

ent on disturbance. A landscape can be viewed as a collection of patches of varying size and undergoing changes influenced by disturbance, as well as by the patches that surround it, and at any time, different parts of a forested landscape will be at different successional stages. A Pacific Northwest forest could comprise an evenly aged stand of red alder that eventually is replaced by Douglas-fir, which might then be replaced by hemlock or cedar.

WHAT IS AN OLD-GROWTH FOREST?

Late-successional, or late-seral, has commonly referred to forests in which shade-tolerant tree species, such as western hemlock and grand fir, begin to attain dominance (Spurr and Barnes 1973). FEMAT (1993) defined late-successional quite differently, as the period from fires merchantability to culmination of mean annual increment. As traditionally defined (e.g., by Spurr and Barnes), late-successional conditions in Pacific Northwest forests occurred rarely, only after many years in the old-growth condition and in the absence of significant disturbances that maintained dominance of less shade-tolerant species (most commonly Douglas-fir or ponderosa pine). Under FEMAT's definition, however late-successional has nothing to do with dominance by shade-tolerant species, but rather is a stage of development of all forests that occurs well before, rather than in the later stages of, old-growth conditions. Unless noted otherwise, our use of late-successional will follow Spurr and Barnes (1973).

In the absence of fire or other disturbance, Douglas-fir in moderately moist Westside forests is gradually replaced over many centuries by shade-tolerant species, most commonly western hemlock. However, because of intermittent fires, shade-tolerant species rarely replace Douglas-fir altogether (Agee 1993). Similarly, frequent fires maintained dominance by ponderosa pine throughout most of the low- and mid-elevation forests in the interior of the Pacific Northwest; hence, forests dominated by shade-tolerant species were a minor component of the region. Late-successional forests have been more common at higher elevations in interior Oregon and Washington.

Old-growth forests are forests that have accumulated specific characteristics related to tree size, canopy structure, snags and woody

3

OLD-GROWTH FORESTS

INTRODUCTION

Issues surrounding old-growth forests are at the very center of discussions about forest management in the Pacific Northwest. Terms such as "overmature," "late successional," "ancient forest," "forest primeval," as well as "old growth," often are used interchangeably, adding to the confusion of these discussions. Furthermore, public perceptions of what an old-growth forest is might not jibe with quantitative definitions of forest scientists and managers (Ribe 1989).

This chapter describes the attributes that characterize old-growth forests. Variations among forest types are described with respect to those attributes, as well as variations in the age at which forests acquire particular characteristics after disturbance. The characteristics impart several unique ecological features of old-growth forests, such as complexity and high biodiversity, low susceptibility to disturbance, and mesic microclimate.

WHAT IS VEGETATIVE SUCCESSION?

Succession implies structural and compositional change in the species that dominate a plant community (and frequently an animal community as well). Fire, wind, disease, and other disturbance processes of varying intensity and frequency select for adaptations in a landscape's biota, making some species more resistant to and other species more resilient to effects of disturbance; some species have evolved to become depend-

debris, and plant associations. Ecological characteristics of old-growth forests emerge through the processes of succession. Certain features—presence of large, old trees, multilayered canopies, forest gaps, snags, woody debris, and a particular set of species that occur primarily in old-growth forests—do not appear simultaneously, nor at a fixed time in stand development. Old-growth forests support assemblages of plants and animals, environmental conditions, and ecological processes that are not found in younger forests (younger than 150–250 years) or in small patches of large, old trees. Specific attributes of old-growth forests develop through forest succession until the collective properties of an older forest are evident.

The U.S. Forest Service (USFS) Old-Growth Definition Task Group (1986) defined old-growth forests as the third of three basic stages in forest development. These forest stages are young, mature, and old; or, as sometimes distinguished by foresters, immature, mature, and overmature. In

Old-growth forests are forests that have accumulated specific characteristics related to tree size, canopy structure, snags and woody debris, and plant associations.

relatively stable stage with substantial continued growth and biomass accumulation, albeit at a slower rate than in the young forest. Transition from the mature to the old-growth stage is gradual. Douglas-fir stands do not begin to show the characteristics usually associated with old-growth until they are 175 to 200 years old.

Ecological characteristics of old-growth forests vary from one forest type to another (Tables 3-1 and 3-2) (Franklin and Spies, 1991a; Spies and Franklin, 1991), and therefore, no single definition of old growth is appropriate. Increasingly, definitions rely on indexes of successional development based on multiple forest characteristics (e.g., Spies 1991). USFS interim definitions for all types involve specific values or states for five criteria—number of large, old trees; variation in tree diameter; degree of tree decadence; amount of large, dead wood; and characteristics of the canopy architecture (USFS 1993b; Williams 1992).

• *Number of large, old trees.* The minimum density of large, old trees necessary for a stand to qualify as old growth varies from 16 to 50 per

overmature. In

Douglas-fir forests of the Pacific Northwest, maturation typically occurs at 80 to 110 years. The mature forest represents a

TABLE 3-1. Biomass and Production by Ecosystem Components for Eastside and Westside Forests

Species	Location ¹	Age (years)	Above-ground biomass (Mg/ha)	Below-ground biomass (Mg/ha)	Detritus wood (Mg/ha)	Forest floor mass (Mg/ha)	Soil organic matter (Mg/ha)	Total live and dead biomass (Mg/ha)	Above-ground NPP ² (Mg/ha/yr)	Total NPP (Mg/ha/yr)
WESTSIDE FORESTS										
Douglas fir	WA	36	173	33	6	16	112	340	-	-
	WA (SQ4)	22-73	132-304	-	-	-	-	-	5.1-9.3	-
	WA (SQ2)	40	453	-	-	-	-	-	13.7	-
	OR	50	301	67	12	7	88	475	-	-
	OR	70	464	-	-	29	251	-	-	-
	WA (SQ4)	40-70	170-256	30-44	-	27-28	50-70	277-398	9.1-8.9	12-12.5
	WA (SQ2)	40-70	306-379	56-67	-	23-23	70-120	455-589	11.1-15.8	13.7-18.8
	WA (SQ4)	150	763	141	-	30	50	984	13.5	17.8
	WA (SQ2)	150	812	154	-	20	110	1,096	9.6	11.5
	OR	90-110	661	-	-	-	-	-	12.7	10.9
	OR	150	865	-	-	-	-	-	10.5	-
	OR	450	718	153	215	51	113	1,250	8	10.9
Western hemlock/sitka spruce	OR	26	193	38	90	22	770	1,113	32.2	34.9
	OR	121	916	187	21	34	776	1,934	22.8	25.4
Noble fir/Douglas fir	OR	100-130	880	-	-	-	-	-	12.9	-
Mountain hemlock	WA	120-200	278	-	-	-	-	-	4.2	-

TABLE 3-1. (Continued)

Species	Location ¹	Age (years)	Above-ground biomass (Mg/ha)	Below-ground biomass (Mg/ha)	Detritus wood (Mg/ha)	Forest floor mass (Mg/ha)	Soil organic matter (Mg/ha)	Total live and dead biomass (Mg/ha)	Above-ground NPP ² (Mg/ha/yr)	Total NPP (Mg/ha/yr)
Pacific silver fir	WA	130	453	-	-	-	-	-	4.9	-
	WA	180	446	138	240	150	273	1,247	2.3	14.5
	WA	300-350	542	-	-	-	-	-	-	-
EASTSIDE FORESTS										
Ponderosa pine	WA	120-200	136	-	-	-	-	-	-	-
Lodgepole pine/ western larch	WA	70	199	-	-	-	-	-	8.6	-
	WA	>180	339	-	-	-	-	-	-	-
Lodgepole pine	WA	65-70	-	-	-	-	-	-	2.6	-
Western white pine	IDAHO	100-250	265-330	-	-	-	-	-	4.7-10	-
	IDAHO	103	415-675	-	-	-	-	-	11.4-17.6	-
	IDAHO	103	488-794	-	-	-	-	-	13.1-20	-

¹WA=Washington; OR=Oregon; SQ2=site quality 2; SQ4=site quality 4. Site quality is an index by which forests are grouped into classes based on past growth of trees on a site to predict future growth for a site. Site quality 2 is a high-productive site, while site quality 4 is a low-productive site.

²NPP=net primary production.

Source: Data from Vogt 1987, Gower et al. 1989, Vogt 1991, Vogt et al. 1996.

TABLE 3-2. Major Tree Species and Several of Their Dimensions in the Pacific Northwest

Species	Occurrence ¹	Fire tolerance ²	Shade tolerance ³	Modal (maximum age)	Number mycorrhizal species	Major abiotic and biotic constraints ⁴
WESTSIDE FORESTS						
<i>Abies amabilis</i> (Pacific silver fir)	OR, WA	-	VT	350 (>500)	9	APH, T, W
<i>Abies procera</i> (Noble fir)	OR, WA	-	INT	400+(>700)	1	NTM
<i>Picea sitchensis</i> (Sitka spruce)	CA, OR, WA	-	T	500 (>750)	21	NTM, W
<i>Sequoia sempervirens</i> (Redwood)	CA, OR	0 (young), + (mature)	T	1,000+ (>2,000)	?	M
<i>Thuja plicata</i> (Western redcedar)	CA, ID, OR, WA	-	T	200-500 (>1,200)	1 (vesicular-arbuscular)	APH, NTM
<i>Tsuga heterophylla</i> (Western hemlock)	CA, ID, OR, WA	-	VT	200+ (>500)	21	APH, BTR, DM, NTM, W
EASTSIDE AND WESTSIDE FORESTS						
<i>Abies concolor</i> (White fir)	CA, ID, OR, WA	- (young), 0 (mature)	VT	200 (300)	1	APH, DM, T, W
<i>Abies grandis</i> (Grand fir)	CA, ID, OR, WA	0	T	90-120 (250-280)	4	APH, BTR, M, T, W
<i>Pinus contorta</i> (Lodgepole pine)	ID, OR, WA	+	INT	200 (400)	25	BB, DM, M, W
<i>Pinus monticola</i> (Western white pine)	CA, ID, OR, WA	0	I	200 (500)	19	API, BB, DM, M, RR, T
<i>Tsuga mertensiana</i> (Mountain hemlock)	OR, WA	-	T	400+ (>800)	2	T, W

TABLE 3-2. (Continued)

Species	Occurrence ¹	Fire tolerance ²	Shade tolerance ³	Modal (maximum age)	Number mycorrhizal species	Major abiotic and biotic constraints ⁴
<i>Larix occidentalis</i> (Western larch)	ID, OR, WA	0 (young), + (mature)	INT	300+ (>700)	19	APN, DM, IP, M, RR
<i>Picea engelmanni</i> (Engelmann spruce)	CA, ID, OR, WA	-	T-VT	300+ (>500)	6	M, RR, W
<i>Pinus ponderosa</i> (Ponderosa pine)	ID, OR, WA	- (young), + (mature)	INT	200+ (500)	19	API, DM, BB, M, T

¹CA=California; ID=Idaho; OR=Oregon; WA=Washington.

²fire tolerance scale = + (high); - (detrimental); 0 (intermediate).

³shade tolerance scale = VT (very tolerant); T (tolerant); I (intermediate with seedlings more tolerant but mature trees less); INT (intolerant).

⁴major environmental constraint to growth = APH (highly sensitive to air pollution); API (intermediate sensitivity to air pollution); APN (not sensitive to air pollution); BB (bark beetles); BTR (butt and trunk rot); DM (dwarf mistletoe problems); IP (insect pest problems); M (moisture levels to low); NTM (no low temperature or moisture limits to growth); RR (root and butt rot); T (low temperatures, spring frosts); W (wind)

Source: Data from Trappe 1962; Hepting 1971; Franklin and Dyrness 1973; Franklin, 1979; Vogt et al. 1981; Molina and Trappe 1982; Parke et al. 1983.

Old-Growth Forests

ha, depending on forest type, with minimum sizes ranging from 52 cm diameter at breast height (dbh) on less-productive sites (generally in the interior) to 92 cm dbh on more-productive sites west of the Cascade crest. Old-growth forest might have 2 to 3 times that density of large, old trees. Minimum ages for these large dominant trees range from 150 years for the major interior forest types to 200 years for forests in western Oregon and Washington.

Old-growth Douglas-fir and ponderosa pine stands typically contain trees some 700 years old, and in some cases, more than 1,000 years. Old-growth Douglas-fir in western Oregon and Washington most commonly range from 350 to 700 years of age (Franklin et al. 1981). Under some circumstances, forests younger than 150-200 years produce trees that meet minimum size requirements, but those trees do not have characteristics of old-growth trees, such as thick, deeply incised bark and various manifestations of decadence as discussed below (Spies and Franklin 1991).

- *Variation in tree diameter.* Variation in tree diameters is greater in old-growth forests than in younger forests. For example, in the western hemlock zone of western Oregon and Washington, the standard deviation of tree diameters in stands 200 years or older is 2 to 3 times that of younger stands. In many forest types, that difference in diameter reflects the increasing abundance of shade-tolerant tree species in the understory as forests age. In other cases, such as ponderosa pine, it is due to small patches of young pine regenerating within the old-growth matrix.

- *Tree decadence.* In western Oregon and Washington, stands of Douglas-fir that are considered old growth have greater numbers of trees with broken tops, excavated bole cavities, root collar cavities, and bark resinosis than either young or mature stands (Spies and Franklin 1991). Those characteristics are typical of old trees throughout the region; old grand fir trees, for example, are commonly infected with a heart rot called Indian Paint fungus (*Echinodontium tinctorium*).

- *Presence of large dead wood.* Large, standing snags and fallen tree boles typify all types of old-growth forests. On average, 25-35% of the standing boles in old-growth Douglas-fir stands are snags comparable in size to living trees, with more than half of the snags larger than 50 cm diameter (Franklin and Spies 1991b). Large logs are also common on the forest floor (termed "down wood") in Douglas-fir old growth forests, as

well as in high-elevation forest types. Down wood occurs in dry forest types, such as ponderosa pine, but less commonly than in more mesic forests. Snags and logs are important structural features of old-growth forests in providing wildlife habitat (Maser et al. 1979; Thomas et al. 1979; Harmon et al. 1986). In the Blue Mountains, for example, 39 bird and 23 mammal species use snags, and 179 vertebrate species make at least some use of down wood (Thomas et al. 1979; Maser et al. 1979).

Young, naturally established stands also can have large dead wood as legacies from the previous stand. Hence, presence of large, dead wood does not distinguish an old-growth forest as reliably among natural stands of different ages as does the number of large trees (Franklin and Spies 1991b; Spies and Franklin 1991).

• *Canopy architecture.* Large variation in tree diameters in old-growth forests is accompanied by a high degree of structural complexity in the forest canopy. Old-growth forests contain multiple tree-canopy layers (in addition to herb and shrub layers), a feature common to all types except ponderosa pine, lodgepole pine, and Eastside Douglas-fir. That layering reflects the growth of saplings (mostly shade-tolerant trees) into midcanopy strata as stands age. Old-growth forests in western Oregon and Washington also tend to have greater shrub and herb cover than younger stands (Spies and Franklin 1991). That is largely a function of overstory canopy density, inasmuch as open-grown younger stands generally have abundant shrub cover. Frequent ground fires retard understory growth in ponderosa pine and Eastside Douglas-fir forests.

A typical old-growth forest also has areas with little or no understory, resulting in a patchy spatial structure. Patchiness is a distinguishing characteristic of old-growth ponderosa pine, in which small islands (roughly 0.25-0.5 ha) of regenerating pine occur scattered through a matrix of older trees. Viewed from above, the pattern of canopy cover in old-growth stands is distinct from younger stands. Cohen et al. (1990) used low-altitude remote images from the central Oregon Cascades to calculate semivariance, a geostatistical technique that quantifies average patterns of variance. Different age classes of forests were easily distinguished visually using the red bands of the spectrum. Nel et al. (1994) assessed the value of remote imagery of canopy reflection to identify old growth in spruce-fir forests of the interior West. They found the same general patterns as Cohen et al. (1990) but concluded that although remote imagery was a useful guide to old-growth stands, it was not sufficient to identify old-growth stands with certainty.

Time Required for Old-Growth Development

Development of old-growth characteristics forests is progressive and varies among forest types. Some characteristics first appear about a century after a disturbance that destroys a forest stand (Table 3-3). Across the region, many old-growth characteristics develop during the second century of stand development, but forests do not typically display all of the properties described above before they are 200 years old.

Rates of succession differ from site to site depending on environmental conditions, nutrient and moisture availability, and residual forest components from the previous stand. To deal with the spatial and temporal variability in succession, Franklin and Spies (1991b) developed a continuously varying index of old growth based on the following five criteria for naturally established stands in the Oregon coast range, Cascades, and the southern Washington Cascades:

- density of large trees (e.g., more than 80cm Dbh)
- density of shade-tolerant trees
- amount of crown decadence (e.g., broken tops and multiple tops)
- density of large snags
- log biomass (using 60 Mg per ha as the base value)

On the Westside, Douglas-fir stands younger than 200 years generally have a low old-growth index (Franklin and Spies 1991b). Forests in that region have been classified as old growth at ages ranging from 150-250 years (Franklin and Spies 1991b; Johnson et al. 1991; Bonnicksen 1993; FEMAT 1993; Bolsinger and Waddell 1993). There is, however, considerable change in old-growth features across that age span. In the Franklin and Spies (1991b) study region, the old-growth index averaged a little more than 2.0 for stands younger than 100 years (range, 0-6.0), 3.0 for stands between 100 and 300 years (range, 0.3-5.0), and 6.0 for stands older than 300 years (range, 1.0-10.0) (Spies and Franklin 1991).

Old-Growth Landscapes

Ideas about how forests developed following major natural disturbances

TABLE 3-3. Standard of Old-Growth Characteristics for Different Forest Types in Oregon and Washington

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	Live Trees			Variation in Tree Diameter	Tree Decadence	Tree Canopy Layers	Dead Trees			
	Main Canopy		Standing				Down			
WESTSIDE FORESTS	DBH*	TPA*	AGE*	(Yes or No)	TPA	Number	DBH	TPA	Diameter	Pieces
Douglas-fir										
High Sites (1,2,3)	37" (94cm)	8 (20tph)	190	Yes	No	2	13" (33cm)	1 (3tph)	24" (61cm)	4 (10/ha)
Medium Sites (4)	34" (86cm)	9 (22tph)	205	Yes	Yes	2	15" (38cm)	1 (3tph)	24" (61cm)	4 (10/ha)
Low sites (5)	24" (61cm)	10 (25tph)	200	Yes	Yes	2	17" (43cm)	1 (3tph)	24" (61cm)	4 (10/ha)
Western Hemlock										
Site Class 1	42" (107cm)	8 (20tph)	200	Yes	Yes	2	20" (51cm)	4 (10tph)	12" (30cm)	69 (170/ha)
Site Class 2	35" (89cm)	8 (20tph)	200	Yes	Yes	2	20" (51cm)	4 (10tph)	12" (30cm)	37 (91/ha)
Site Class 3	31" (79cm)	8 (20tph)	200	Yes	Yes	2	20" (51cm)	4 (10tph)	10" (25cm)	15 (37/ha)
Site Class 4 & 5	21" (53cm)	8 (20tph)	200	Yes	Yes	2	20" (51cm)	4 (10tph)	8" (20cm)	29 (72/ha)
Pacific Silver Fir										
Sites 2 & 3	26" (66cm)	6 (15tph)	180	Yes	Yes	2	22" (56cm)	6 (15tph)	24" (61cm)	4 (10tph)
Site 4	25" (64cm)	7 (17tph)	200	Yes	Yes	2	22" (56cm)	4 (10tph)	24" (61cm)	4 (10tph)
Site 5	22" (56cm)	9 (22tph)	260	Yes	Yes	2	22" (56cm)	1 (2tph)	24" (61cm)	4 (10tph)
Site 6	22" (56cm)	1 (2tph)	360	Yes	Yes	2	22" (56cm)	12 (30tph)	24" (61cm)	4 (10tph)
Port Orford Cedar										
All Sites	32" (80cm)	16 (40tph)	240	Yes	No data	2	14" (36cm)	6 (15tph)	13" (33cm)	27 (68/ha)
Tanoak (Redwood)										
All Sites	32" (80cm)	8 (20tph)	240	Yes	No data	2	32" (80cm)	3 (7.5tph)	13" (33cm)	20 (50/ha)
EASTSIDE FORESTS										
White fir/Grand fir (Central Oregon)										
Low & Medium Sites	21" (53cm)	10 (25tph)	150	Yes	Yes	2	14" (36cm)	1 (2.5tph)	12" (30cm)	5 (13/ha)
High Sites	21" (53cm)	15 (38tph)	150	Yes	Yes	2	14" (36cm)	1 (2.5tph)	12" (30cm)	5 (13/ha)

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TABLE 3-3. (Continued)

	Live Trees			Variation in Tree Diameter	Tree Decadence	Tree Canopy Layers	Dead Trees			
	Main	Canopy					Standing		Down	
White fir/Grand fir (Blue Mountains)										
Low & Medium Sites	21" (53cm)	10 (25tph)	150	Yes	Yes	2	14" (36cm)	1 (2.5tph)	12" (30cm)	5 (13/ha)
High Sites	21" (53cm)	20 (50tph)	150	Yes	Yes	2	14" (36cm)	1 (2.5tph)	12" (30cm)	5 (13/ha)
Ponderosa Pine										
Low Sites	21" (53cm)	10 (25tph)	150	Yes	---	1	14" (36cm)	3 (7.5tph)	---	0
	31" ¹ (79cm)	2 (5tph)	200	Yes	Yes	1	Same	Same	Same	Same
Medium & High Sites	21" (53cm)	13 (33tph)	200	Yes	---	1	14" (36cm)	3 (7.5tph)	---	0
	31" ¹ (79cm)	3 (8tph)		Yes	Yes	1	Same	Same	Same	Same
Douglas-fir										
All Sites	21" (53cm)	8 (20tph)	150	Yes	2 (5tph)	1	12" (30cm)	1 (2.5tph)	12" (30cm)	2 (5tph)
Lodgepole Pine (Sierra)										
All Sites	12" (30cm)	60 (150tph)	120	Yes	No data	1	12" (30cm)	5 (13tph)	---	0

*Required minimums

(Metric equivalents in parenthesis)

¹Very late seral (decadent) conditions

in the Douglas-fir region are changing significantly as a result of new information developed from historic stand reconstructions. The traditional view for coniferous forests (excepting ponderosa pine) is based on experience during the 20th century with stand development after logging (Oliver 1981; Oliver and Larson 1996). In that model, all trees composing the forest originate from the same disturbance, hence the stand is relatively even-aged. Trees grow into competition with one another and stands enter a self-thinning or "stem exclusion" phase, followed some time later by an "understory reinitiation stage" in which shade tolerant trees and shrubs become established. Over time, stands eventually attain old-growth status.

A growing number of studies suggest the traditional model does not accurately describe development of old growth in the Douglas-fir region (Tappeiner et al. 1997). Historic reconstructions performed to date, covering a wide area of western Oregon including the Cascade, Siskiyou, and Coast Range mountains, have consistently found old-growth stands consisted of multiple age classes of overstory trees spanning many tens of decades rather than a single age class (Franklin and Hemstrom 1981; Tappeiner et al. 1997). In their study of 10 old-growth stands in the Oregon Coast Range, Tappeiner et al (1997) concluded the oldest trees had established at low densities, with additional trees filling in over many years. They also found considerable patchiness within stands, some plots having a narrow age range of overstory trees and others having a wide range.

The picture now emerging is different and more complex than the traditional view, with considerable spatial and temporal heterogeneity, much less self-thinning than occurs in the even-aged stands created by clearcutting, an abundance of biological legacies, and intimate mixtures of older and younger trees intermingled both as individuals and in discrete patches. If a significant cover of hardwoods existed along with the conifers, which is suggested by the relative low conifer stocking, susceptibility to crown fires would have been low except under extreme weather conditions (Perry 1988a), and conifer diseases, a problem in many plantations, would have spread less readily than in densely stocked pure conifer stands (Manion 1981; Simard and Vyse 1994). The resulting old-growth landscape would have been dynamic but, because of a structure that tended to damp the spread of catastrophic disturbances, also relatively stable (Perry 1995a). While older trees, with their

unique structure and habitat values, are a vital component (Bull et al. 1992; FEMAT 1993; Peck and McCune 1997), the structure and functioning of old-growth landscapes emerges not from age alone, but from variable patterns of disturbance and succession within a more or less stable landscape matrix of older trees. The scale over which these dynamics played out historically, hence the characteristic spatial patterns of age classes and other structural attributes, varied among regions (e.g., from mesic to dry forests; SNEP 1996a,b), within watersheds (e.g., from southerly to northerly aspects and with elevation, Cissel et al. 1998), and over time in any one area due to the influence of varying macroclimate (Fryer and Johnson 1988; Swetnam 1993). As we discuss later, this view of a dynamic yet stable old-growth landscape serves as a basis for some of the new approaches to forest management being applied in the region.

Managed Forests and Old-Growth Characteristics

Managed forests can be thinned to produce large trees and structural heterogeneity at a relatively early age, especially in areas of high site quality. For example, a 75-year-old stand on the Black Rock State Forest (Oregon coast range), thinned to 125 trees per ha 30 years ago, now has an average tree diameter approaching the minimum old-growth requirement. But the degree to which such forests can be managed to mimic old-growth habitat and processes is unclear. Many managed forests either have no large dead wood or have much less than occurs in natural stands, which significantly reduces their habitat value for many animal species.

Some important characteristics of old trees are not related strictly to size and may be difficult to attain in trees younger than 175-200 years. For example, pileated woodpeckers, keystone species that excavate cavities used by numerous other bird and mammal species, prefer to roost in large grand fir trees extensively decayed by Indian paint fungus (Bull et al. 1992). The fungus is believed to enter through broken tops, which usually occur in older trees, and takes at least 20 years after entry to create sufficient decay for woodpecker use. Similarly, marbled

murrelets prefer nest trees "in declining condition and (with) multiple defects (including) mistletoe blooms, unusual limb deformations, decadence, and tree damage" (Hammer and Nelson 1995). Alecroid lichens and cyanolichens — critical links in the food chain and, in the case of the latter, the nitrogen cycle — are much more diverse and abundant in old-growth than in young and mature stands, a phenomenon related in part at least to limited dispersal (Peck and McCune 1997), hence a matter of time. However, the time required for populations to recover may be shortened by the presence of hotspots of lichen diversity within young stands, especially old, remnant trees and hardwoods associated with gaps in the conifer canopy (Neitlich and McCune 1997).

Producing managed stands with large, old living and dead trees, dedicated to stay on site, is a primary objective of the relatively new silvicultural approach termed "variable retention" (Franklin et al. 1997). Such techniques attempt to mimic natural disturbances by preserving legacies such as decaying logs and accumulations of soil organic matter (Franklin 1993a). In time, practices that mimic natural disturbance patterns in managed stands might produce managed forests with at least some old-growth characteristics. However, the degree to which that is true can be determined only by extensive testing.

Stand Size

Edge effects (such as altered light conditions, animal activities, or species composition) can extend more than 100 m into a stand (Chen et al. 1992), which means that a 3-ha stand might exhibit edge effects throughout. The ecological relevance of edge effects depends on numerous factors. Small fragments are normally more vulnerable to drying (and hence to fire and wind damage) than large stands, but an old-growth fragment surrounded by mature forest presents a different situation than one surrounded by clearcuts. A fragment might be too small to provide habitat for some species, but it might be large enough for others. Furthermore, finding individuals of a given species in a fragment does not necessarily indicate the quality of the habitat. For example, marbled murrelets (*Brachyramphus marmoratus*) will nest in

very small old-growth patches, but some evidence suggests that they are vulnerable to predators in such restricted habitats (Ralph et al. 1995).

The minimum size necessary for a stand to qualify as old growth has been subject to much debate. The Old-Growth Definition Task Group (1986) originally suggested 32 ha as a minimum, reasoning that, "patches of smaller size were not . . . viable old-growth units because of their dominance by edge effects (penetration of external environmental influences) and vulnerability to major disturbances such as windthrow." However, that requirement was dropped because "minimum acreages for old-growth depended on management objectives and the nature of surrounding areas" (Old-Growth Definition Task Group 1986).

Fragmentation of intact old-growth stands increases vulnerability to disturbance and diminishes habitat values for at least some species; however, even very small old-growth fragments may retain some important biological values. The vulnerability and biological values of small patches depend heavily on the character of the landscape in which they are imbedded. Thus, no absolute statement regarding minimum size of old-growth stands can be made.

BIOLOGICAL FUNCTIONS OF

OLD-GROWTH AND LATE-SUCCESSIONAL FORESTS

The biological functioning of old-growth and late-successional forests is an important consideration in management of the Pacific Northwest terrestrial and aquatic ecosystems. To provide some understanding of the role of old-growth forests in the region, the discussion below centers on significant biological features and how biotic diversity of old-growth forests compares with that of younger forests.

Old-growth forests are biotically more complex than forests in earlier successional stages, and many species depend on the unique environmental features of old-growth forests for survival. Compared with younger forests, old-growth forests have a greater diversity of ecosystem components and specialized organisms and produce more food for some animal species (e.g., red-backed voles and spotted owls). They have higher total amount of live and dead biomass (mainly due to the

increased presence of coarse wood) and a higher amount of woody debris in streams and terrestrial areas. Old-growth forests are also less susceptible to large-scale disturbances and pest outbreaks, and they have a lower incidence of root-rot problems. Old-growth forests have unique microclimates and might have an effect on regional climate as well.

Species Diversity

The Scientific Analysis Team (SAT 1993) listed 80 terrestrial vertebrate species (16 amphibians, 38 birds, and 26 mammals) that were "closely associated" with old-growth stands in the range of the northern spotted owl, along with 99 invertebrate species and 111 vascular plant species. In his analysis of forests in western Oregon and Washington, Harris (1984) estimated that 118 terrestrial vertebrate species used old growth as primary habitat, 135 species used young forests (before canopy closure), and 90 species used mature forests. He also noted that "all of the species that meet their primary habitat requirements in...early stage forests find abundant habitat throughout the western Cascades and are generally common. Forty of the species finding primary habitat...in old-growth or mature forest cannot meet their habitat requirements outside this forest type."

Thomas et al. (1979) found somewhat different patterns in the Blue Mountains of eastern Oregon and Washington. In all forest types in the Blue Mountains, more terrestrial vertebrate species reproduced in mature and old-growth stands than in early-successional stands, but little difference was seen between old-growth and mature stands. The Blue Mountains and the Cascades have significantly different environments and hence, different patterns of forest development.

Arthropods and other small or inconspicuous organisms account for the bulk of diversity but have been largely overlooked until recently (Parsons et al. 1991), despite their importance in terms of numbers, species diversity, and functional importance. Lattin (1990) estimated that 8,000 arthropod species are found in the H.J. Andrews Experimental Forest in the central Cascades, compared with 143 vertebrate species and 460 vascular plant species. Many of those arthropods live either in

canopies or soils, the least studied subsystems in forests. Schowalter (2000) compiled data from 9 forest, grassland, desert, and marsh ecosystems where extensive species inventories are available to show that arthropods commonly account for at least 70-90% of all species present.

The few studies that have been completed found striking differences between old-growth and younger forests in epiphyte, arthropod, and lichen communities. For example, one of the distinguishing characteristics of old-growth Douglas-fir forests is the abundance of epiphytic plants (mosses and lichens), especially the nitrogen-fixing lichen *Lobaria oreгона*. *Lobaria* occurs in younger stands but not nearly as abundantly as in old-growth forests (Franklin et al. 1981).

Arthropod communities in old-growth canopies are significantly more diverse than in young plantations. Schowalter (1989, 1995) measured more than 70 species of arthropods associated with Douglas-fir and western hemlock foliage in old-growth forests in the central Cascades and only 15 species associated with Douglas-fir in 7- to 11-year-old stands. Diversity was 5-6 times greater in old-growth stands than in younger stands, with some of the most striking differences occurring in the diversity of predatory arthropods, such as spiders (Schowalter 1995). Moreover, the structure of arthropod communities differed significantly between young and old forests. In the former, the biomass of phytophages (largely aphids) was 800% greater than that of predators (e.g., ants, wasps, and spiders), while in the latter, the biomass of plant eaters (largely defoliators) was only 20% greater than that of predators. That pattern suggests more effective internal controls over plant eaters in old-growth stands than in younger stands.

The dominance of hardwoods and shrubs in young forests in part reflects the suppression of conifers by insects and pathogens at this stage. Conifers become re-established after populations of insects and pathogens have been reduced because they have so few conifer hosts (Goheen and Hansen 1993). The pines, western larch, western red cedar, Engelmann spruce, and western hemlock have higher tree mortality associated with root disease in early stages of stand development (younger than 30 years), but mortality decreases thereafter (Hagle and Goheen 1988).

Indigenous insects and diseases might have important roles in stand

development by mitigating the effects of biomass accumulation and competitive stress through natural pruning, thinning, and cycling nutrients. Old-growth forests generally have higher populations of predatory insects than younger forests; those insects might help maintain populations of herbivorous insects at lower levels than in young stands (Schowalter 1989, 1995). Management practices that focus on short rotations or plantations of single species result in an overall loss of predators. Pests also are better able to find their hosts in such managed forests, and the systems become more susceptible to insect outbreaks (Hagler and Schmitz 1993, Schowalter 1995).

Logs and Woody Debris

Much of the influence of old-growth forests on environmental conditions is conferred by their large persistent structures. Whereas younger or smaller trees decompose relatively quickly (Harmon et al. 1986), large boles of old trees contain terpenoid and phenolic compounds in the heartwood that inhibit decay and provide structure and resources for soil and aquatic systems for centuries after tree death and fall (Harmon et al. 1986; Schowalter et al. 1992; Schowalter et al. 1998; Progar 2000).

Logs decomposing on slopes stabilize soils, retain moisture during dry periods (often more than 200% of wood dry weight, especially after a period of decay has increased porosity), and provide organic matter and nutrients that are tapped by mycorrhizae and roots penetrating wood from surrounding plants (Harmon et al. 1986; Schowalter et al. 1992). Logs falling into streams create the pool-and-riffle structure that contributes to aquatic biodiversity. Logs are essential components of salmon habitat, slowing erosion from upslope and minimizing scouring of streambeds that degrade salmon habitat.

Although amounts of woody debris that can function in conserving mycorrhizal inoculi are highest in late-successional forests (Vogt et al. 1995), the actual diversity and biomass of mycorrhizal fungi may peak in the early stages of stand development. Only limited data exist on the pattern of mycorrhizal development with stand age (Vogt et al. 1992), but existing information suggests that the number of mycorrhizal species and the associated sporocarp biomass peak at canopy closure. Thus, total diversity of mycorrhizal fungi may be more closely tied to

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the net primary production of a forest than to structural components such as coarse wood. In contrast, the diversity of certain groups, such as the truffle formers, is higher in old-growth stands than in young stands (Amaranthus et al. 1994).

The number of sites for mycorrhizal fungal colonization of root tips is maximal at canopy closure (Vogt et al. 1983). The peaking of mycorrhizal fungi in early states of stand development might indicate a carbon cost to plants to maintain mycorrhizal associations (Vogt et al. 1991); hence, less carbon might be available to sustain all plant parts after that stage (Grier and Logan 1977). All Pacific Northwest forest tree species have a good complement of different mycorrhizal species that are capable of colonizing tree-root systems (e.g., almost 1,000 species mycorrhizal associates have been reported for Douglas-fir (Perry et al. 1992)). Many of the trees share similar species of mycorrhizal associations.

Insects and pathogens are instrumental in directing succession through their selection of plant species. Although

Old-growth forests are more resistant to crown fires than are younger forests....

tree characteristics have been emphasized in most studies of successional insects, pathogens, and other taxa influence seed production and dispersal, tree growth and survival, nutrient cycling, and soil-fertility patterns, and therefore affect the rate and direction of succession transformation. For example, several insects and root pathogens that kill Douglas-fir trees are instrumental in accelerating the transition hemlock or cedar forest but also might provide litter accumulation sufficient to fuel a stand replacement fire (Goheen and Hansen 1993). Insects and root diseases responsible for stand replacement also can retard germination and growth of young conifers after disturbances.

Susceptibility to Disturbance

Old-growth forests are more resistant to crown fires than are young forests, perhaps because of high humidity and litter moisture (Perry 1988a; Franklin et al. 1989; Chen et al. 1993). The hardwood and shrub species in the old-growth understory also appear to inhibit fire spread.

and to protect interspersed conifers. Young, evenly aged conifer forests are the most flammable and are particularly vulnerable to reburns (Agee 1993). Old-growth forests might be most vulnerable to fire where adjacent younger, drier, and more flammable forests provide the necessary heat and fuels to carry flames into the forest canopy. However, the heterogeneous structure of old-growth forests and the water-saturated logs provide barriers to fire spread, allow trees to survive, and provide open spaces for growth of understory (Perry 1988a; Palazzi et al. 1992).

AQUATIC ECOSYSTEMS

Streamside disturbance and flooding have important impacts on virtually all components of aquatic ecosystems (Reiter and Beschta 1995); however, no component has received more attention than salmon and trout. Seven species of salmon exist in the Pacific Ocean, and five occur on the North American continent: chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), and sockeye salmon (*O. nerka*). In addition, there are anadromous trout, steelhead or rainbow trout (*O. mykiss*), coastal cutthroat trout (*O. clarki*), and Dolly Varden trout (*Salvelinus malma*). Those salmonid species do not obligately require old-growth forests for survival, but they did evolve across a geographic range that closely overlaps that of the Northwestern coniferous forests.

Anadromous salmon and trout spawn in freshwater streams. Fry and juveniles rear in streams and rivers (sockeye in lakes), migrate to the ocean, spend varying amounts of time (depending on species and stocks), return as adults to their natal streams, spawn, and die. All Pacific salmon die after spawning, but a small fraction of anadromous trout are capable of repeated ocean migration and spawning. All eight species of the anadromous salmon and trout spend a portion of their lives in freshwater habitats in forested areas of the Pacific Northwest. As a result, their survival and production are closely linked to the forest ecosystem and are influenced by changes caused by forest practices (NRC 1996).

Disturbance, which is a critical feature of streams and rivers, strongly influences the survival of salmon and trout. Floods are a natural and

essential component of rivers. Streams are shaped by floods, and rivers are more productive after flooding. Although productivity might decline immediately after flooding, flooding in streams creates pools, cleans gravels, and delivers dissolved and particulate nutrients. Refuges, such as deep pools, boulders and logs, off-channel habitats on floodplains, and stems and roots of streamside forests, are required for aquatic organisms to survive frequent disturbances. Over short- and long-term scales, old-growth forests along streams and floodplains create sizes and amounts of woody debris that cannot be provided by younger forests. Floodplain habitats, large woody debris, and pool habitats have declined substantially in recent years, and conversion of old-growth forests to younger stands is one of the causes of habitat losses related to the decline of Pacific salmon (NRC 1996). Many processes mediated by old-growth trees can be provided in riparian reserves or stream-management zones, but riparian management must be integrated with watershed conditions and land-use practices.

EXTENT AND STATUS OF OLD-GROWTH FORESTS

Differences in estimates of the past and present extent of old-growth forest in the Pacific Northwest reflect differences in the definitions used in each study: the time frame (e.g., presettlement, early settlement, pre-World War II, or current), the geographic area (e.g., states, Eastside forests, or Westside forests), land-use types (e.g., forest lands only or combinations of forest, agricultural, residential, and urban lands), and type of ownership (e.g., public, private, or national park). Eight studies have attempted to evaluate the current extent of old-growth forest in the Pacific Northwest, and eight studies have attempted to reconstruct the past distribution (Table 3-4). When allowances are made for the factors above, the study results are much the same.

Regional patterns of forest age classes and structure before logging resulted from the frequency and severity of natural disturbances, primarily fire, and to a lesser degree, wind, insects, and pathogens. The natural fire regime is closely linked to climate and, as a result, historic patterns of forest succession have varied within the region.

Estimates of the extent of old-growth before logging in the Douglas-fir

TABLE 3-4. Comparison of Studies of the Historical Extent of Old-Growth Forests in the Pacific Northwest

Study	Timeframe	Region	Landbase	Extent
Bonnicksen 1993	Pre-1850	W OR, W WA	Public and private forest land	42%-77%
Booth 1991	Pre-1850	W OR, W WA	Public and private forest land	62%
Teensma et al. 1991	1890	Coastal OR	Public and private forest land	46%
Morrison 1991	Pre-1850	W OR, W WA	Public and private forest land	66%
Morrison and Swanson 1990	1200-1990	Central Cascades, OR	Public forest land only	25%-49%
Andrews and Cowlin 1940	Mid-1930s	W OR, W WA, NW CA	Public and private forest land	44%
Cowlin et al. 1942	1936	E OR, E WA (excludes 2 counties)	Public and private forest land	73%
Lehnkuhl et al. 1994	1932-1959	E OR, E WA	Public forest only (6 national forests)	Mean-8.8%
Bolsinger and Berger 1975	mid-1950	E OR	Public land only (Ochoco National Forest)	44%
Hemstrom and Franklin 1982	1980 (represents historical)	Mt. Rainer National Park	Public forest land only	65%

region west of the Cascades crest, inferred largely from fire histories, range from 5.6 million ha to nearly 8 million ha, or 54-70% of the commercial forest area (Andrews and Cowlin 1940; Franklin and Spies 1984; Norse 1990; Booth 1994). The first inventory of Pacific Northwest

forests on the west side of the Cascades, conducted in the mid-1930s after a period of heavy logging in the lowlands and severe logging-related fires, recorded old-growth forests covering 4 million ha, or 44% of the commercial forest (Andrews and Cowlin 1940). In southwestern Oregon, where little logging had occurred by the 1930s, old-growth trees of various species accounted for 73% of the commercial forest (Cowlin et al. 1942). In the Oregon Cascades and eastern coast range, only 8% of forests had been cut by the mid-1930s, and 57% remained in old-growth stands. In western Washington, 18% of the commercial forest had been logged by the 1930s, leaving 45% in old-growth stands.

Most reconstructions of presettlement conditions estimate that old-growth forests covered 54-70% of the forest area in western Washington and Oregon. Timber harvest and development have reduced this to 13-18% (Table 3-5).

Using a landscape simulation model driven by climate change and its coupling to fire, Wimberly et al. (2000) estimated that old-growth forest coverage in the Oregon Coast Range varied from 25-75% during the past 3000 years. The earliest quantitative estimate for the Oregon coast range was that old-growth trees covered 33% of the commercial forest in the mid-1930s (Andrews and Cowlin 1940). By that time, a significant amount had been logged, and large areas of old-growth trees had been destroyed by rampant wildfires. If logged areas and the Tillamook burn are added to the 1930s inventory, estimates of old-growth stands in presettlement coast range forests rises to 47%, which is consistent with the Teensma et al. (1991) estimate of 46% in 1890. Slightly more than one-third of coast range forests were between 90 and 200 years old in the 1930s survey. Because of logging-related fires, estimates of fire patterns based on wildfires during the past century are likely to overestimate presettlement fire frequency and, thus, underestimate the original extent of old-growth forests.

At the time of the 1930s survey, an additional 2.5 million ha in western Oregon and Washington were 90- to 160-year-old stands that had been established by fire. About 50% of those stands had trees averaging 50 cm dbh or more and were beginning to take on old-growth characteristics. Thus, by the 1930s, despite extensive logging, 68% of commercial forest land in western Oregon and Washington remained in what FEMAT (1993) classified as "late-successional/old-growth" (stands 80 years of age or older). Based on that figure, when Euro-Americans

TABLE 3-5. Comparison of Studies of the Existing Extent of Old-Growth Forests in the Pacific Northwest

Study	Timeframe	Region	Landbase	Extent
Morrison 1991	Mid 1980s	W OR, W WA	Public and private forest land	13%
Lehmkuhl et al. 1994	1985-1990	E OR, E WA	Public forest only	Mean-4.5%
FEMAT 1993	1990	W OR, W WA, NW CA	Public forest only	<20%
Hann et al. 1994	1992	W MT	Public forest only (Beaverhead N.F.)	3%-21%
Bolsinger and Waddell 1993	1992	W OR, W WA, NW CA	Public and private forest lands	18%

arrived in the area in the 1800s, as much as 80% of the forests in western Oregon and Washington were older than 80 years and about two-thirds were older than 200 years.

Forests of interior Oregon and Washington were also dominated by old-growth stands. The first comprehensive survey of forest resources in eastern Oregon and Washington (excluding northeastern Washington) was completed in 1936, at which time "the area of commercial forestland [was] characterized by a high proportion of old-growth" (Cowlin et al. 1942). The 1936 survey found that old-growth forests of all types made up 89% of the sawlog-sized stands and 73% of all commercial forest in eastern Oregon and Washington. Nearly two-thirds of Eastside forest lands covered by the 1936 survey were dominated by ponderosa pine, which, even after a period of heavy cutting that began in the early 1920s, was still mostly old-growth. If adjustments are made for logging before 1936, the original low-and-mid-elevation ponderosa pine forests were nearly 90% old growth. Those stands typically contained trees up to 60-70 in dbh with most of the stand volume concentrated in trees 20-44 in dbh (Cowlin et al. 1942).

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In the late 1800s on what is now the Ochoco National Forest, surveyors recorded ponderosa pine at 93% of the section corners in all but the wettest forest types (north slopes above 5,000 feet in elevation).

Various tree species other than ponderosa pine dominated forests at higher elevations and on moist sites at mid-elevations in the interior. In the 1936 survey, those species were classified as either large or small rather than as old-growth or second-growth, which was the case with ponderosa pine and Douglas-fir. In 1936, 71-96% of species other than ponderosa pine were classified as large, which almost certainly would fit within current definitions of old-growth for these types. In 1936, 11% of Eastside forest lands were lodgepole pine, a pioneer tree species that colonizes sites after wildfire. Most of those stands were classified as medium-sized and probably were not old-growth.

No comprehensive early surveys exist for Idaho, western Montana, and extreme northeastern Washington. Forest types of central Idaho are quite similar to those in the Blue Mountains of Oregon and Washington, and historic patterns are unlikely to have differed substantially between the two areas. In contrast, forest types in northeastern Washington and northern Idaho are unlike other Eastside forests, having higher proportions of Douglas-fir and a representation of species such as western hemlock and western red cedar that are more typical of Westside forests.

Historically, northeastern Washington and northern Idaho had extensive stands of western white pine that were probably mostly old growth. These have either been logged or killed by white pine blister rust (an introduced pathogen). The moist western red cedar stands, common in northeastern Washington and northern Idaho, probably had a relatively large proportion of old growth, because fires were infrequent and of a low intensity that seldom killed large overstory trees.

The most extensive and recent analysis of the current extent of old-growth forest included all federal, state, and private forest lands in western Washington, western Oregon, and northern California (Bolsinger and Waddell 1993). Old-growth forests were estimated to occupy 18% of the existing forest lands in the area. That analysis was based on recent maps and interpretations by the array of institutions and ownerships that have been responding to the debate over old-growth stands during the past 2 decades.

Conditions of Eastside forests were reviewed by the Eastside Forests Scientific Panel (Henjum et al. 1994), which concluded that approximately 25% of the land on eight national forests in eastern Washington and Oregon was old-growth forest. When public and private lands are considered, that proportion decreases to less than 20%, which is consistent with the distribution of old growth estimated for Westside forests (Bolsinger and Waddell 1993).

The composition of Pacific Northwest forests has changed dramatically over the past 10,000 years since the last ice age. Thus, the distribution and amount of old-growth forests before settlement represents only one point along a continuum of natural forest change. In some prehistoric periods, old-growth coniferous forests made up less than the 60-70% of the forest that settlers encountered when they first came to the Northwest (Brubaker et al. 1992; Whitlock 1992). Regardless of the extent that old-growth forest might have increased and decreased naturally over thousands of years, the reduction of old-growth over the past century is a more abrupt change than the forests have undergone since the last ice age.

SUMMARY

Because the ecological characteristics of old-growth forests vary from one forest to another, no single definition of old growth is appropriate. However, as knowledge has progressed, various indexes of successional development have been developed to characterize forests. Old-growth forests are biotically complex, with some species depending on unique features of old growth to survive, and the biological functioning of old-growth and late-successional forests is important to management of terrestrial and aquatic ecosystems.

Fifty percent of Pacific Northwest land is forested. Depending on locality, late-successional and old-growth forests originally made up from 54-70% of the forests, but now they are only 10-18%. Harvest since 1850 has removed more than 80% of the late-successional and old-growth forests of the Pacific Northwest; nonetheless, more than 80% of the remaining old-growth forests occur in national forests.

4

THE STATUS AND FUNCTIONING OF PACIFIC NORTHWEST FORESTS

INTRODUCTION

In this chapter, the status, condition, and sustainability of the forested ecosystems and associated plant and animal species of the Pacific Northwest are reviewed and assessed. The effects of forest-use patterns and management practices on timber and nontimber species are evaluated, and the discussion includes an analysis of species that are threatened or endangered by forest cutting and habitat fragmentation. The chapter ends by considering the long-term effects of the loss of biological diversity on the stability and functioning of ecosystems in general. The findings presented in this chapter provide important bases for the assessment of forest management practices in Chapters 7 and 8.

FOREST CONDITION

General Criteria of Condition

A system that is in good condition is one that retains its basic structures and processes (Rapport 1989). The condition of an ecosystem represents more than the absence of disease. It is also the ability to resist or recover quickly from environmental stressors. Because ecosystems seldom have clear boundaries, ecological condition spans spatial scales. The structure of landscapes, for example, shapes processes (e.g., hydrology and propagation of disturbances) that influence the integrity of stands and