape of a disturbance can influence the amount of edge and hence the microclimatic characteristics of the stand (Geiger 1965), so patches with high edge-to-area ratios may influence habitat quality for species sensitive to microclimate (e.g., relative humidity).

Intensity. Disturbance intensity influences the amount of organic material destroyed or redistributed by the disturbance (table 1). The residual organic material after disturbance can influence the direction of succession and the rate of subsequent development (Harmon et al. 1986). The remaining structures might directly or indirectly provide habitat for mature-forest species. Disturbances that cause gaps in mature and old-growth forests also produce snags and logs, and subsequent vegetative growth enhances the stand's vertical complexity (Hunter 1990, Spies et al. 1990). Lower numbers and lower frequencies of most mature-forest vertebrates were detected in young, structurally diverse, unmanaged stands than in older unmanaged stands (Ruggiero et al. 1991). The large trees and dead wood present following coarse-scale disturbances might persist into the closed-canopy stage and provide the larger trees and snags associated with mature-forest vertebrates. The hypothesis is that the absence of large trees and dead wood in managed stands would further degrade habitat quality for these species.

Frequency. Disturbance frequency will influence species composition and the amount of living and dead organic mate-

rial on the site over time (Harmon et al. 1986, Spies et al. 1988). Frequent coarse-scale disturbances can delay the onset of mature forest development or preclude it. Infrequent fine-scale disturbances may delay the development of multilayered stands, large snags, and large logs (Spies et al. 1990). Frequency can be characterized in several ways: disturbance rate per unit area, percent of a stand disturbed annually, or time between disturbances.

Density and pattern. Disturbance density is the percentage of the stand or landscape occupied by the type of patch created by specific disturbances. The density of disturbances influences the abundance of structural features produced. For a given gap size, a stand in which 1% of the stand is in canopy gaps less than 30 years old probably will have a less well developed vertical foliage structure and fewer large pieces of dead wood than one in which 15% is in gaps. The disturbance pattern also might influence habitat quality for species sensitive to habitat contiguity. Clumped distributions of fine-scale disturbances may result in a cumulative decrease in habitat availability.

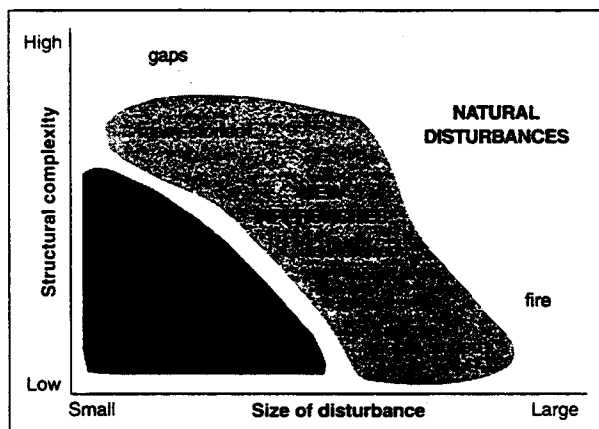


Figure 2. Illustrative comparison of the disturbance effects of traditional silvicultural systems, natural disturbances, and new silvicultural approaches.

Stand Objectives for Managed Forests

No one stand management system will precisely match the variability inherent in natural stands that resulted from a variety of disturbances. But some of the variation can be incorporated into managed landscapes by using a variety of silvicultural systems. The choice of system will depend on biological, social, and economic objectives for the stand and the

landscape and will imitate natural disturbances to varying degrees. Indeed, existing silvicultural systems with timber objectives reflect the evolutionary regeneration and growth strategies of the commercially important tree species in a region. Intensive silviculture for timber production, as currently practiced, might leave less dead wood and fewer noncommercial plant species than natural disturbances (Harmon et al. 1986, Halpern 1988, Hansen et al. 1991), so it does not imitate natural disturbances for other forest resources as well as it does for timber. Even timber yields may decline over several rotations as a result of net losses of soil organic matter (Harmon et al. 1986, Keeves 1966).

This article proposes that a series of stand condition specifications be developed as target objectives for each stand, including diameter distributions for living and dead wood in naturally-occurring young (40–69), mature (70–200), and old-growth (more than 200-year) stands. The selected unmanaged mature and old-growth stands should support self-sustaining populations of mature-forest vertebrates. The development, structure, and composition of natural stands can serve as goals for stands managed to produce habitat for mature-forest wildlife and timber. The silvicultural goal would be to provide many of the features found in a natural stand during the development of its managed counterpart (figs. 1, 3).

Of the many possible silvicultural approaches to developing such stands, four are discussed here—single-story, few-storied, many-storied, and mature-forest restoration. The first two approaches imitate coarse-scale disturbances; the third is patterned after fine-scale natural disturbances that might be tolerated by some mature-forest species; and the fourth develops a young plantation into a stand with mature-forest structures. The objectives for each stand (targets) are based on data from the Old-Growth Habitat Relationships Program, modified for local conditions. The hypotheses to

be tested include whether mature-forest wildlife use these stands.

The western Willamette Valley version of ORGANON (developed from data on Oregon State University's [OSU] McDonald Forest) was used to develop stand predictions. This model was tested in nearby stands managed under tree densities from 50/acre to 400/acre and ages 35–85. ORGANON predicted basal area, volume, and mortality well in these stands (pers. commun., D. Hann, Oregon State University, Corvallis, 1993). Certain assumptions were made: (1) extrapolations of tree growth outside the data on which ORGANON was based (e.g., tree growth greater than 135 years) would reasonably estimate stand development; (2) estimates of mortality from suppression reasonably reflected snag recruitment; (3) the Snag Recruitment Simulator model (Marcot 1991) would provide a reasonable estimate of snag abundance for dead wood-dependent species when the management objective is set at 100% of maximum potential population level for primary cavity-nesters (3.7/acre); and (4) no snags were retained at initial harvest—that is, all snags must be created from green trees or recruited through suppression mortality. The latter assumption was a conservative approach that meant retaining adequate green trees for snag replacement to meet current and future dead wood needs, and hence resulted in the greatest impact on timber volume. The models also included four operational assumptions: (1) any natural advance regeneration that was present would be maintained to enhance species composition; (2) control of competing vegetation might be needed to ensure regeneration success; (3) retained green trees would be windfirm and have high diameter-to-height ratios and deep crowns to increase postrelease growth rates; and (4) no major blowdown loss occurred.

The starting points for stand development predictions were data from a 115-year-old unmanaged stand (site index = 121 feet at 50 years for the single-, few-, and many-storied examples) and a 40-year-old plantation (site index = 127 feet for the mature-forest restoration example) on the OSU McDonald Forest. Stand exam data from a 20-year-old plantation became the basis for regeneration in the single- and few-storied and mature-forest restoration examples, and from nat-

Table 2. Biological effects shortly after disturbance for two natural-disturbance patterns and three hypothetical silvicultural systems that consider both timber removal and mature-forest wildlife habitat.

Effect	Natural disturbance		Managed stand		
	Coarse	Fine	Coarse		Fine
			Single-story	Few-storied	Many-storied
Plant community, stand scale					
Early seral shrubs and herbs	Abundant	Rare	Abundant	Common-abundant	Rare
Shade tolerance of tree regeneration	Intolerant/tolerant	Tolerant	Intolerant	Intolerant/tolerant	Tolerant/intolerant
Wildlife habitat following disturbance					
Vertical structure	Low-moderate	High	Low	Moderate	High
Edge effects ¹	Moderate	Low	High	Moderate	Low
Horizontal patchiness	Moderate-high	High	Low	Moderate	High
Forest floor effects	Low-moderate	Low	Moderate	Moderate	High

¹Assuming adjacent stands are mature forest.

ural regeneration in a partially harvested stand in the many-storied example. Volume production from single-, few-, and many-storied stand management through stand age 70 years (table 3) were compared to volume production in the same stand 70 years following clearcutting, planting, and thinning at age 35 and 60; no snags or down logs were created in the latter stand. Including clearcut harvest and standing volume at age 70, this stand produced 125 mbf/acre.

An adaptation of Morisita's community similarity index (Brower et al. 1990) allowed comparisons between the diameter distribution of target stands and managed stands (figs. 1, 3). It was assumed that diameter distributions would reasonably represent tree sizes and hence vertical foliage distribution in the stands. Morisita's index was chosen because it allows comparison of community structure between two communities with different densities of organisms (Brower et al. 1990). This index describes the probability that a woody stem randomly selected from each of two stands would belong to the same diameter class, relative to the probability of randomly selecting a pair of woody stems of the same diameter class from one of the stands. A value of 0% meant no similarity between the stands; 100% indicated that the number of stems in each diameter class was identical for both stands. For instance, natural mature and old-growth stands were quite similar. The average community similarity between all possible pairs of six natural stands (ages 80–300 years) from the Old Growth Habitat Relationships Program (figs. 1, 3) was 93.2% (SE = 1.42). Average similarity between these natural stands and the simulated 70-year-old

stand resulting from clearcutting was 37% (SE = 4.0). Hence a similarity greater than 45% (at the 95% confidence interval) between managed and target stands would represent improvement over traditional stand management for timber production.

Single-Storied Application

Coarse-scale disturbances such as patchy fires and slope failures can result in a primarily even-aged stand with few residuals (fig. 1A). Its managed counterpart (table 2), a single-storied stand, represents a slight but important modification of current clearcuts, which produce relatively uniform stands for timber production under an even-aged regeneration system. The prescription system can be based on clearcutting, shelterwood, or deferred rotation (Smith et al. 1989) but reserve green-tree and snag structures should be designated.

In this example, two remnant trees larger than 30 inches dbh were retained for each acre, and six snags larger than 25 inches dbh at final harvest. Harvest resulted in net production of 71 mbf/acre, with an additional 4 mbf/acre retained as snags, logs, and green trees. The regeneration (265 trees/acre) was 85% Douglas-fir and 15% grand fir (*Abies grandis*) and hardwoods. At age 45 years, 30% of the 8- to 20-inch trees were thinned (3 mbf/acre of timber, 2 mbf/acre allocated to snags and logs). Standing volume at age 70 was predicted to be 49 mbf/acre for a total timber volume production of 123 mbf/acre. Mean annual increment at age 70 was similar to the clearcut stand (table 3). Similarity between the managed stand and the target stand was 63%, while similarity between the traditional clearcut at

age 70 and the target stand was 46%.

Only thinning methods that assumed uniform spacing of residual trees were available, but variable density planting and thinning could economically produce a stand of heterogeneous tree sizes within an even-aged stand. Thinning for timber production usually leaves the remaining trees uniformly spaced with adequate room among crowns for continued volume growth. Thinnings that are variable in intensity within the stand will allow rapid growth by some trees and reduced growth or death (snags) by others.

Harvest disturbances in a single-story system are more intense and leave fewer large trees, snags, and logs, except when fires have been frequent or intense. This system represents the low end of within-stand natural variation in patch size, canopy cover, and large live-tree survival. This hypothetical stand might begin to provide habitat for most species typical of mature forest after about 70 years.

Few-Storied Application

Stands with two or three canopy layers can be created either by regenerating two or three age classes (Long and Roberts 1992), or by regenerating a single age class composed of two or three species with different growth rates and potential sizes. The first approach (shelterwood with reserves) would apply where existing old stands are being cut and where windthrow is not likely. The second approach (mixed-species clearcut) could be applied in existing young plantations or where windthrow and root-rot potential is high.

Few-storied stands do not fit into traditional concepts of either even-aged stands or uneven-aged stands—Smith

(1989, p. 17) described these stands as intermediate. Traditional approaches to creating balanced uneven-aged stands with more than three age-classes and canopy layers have used selection regeneration methods, in which individual or small groups of trees are cut in a mosaic pattern. Such cutting partially imitates gap disturbances from windfall and small patches of insect and disease mortality. In the Douglas-fir region, however, ground fires, wind, and other low-intensity, coarse-scale disturbances have created uneven-aged old-growth stands of Douglas-fir and western hemlock (*fig. 1B*). Many old-growth stands contain more than one size class of Douglas-fir with several size classes of western hemlock. The diameter distribution in the first diagram in *figure 1B* probably developed following wind-throw or moderately severe wildfires that killed 10%–75% of the

canopy Douglas-firs and western hemlocks (Morrison and Swanson 1990). Relatively even-aged clumps of Douglas-fir or western hemlock became established beneath the scattered or clumpy overstory of the canopy survivors.

A regeneration system that partially imitates this type of stand would have elements of both even-aged and uneven-aged management. Like even-aged systems, disturbance and establishment would occur relatively infrequently. Like uneven-aged systems, more than two age classes would be present in the stand. This example retained six trees larger than 30 inches dbh/acre and created four snags more than 24 inches dbh/acre at harvest (70 mbf/acre removed as timber, with 5 mbf/acre retained to create snags and logs). Regeneration (265 trees/acre) was 85% Douglas-fir and 15% grand fir and hardwoods. Following creation of 3

snags/acre at age 35 years (2 mbf/acre), regeneration was thinned at age 45 years to 50 trees/acre (producing 12 mbf/acre) and underplanted with 265 trees/acre (23% Douglas-fir, 77% grand fir). One additional snag/acre was created from the 55-year-old trees, and stocking of regeneration reduced by 70% at age 70. The predicted standing volume 70 years after initial harvest was 30 mbf/acre, resulting in a predicted net timber volume production of 112 mbf/acre, plus 8 mbf/acre allocated to trees, snags, and logs (*table 3*). The mean annual increment for the few-storied stand at age 70 was 15% less than for a traditional clearcut. Birch and Johnson (1992) predicted a reduction of 15% volume production over 60 years using a similar approach, but they did not consider retained green trees as potential volume for harvest in the future. Predicted similarity between the target stand and the managed few-storied stand at age 70 was 90%. Similarity between the target stand and a 70-year-old clearcut was 27%. This is similar to the approach being taken in some new forestry units (Franklin 1989), except that trees to be retained for specific purposes should be marked prior to harvest by biologists and silviculturists, and approved by loggers (to ensure logger safety).

Mortality in the 185-year-old trees (larger than 40 inches dbh) was predicted to be less than 1/acre over 70 years using ORGANON. This mortality would not be salvaged, resulting in large snags or logs. Although the model projected stand growth for only 70 years, about three or four 70-year-old trees/acre, in addition to the 185-year-old trees, could be left if the stand was harvested at age 70. The process of maintaining a 70-year rotation for timber production in conjunction with a natural rotation of larger trees could provide a long-term multilayered stand similar to a stand that developed following natural disturbance (*fig. 1B*).

Creating a stand of trees with varied growth rates might be most applicable where windthrow is a concern or where management is focused on young, uniform plantations. New stands could be established in plantations (similar to single-story systems) and a mix of slow- and fast-growing species (e.g., Douglas-fir, red alder [*Alnus rubra*], black cottonwood [*Populus trichocarpa*], and western redcedar [*Thuja plicata*]) planted to produce a stand with more than two canopy layers.

Table 3. Predicted growth and harvest from three 115-year-old stands and a 40-year-old stand, McDonald Forest, Benton County, Oregon.

Stand	Age	Mean annual increment	Standing volume	Timber harvest	Retention
	yrs	mbf/ac/yr		mbf/ac	
Clearcut	115	0.65	75	75	0
	35	0.40	6	8	0
	45	0.47	13	0	0
	55	0.58	24	0	0
	70	0.71	35	42	0
Total				125	0
Single-story	115	0.65	75	71	4
	35	0.47	16	0	0
	45	0.60	22	3	2
	55	0.67	32	0	0
	70	0.77	49	49	0
Total				123	6
Few-storied	115	0.65	75	70	5
	35	0.49	17	0	2
	45	0.60	15	12	0
	55	0.60	21	0	1
	70	0.60	30	30	0
Total				112	8
Many-storied	115	0.65	75	57	18
	25	1.20	24	4	2
	35	0.97	28	0	0
	45	0.87	33	0	0
	50	0.82	28	5	2
	55	0.78	30	0	0
	70	0.73	38	38	0
Total				104	22
Plantation	40	0.50	19	12	2
	45	0.49	7	0	1
	55	0.51	13	0	0
	70	0.66	29	0	2
	90	0.78	56	13	0
	110	0.85	66	0	2
Total	115	0.85	71	71	0
				96	7

Table 4. Management activities to provide habitat for mature forest wildlife.

Habitat characteristic desired	Single-story stand	Few-storied stand	Many-storied stand
Large tree size	Extend rotation; thin; fertilize	Extend rotation; thin; fertilize	Large target tree size; low Q^1
Snags and logs	Reserve at harvest; control stand density; kill trees	Reserve at harvest; control stand density; kill trees	Reserve at each cutting cycle
Vertical complexity	Thin; plant mixed species; fertilize	Thin; plant mixed species	Control density and species when thinning
Horizontal patchiness	Nonuniform planting; thin	Nonuniform planting; thin	Nonuniform thinning
Edge effects	Retain green trees, stand size, and shape; schedule harvest	Retain green trees, stand size, and shape; schedule harvest	Scatter gaps, small gap size
Forest floor	Harvest with cable yard or helicopter; low intensity site preparation	Harvest with cable yard or helicopter; low intensity site preparation	Designate skid trails
Human disturbance	Gate roads; infrequent entry	Gate roads; infrequent entry	Gate roads and skid trails

¹ Q -factor is a number multiplied by the number of trees/acre in one diameter class to estimate the appropriate number of trees/acre in the next smallest diameter class and produce an inverse J-shaped curve. A low Q -factor would have fewer smaller trees and more large ones than a high Q given the same target tree size. Target tree size is the maximum dbh tree grown for timber production.

Existing young, even-aged plantations could be accelerated toward a multistoried condition through precommercial thinning of variable intensity to release some trees. Shade-tolerant species (grand fir, western redcedar, western hemlock) could be underplanted to provide additional layers as the stand develops, but thinning both layers may be necessary to maintain growth in this lower layer (pers. commun., D. Marshall, Oregon State University, Corvallis, 1992). These stands could then be managed as few-storied stands.

Few-storied stands produce greater variability in vertical structure and tree diameter classes than single-story stands. Both types of stands may be smaller in size and more frequently disturbed than some natural stands that developed from coarse-scale disturbances (table 1). Cavity-nesters typically found in mature forests might use these stands within 50 years as the crowns close, especially where large trees are close to snags.

Many-Storied Application

Group and single-tree selection systems designed to produce large tree diameters could partially imitate structures produced following natural disturbances such as individual tree death or gap formation. The stands would provide some of the characteristics typical of old-growth stands—large trees, snags, and logs; many-aged; and many sized (Spies and Franklin 1988)—but should not be considered a replacement for old-growth (Hunter 1989). Lower structural complexity and stocking levels are typical following cutting in selection systems for timber because growth is concentrated on commercial tree species and mortality is

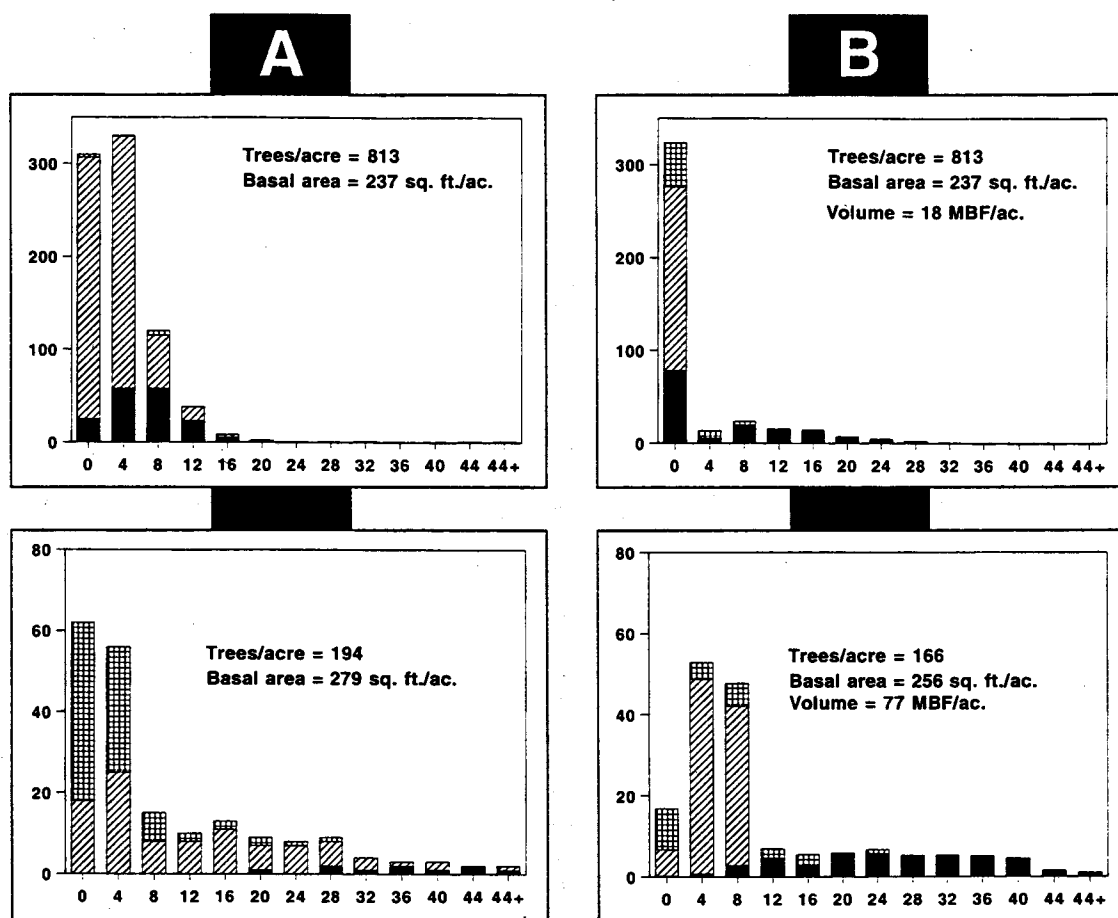
reduced through density management. Producing many-storied stands suitable for mature-forest wildlife may be possible on sites where advanced harvesting techniques, such as designated skid trails or helicopter logging, are feasible. Kellogg et al. (1991) found that harvesting a 115-year-old stand using group selection cost 5% more than clearcutting with ground-skidding systems and up to 35% more than clearcutting with cable systems. Modified selection systems should be re-evaluated in light of advances in harvesting technology and increasing knowledge of the ecological importance of fine-scale disturbances to stand dynamics in Douglas-fir/western hemlock forests.

In this example (fig. 1C), the development of the 115-year-old stand from McDonald Forest was projected for 70 years based on a 25-year cutting cycle. A complete skid trail system could be developed for the stand prior to the first entry that would limit ground impact to less than 10% of the stand (Kellogg et al. 1991). Volume removal from the first entry was predicted to be 57 mbf/acre with 3 mbf/acre allocated to snag creation and 15 mbf/acre retained as growing stock. Regeneration was 120 trees/acre (13% Douglas-fir, 87% grand fir), either planted or natural, following each entry. Previously established regeneration was precommercially thinned to 50%–60% of full stocking during each entry, with selection for Douglas-fir and against grand fir. Replacements for snags, logs, and large green trees could be recruited during each cutting cycle (table 4). Predicted volume removal 25 years after initial entry would be 4 mbf/acre, plus 2 mbf/acre as snags and logs; 50 years after initiating management, 5 mbf/acre would be removed plus

2 mbf/acre for snags and logs. Standing volume at age 70 was predicted to be 38 mbf/acre; mean annual increment 70 years after initiating management was predicted to be comparable to the traditional clearcut (table 3). If grand fir begins to dominate the stand, timber value may decline significantly. Similarity between the managed many-storied stand at age 70 and the target stand was 70%. Similarity between the target stand and a 70-year-old clearcut was 47%.

Although less cost-effective than clearcutting, this system could result in large logs with high biological and economic value on a sustained basis while producing trees up to 44 inches dbh within a multistoried stand. Managed stands would have fewer large trees and lower woody debris levels than typical old-growth stands. A dominance shift to shade-tolerant species may necessitate stand reestablishment with Douglas-fir using single- or few-storied approaches. Alternatively, cutting gaps larger than most natural canopy gaps in combination with thinning to favor Douglas-fir may allow shade-intolerant species to persist. This system would have high within-stand variability in tree size and vertical complexity. Compaction along designated skid trails may have adverse effects on some burrowing species and on long-term site productivity, but carefully designed harvesting systems impact less than 10% of the stand (Kellogg et al. 1991). Disturbance between entries should be minimized. This system might provide acceptable habitat for mature-forest species such as red tree voles, Douglas squirrels, and pileated woodpeckers while allowing regular timber removal.

Figure 3. Diameter distributions for (A) unmanaged stands at 80 years (top) and 300 years (bottom); and (B) their hypothetical managed counterparts at 60 years (top) and 120 years (bottom) as predicted by ORGA-NON. Vertical axis indicates trees/acre; horizontal axis is dbh in inches.



Plantation Restoration

Because millions of acres of plantations have been created without retention of large trees, restoration to resemble mature and old-growth stands within some forests should be a high-priority management goal. In attempting to develop a 40-year-old plantation (319 trees/acre) structure resembling unmanaged young, mature, and old-growth stands, the stand was thinned to 81 trees/acre at age 40, removing 12 mbf/acre of timber and allocating 2 mbf/acre to snag creation (table 3). The stand was planted to 265 trees/acre (28% Douglas-fir, 72% grand fir).

During stand development, snags of a size potentially usable by pileated woodpeckers could be created, so 1 mbf/acre was allocated at age 45, 2 mbf/acre at age 70, and 2 mbf/acre at age 110. Twenty years after thinning and regeneration, predicted similarity between the plantation and an unmanaged, 80-year-old stand (fig. 3) was 67%. Thinning of the stand at age 90 was simulated by reducing the density of trees less than 30 inches dbh by 40% (13 mbf/acre was removed); at this time the predicted similarity between the managed stand and an unman-

aged, mature stand was 91%. At predicted stand development at age 115, predicted similarity in diameter distribution between the managed stand and an unmanaged 300-year-old old-growth stand was 79%. Standing volume at age 115 was predicted to be 71 mbf/acre, for a total production of 103 mbf/acre not including the allocation to snags and logs (table 3). Mean annual increment was predicted to increase from stand age 40 to 120. At age 115, either a single- or a few-storied stand management approach could be initiated, or the old-forest character of the stand could be maintained using a many-storied management approach.

Landscapes by Design

We are inheriting landscapes created by past disturbances and timber-driven management objectives on mixed ownerships that do not consider large-scale habitat patterning. Combining a range of available silvicultural systems on the landscape in a manner that considers size and connectedness of mature stands over landscapes through time would be one step toward designing forest patterns. For instance, harvest of stands within a land-

scape should not excessively fragment currently suitable habitat. Within a "habitat management block" for mature-forest species, constraints would be needed on the proportion of the area that would be allowed to consist of other than old-forest habitat. The amount of old-forest habitat, connectivity, and volume removals could be predicted at the landscape scale using a scheduling and network analysis program such as SNAP (Sessions and Sessions 1992).

The four proposed prescriptions should be considered as examples; they will not apply in all situations nor will they meet all ecosystem objectives. Silviculturists will have to work with wildlife biologists, forest ecologists, harvesting specialists, and other resource managers to identify clear objectives for wildlife habitat and timber; identify existing examples of conditions that meet the objectives; design prescriptions specific to local conditions that can attain stand objectives; and plan stand locations to create landscape patterns that meet the objectives.

As an example, consider how these approaches might be distributed on a land-

scape to meet a management objective of maintaining mature-forest species while allowing some timber removal. Because ground-skidding is generally limited to slopes less than 35%, areas with such slopes that are known to support mature-forest species could be managed by producing many-storied stands to maintain these species and provide connectivity among other stands. Single- and few-storied stands could be used on steep side-slopes. Few-storied stands might be most appropriate on steep slopes adjacent to riparian buffer strips because they would provide at least a low contiguous canopy cover and a source of large logs for the riparian system. Restoration could be applied to young plantations.

The resulting landscape would be a mosaic of many-storied stands interspersed with single- and few-storied stands in various stages of development. Managers would have to be committed to designing the landscape to meet the needs of mature-forest species over time. Once stand and landscape conditions supported populations of species associated with old forests, stand conditions could be prolonged by using selection systems that create many-storied stands. Indeed, this progression from coarse-scale disturbance (single- and few-storied stands) to fine-scale disturbance (many-storied stands) is typical of natural development of mature and old-growth forests (Spies et al. 1990). Decisions regarding use of coarse-scale disturbances in managed stands should be based on landscape objectives. Further, silviculturists must be aware that natural disturbances (e.g., root rots, fire, wind) will continue to alter stand structure in managed stands.

Unless a landscape had been cut to the point that further harvest would excessively fragment the area, volume removals (though low) would continue until the areas became fully managed; then timber production would increase (Gagliuso and McComb 1992). Volume removals would be lower and species mix may differ from stands managed solely for timber production. The level of removals will depend on site quality, species composition, desired structures, current structure, relative value placed on wildlife by landowners, and legislative mandates.

Hypothesis Testing


Forest management is entering an era of ecosystem management. New ap-

proaches are often being implemented faster than research can provide information on impact and effectiveness. All of the approaches illustrated in this article are based on ecological concepts that need to be tested with long-term studies. A deductive approach to hypothesis testing should be used to assess (1) the likelihood that predicted stand development will be achieved, including disturbance as well as suppression mortality and changes in species composition; (2) economic feasibility of the systems; and (3) responses of mature-forest wildlife to silvicultural systems (Romesburg 1981).

Research is being conducted in east-central Coastal Range stands in Oregon to examine the growth of residual and regenerated trees, harvesting costs, site preparation costs and effectiveness, wildlife population responses, and esthetic values associated with similar treatments (Brunson and Shelby 1992). However, experiments must be conducted at both stand and landscape scales. Stand-level studies can provide information on regeneration and residual tree responses, harvesting system approaches and costs, and responses of species with small home ranges. Large manipulations (thousands of acres) should be the basis for testing species responses to treatments, especially for species with large home ranges.

Traditional divisions between research and management must be minimized for experiments to succeed. Researchers must work with managers to achieve stand and landscape patterns that meet the goals for both experimental designs and multiple-use management. Managers must appreciate the importance of replicated experimental designs. Although Bayesian statistics may be necessary approaches to understanding large-scale processes (Reckhow 1990), cause-and-effect relationships could be assessed using a repeated measures experimental design (Gurevitch and Chester 1986) at the landscape scale. Replicated studies of habitat and wildlife would have to occur on large scale. DCAs could serve as control areas, with manipulations occurring on landscapes paired with DCA controls to provide a basis for comparing species and community responses to changes. Although DCAs already contain many second-growth stands, animal responses to developing habitat conditions in DCAs without subsequent management could be com-

pared to responses to habitat development outside DCAs in areas managed using techniques discussed in this article.

Monitoring correct implementation and prescription effectiveness will be critical to give managers the flexibility to alter approaches over time in an adaptive management approach. Adaptive management will allow managers to incorporate monitoring results into new prescriptions, thereby increasing the likelihood of reaching their objectives. 

Literature Cited

- BIRCH, K.R., and K.N. JOHNSON. 1992. Stand-level wood production costs of leaving live, mature trees at regeneration harvest in coastal Douglas-fir stands. *West. J. Appl. For.* 7:65-68.
- BROWN, E.R., tech. ed. 1985. Management of fish and wildlife habitats in forests of western Oregon and Washington. USDA For. Serv. PNW Rep. R6-F&WL-192-1985. 332 p.
- BROWER, J.E., J.H. ZAR, and C.N. VON EENDE. 1990. Field and laboratory methods for general ecology. Ed. 3. Wm. C. Brown, Publ., Dubuque, IA. 237 p.
- BRUNSON, M., and B. SHELBY. 1992. Assessing recreational and scenic quality—how does new forestry rate? *J. For.* 90:37-41.
- BURY, R.B. and P.S. CORN. 1988. Douglas-fir forests in the Oregon and Washington Cascades: relation of the herpetofauna to stand age and moisture. *In* Management of amphibians, reptiles, and small mammals in North America—proceedings of the symposium, R.C. Szaro, K.E. Severson, and D.R. Patton, tech. coords., p. 11-22. USDA For. Serv. Gen. Tech. Rep. RM-166.
- CAREY, A.B. 1985. A summary of the scientific basis for spotted owl management. *In* Ecology and management of the spotted owl in the Pacific Northwest, R.J. Gutierrez and A.B. Carey, tech. eds., p. 100-14. USDA For. Serv. Gen. Tech. Rep. PNW-185.
- CLEARY, B.D., R.D. GREAVES, and R.K. HERMANN, eds. 1978. Regenerating Oregon's forests. *Oreg. State Univ. Ext. Serv., Corvallis.* 286 p.
- CORN, P.S., R.B. BURY, and T.A. SPIES. 1988. Douglas-fir forests in the Cascade Mountains of Oregon and Washington: Is the abundance of small mammals related to stand age and moisture? *In* Management of amphibians, reptiles and small mammals in North America—proceedings of the symposium, R.C. Szaro, K.E. Severson, and D.R. Patton, tech. coords., p. 340-52. USDA For. Serv. Gen. Tech. Rep. RM-166.
- FORSMAN, E.D., E.C. MESLOW, and H.M. WIGHT. 1984. Distribution and biology of the spotted owl. *Wildl. Monogr.* 87. 64 p.
- FRANKLIN, J.F. 1989. Toward a new forestry. *Am. For.* 12:37-44.
- FRANKLIN, J.F., and D.S. DeBELL. 1988. Thirty-six years of tree population change in an old-

- growth *Pseudotsuga-Tsuga* forest. Can. J. For. Res. 18:633-39.
- FRANKLIN, J.F., and T.A. SPIES. 1991. Ecological definitions of old-growth Douglas-fir forests. In *Wildlife and vegetation of unmanaged Douglas-fir forests*, L.F. Ruggiero, K.B. Aubrey, A.B. Carey, and M.H. Huff, tech. coords., p. 61-69. USDA For. Serv. Gen. Tech. Rep. 285.
- GAGLIUSO, R., and W.C. McCOMB. 1992. Designing landscapes for wildlife and timber. In *Managing forest information over space and time*, G. Wood and B. Turner, tech. eds., p. 379-88. IUFRO ANUTECH Pty. Ltd., Canberra, Australia.
- GEIGER, R. 1965. The climate near the ground. Harvard Univ. Press, Cambridge, MA. 611 p.
- GREBER, B.J., K.N. JOHNSON, and G. LETTMAN. 1990. Conservation plans for the northern spotted owl and other forest management proposals in Oregon: the economics of changing timber availability. *Oreg. State Univ., Corvallis*. 50 p.
- GUMTOW-FARRIOR, D.L. 1991. Cavity resources in Oregon white oak and Douglas-fir stands in the mid-Willamette Valley. MS thesis, *Oreg. State Univ., Corvallis*. 89 p.
- GUREVITCH, J., and S.T. CHESTER, JR. 1986. Analysis of repeated measures experiments. *Ecol.* 67:251-55.
- HALPERN, C.B. 1988. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecol.* 70:704-20.
- HANSEN, A.J., T.A. SPIES, E.J. SWANSON, and J.L. OHMANN. 1991. Lessons from natural forests. *BioScience* 41:382-92.
- HARMON, M.E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. in Ecol. Res.*, Vol. 15. Academic Press, Orlando, FL. 302 p.
- HARRIS, L.D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. Univ. Chicago Press, Chicago. 211 p.
- HEMSTROM, M.A., and J.F. FRANKLIN. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. *Quatern. Res.* 18:32-51.
- HUNTER, M.L., JR. 1989. What constitutes an old-growth stand? *J. For.* 87(8):33-35.
- . 1990. *Wildlife, forests and forestry—principles of managing forests for biological diversity*. Prentice-Hall, Englewood Cliffs, NJ. 370 p.
- ISAAC, L.A. 1956. Place of partial cutting in old-growth stands of the Douglas-fir region. *USDA For. Serv. Res. Pap.* 16. 48 p.
- KEEVES, A. 1966. Some evidence of loss of productivity with successive rotations of *Pinus radiata* in the southeast of South Australia. *Austral. For.* 30:51-63.
- KELLOGG, L.D., S.J. PILKERTON, and R.M. EDWARDS. 1991. Logging requirements to meet new forestry prescriptions. In *Proceedings of the 1991 COFE annual meeting*, p. 43-49. Counc. on For. Eng., Nanaimo, BC.
- LONG, J.N., and S.D. ROBERTS. 1992. Growth and yield implications of a "new forests" silvicultural system. *West. J. Appl. For.* 7:6-9.
- MACARTHUR, R.H., and J.W. MACARTHUR. 1961. On bird species diversity. *Ecol.* 42:594-98.
- MANNAN, R.W., M.L. MORRISON, and E.C. MESLOW. 1984. Comment: the use of guilds in forest bird management. *Wildl. Soc. Bull.* 12:426-30.
- MARCOT, B.G. 1991. Snag recruitment simulator (computer model). *USDA Reg. 6*, Portland, OR.
- MARTIN, A.C., H.S. ZIM, and A.L. NELSON. 1951. *American wildlife and plants, a guide to wildlife food habits*. Dover Publ., Inc., New York. 500 p.
- MASER, C., B.R. MATE, J.F. FRANKLIN, and C.T. DYRNES. 1981. Natural history of Oregon coast mammals. *USDA For. Serv. Tech. Rep. PNW-133*. 496 p.
- MORRISON, P.H., and F.J. SWANSON. 1990. Fire history and pattern in a Cascade Mountain landscape. *USDA For. Serv. Gen. Tech. Rep. PNW-GTR-254*.
- MUNGER, T.T. 1950. A look at selective cutting in Douglas-fir. *J. For.* 48:97-99.
- NEITRO, W.A., V.W. BINKLEY, S.P. CLINE, R.W. MANNAN, B.G. MARCOT, D. TAYLOR, and F.F. WAGNER. 1985. Management of fish and wildlife habitats in forests of western Oregon and Washington. In *Snags*, E.R. Brown, tech. ed., p. 129-69. *USDA For. Serv. PNW Rep. R6-F&WL-192-1985*. 332 p.
- NELSON, S.K. 1989. Habitat use and densities of cavity-nesting birds in the Oregon Coast Range. MS thesis, *Oreg. State Univ., Corvallis*. 157 p.
- PETERSON, A.T., D.R. OSBORNE, and D.H. TAYLOR. 1989. Tree trunk arthropod fauna as food resources for birds. *Ohio J. Sci.* 89:23-25.
- RAPHAEL, M.G. 1987. Use of Pacific madrone by cavity-nesting birds. In *Symposium on multiple-use management of California's hardwood resources*, p. 198-202. *USDA For. Serv. Gen. Tech. Rep. PSW-100*.
- RECKHOW, K.H. 1990. Bayesian inference in non-replicated ecological studies. *Ecol.* 71:2053-59.
- ROMESBURG, H.C. 1981. Wildlife science: gaining reliable knowledge. *J. Wildl. Manage.* 45:293-313.
- ROSENBERG, K.V., and M.G. RAPHAEL. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. In *Modeling habitat relationships of terrestrial vertebrates*, J. Verner, M.L. Morrison, and C.J. Ralph, eds., p. 263-72. Univ. Wisc. Press, Madison.
- RUGGIERO, L.F., L.C. JONES, and K.B. AUBREY. 1991. Plant and animal associations in Douglas-fir forests of the Pacific Northwest. In *Wildlife and vegetation of unmanaged Douglas-fir forests*, L.F. Ruggiero et al., tech. coords., p. 447-62. *USDA For. Serv. Gen. Tech. Rep.* 285.
- RUNKLE, J.R. 1985. Disturbance regimes in temperate forests. In *The ecology of natural disturbance and patch dynamics*, S.T.A. Pickett and P.S. White, eds., p. 17-34. Acad. Press, New York.
- RUTH, R.H. and R.A. YODER. 1953. Reducing wind damage in the forests of the Oregon Coast Range. *USDA For. Serv. Stn. Pap. PNW-7*.
- SESSIONS, J. 1990. Timber for Oregon's tomorrow, the 1989 update. *Oreg. State Univ., Corvallis*. 183 p.
- SESSIONS, J., and J.B. SESSIONS. 1992. Scheduling and network analysis program (SNAP II), Users Guide 2.01. *Oreg. State Univ., Corvallis*.
- SINGER, S.W., N.L. NASLUND, S.A. SINGER, and C.J. RALPH. 1991. Discovery and observations of two tree nests of the marbled murrelet. *Condor* 93:330-39.
- SMITH, H.C., N.I. LAMSON, and G.W. MILLER. 1989. An esthetic alternative to clearcutting. *J. For.* 87:14-18.
- SPIES, T.A., and J.F. FRANKLIN. 1988. Old-growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Nat. Areas J.* 8:190-201.
- . 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In *Wildlife and vegetation of unmanaged Douglas-fir forests*, L.F. Ruggiero, et al., tech. coords., p. 91-109. *USDA For. Serv. Gen. Tech. Rep.* 285.
- SPIES, T.A., J.F. FRANKLIN, and M. KLOPSCH. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* 20:649-58.
- SPIES, T.A., J.F. FRANKLIN, and T.B. THOMAS. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecol.* 69:1689-702.
- STEWART, G.H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Oregon Cascade Range. *Can. J. For. Res.* 16:558-68.
- 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: report of the Interagency Scientific Committee to address the conservation of the northern spotted owl. *US Gov. Print. Off., Portland, OR. Doc. 1990-791-171/20026*. 427 p.
- US DEPARTMENT OF THE INTERIOR. 1992. Recovery plan for the northern spotted owl—draft. *US Dep. of Int., Washington, DC*. 662 p.

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