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Two Decades of Stability and Change in Old-growth Forest at Mount Rainier National Park

Abstract

We examined how composition and structure of old-growth and mature forests at Mount Rainier National Park changed between the mid-1970s and mid-1990s. We assessed whether the patterns of forest dynamics observed in lower elevation old-growth forests in the Pacific Northwest held true for the higher-elevation forests of the Park. We used measurements of tree recruitment, growth, and mortality on 18 permanent plots that spanned the range of forested environments in the Park. Similar to previous studies, there was little change in stand structure and composition, while a relatively large number of individual stems died or were recruited into the tree population. Most recruitment was of shade-tolerant tree species. Unlike some previous studies, in many stands recruitment of shade-tolerant individuals occurred without substantial mortality of shade-tolerant trees in the upper canopy. Habitat characteristics associated with old-growth forest changed little in most stands. One exception was a mature noble fir stand in which a brief episode of tree mortality, apparently due to drought and pathogens, increased similarity to old-growth structure. Plots in old-growth forest on the coldest and wettest sites in the Park had low similarity to the published definition of upper-slope old-growth forest at both the beginning and end of the study, suggesting that the existing definition may not apply at these environmental extremes.

Introduction

In recent decades, there has been increasing interest in biological diversity and ecosystem functions of old-growth forests. Although very young forests may harbor a greater number of species, old-growth forests often provide habitat for plant and animal species less common in, or missing from, earlier stages of forest development (Spies and Franklin 1996). Old-growth forests may moderate microclimate and store carbon to a greater extent than younger forests (Spies and Franklin 1996, Janisch and Harmon 2002).

Interest in old-growth forest has grown simultaneously as the area occupied by old-growth forest has declined. Over a five-decade period ending in the 1990s, the area of old-growth forest in Oregon and Washington declined by 67% (Bolsinger and Waddell 1993; see Moeur et al. 2005 for more recent trends on federal lands). This decrease in the area of old-growth forest was a key element in the controversy surrounding management of federal forest land in the Pacific Northwest in the 1990s (Thomas 1997). Reserved areas such as Mount Rainier and other National Parks provide significant areas of old-growth forest (Forest Ecosystem Management Assessment Team 1993). Although Mount Rainier National Park is most famous for alpine features, 60% of the Park is forested, and 65% of the forested area consists of stands >200 yr old (Franklin et al. 1988).

Long-term studies are essential for development and testing of ecological theory, and application of ecological knowledge to natural resource management (Franklin 1989). Old-growth forests of the Pacific Northwest are an excellent case in point,

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given that dominant tree species can live for many centuries and intervals between stand-replacing disturbances can be similarly long (Franklin 1989, Acker et al. 1998a, Franklin and Halpern 2000). However, most studies of forest dynamics in the region have focused on the first few decades after stand-replacing disturbance (Franklin and Halpern 2000).

The few studies of dynamics of old-growth forest in the Pacific Northwest have shown that overall species composition can be stable for decades, even while many individual trees die and are replaced by regeneration, measured as ingrowth (Franklin and DeBell 1988, Edmonds et al. 1993). In such stands, recruitment of individuals of shade-tolerant tree species is common, especially under openings in the forest canopy (Huff 1995, Edmonds et al. 1993, Moeur 1992, Franklin and DeBell 1988, Stewart 1986, 1989, DeBell and Franklin 1987). In particular, recruitment of shade-tolerant trees is most likely where the shade tolerant species western hemlock is absent from the forest canopy (Stewart 1986, 1989). Due to the processes of recruitment of shade-tolerant tree species and mortality of dominant, pioneering species, the habitat features of old-growth forest will gradually shift over time (DeBell and Franklin 1987, Barbour et al. 2002, Franklin et al. 2002).

The purpose of this paper is to examine how the composition and structure of old-growth and mature forests at Mount Rainier National Park have changed over the last 20 yr. We asked several questions. Do previously observed patterns, mostly obtained from lower-elevation forests of Douglas-fir and western hemlock, also apply to the higher-elevation forests of the Park where species such as Pacific silver fir and mountain hemlock dominate mature vegetation? Has stand structure and species composition remained relatively constant in the face of loss and recruitment of individual trees? Has recruitment of shade-tolerant trees occurred in response to mortality of shade-tolerant canopy trees? Have habitat characteristics associated with old-growth forests changed?

Our analyses derive from research on basic plant population and ecosystem processes at sites representing the full range of forested environments in the Park (Acker et al. 1998a, Dyrness and Acker 2000). Since study locations were chosen subjectively, it is not possible to draw direct inferences from the study plots to the Park as a whole. However, since the locations are broadly representative of the Park's forests, our analyses should indicate whether forests there are changing dramatically, and whether dynamics are similar to those observed elsewhere in the Pacific Northwest.

Study Sites

Permanent forest plots were established at 18 locations in Mount Rainier National Park between 1976 and 1978 (Table 1). Plots range from 600 m to 1,600 m elevation, encompassing most of the elevation range of closed-canopy forest in the Park (Franklin et al. 1988). Plots are located in the major river drainage basins (Nisqually, Ohanapecosh, White, and Carbon), and include all four corners of the Park. The potential vegetation for forested areas of the Park has been classified into 14 plant associations (Franklin et al. 1988), 11 of which are represented within the permanent plots. Most of the plots are in old-growth forests (Table 1).

Franklin et al. (1988) organized forested plant associations of Mount Rainier National Park into four groups: moist, modal, dry, and cold. Moist forest types represented in the permanent plots include western hemlock/devil's club (*Tsuga heterophylla/Oplopanax horridum*), western hemlock/vanillaleaf (*T. heterophylla/Achlys triphylla*), Pacific silver fir/devil's club (*Abies amabilis/O. horridum*), and Pacific silver fir/coolwort foamflower (*A. amabilis/Tiarella unifoliata*). Dominant tree species in these plots are Douglas-fir (*Pseudotsuga menziesii*), western hemlock, noble fir (*Abies procera*), Pacific silver fir, and western red cedar (*Thuja plicata*).

The modal forest type comprises one plant association, Pacific silver fir/Alaska blueberry (*A. amabilis/Vaccinium alaskaense*). Permanent plots in this plant association type are dominated by Pacific silver fir and western hemlock.

Dry forest types represented in the permanent plots are Pacific silver fir/salal (*A. amabilis/Gaultheria shallon*), Pacific silver fir/dull Oregon grape (*A. amabilis/Berberis nervosa*), and Pacific silver fir/beargrass (*A. amabilis/Xerophyllum tenax*). Dominant tree species in plots in these forest types are western hemlock, western red cedar, Douglas-fir, and Pacific silver fir.

Cold forest types in the plot set include Pacific silver fir/dwarf bramble (*A. amabilis/Rubus*

TABLE 1. Permanent forest plots in Mount Rainier National Park. Plots are ordered from warm and dry to cold and wet using the plant association classification of Franklin et al. (1988).

Plot name	Elev. (m)	Plant association	Seral stage	Dominant tree species
PP17	1116	Douglas-fir-lodgepole pine/pinemat manzanita	Old-growth	Douglas-fir, lodgepole pine
TB13	1018	Western hemlock/dull Oregongrape	Mature	Douglas-fir, western hemlock
TA01	671	Western hemlock/vanillaleaf	Old-growth	Douglas-fir, western hemlock
TO04	668	Western hemlock/devil's club	Old-growth	Western hemlock, Douglas-fir
TO11	604	Western hemlock/devil's club	Mature	Douglas-fir, western hemlock
AG05	951	Pacific silver fir/salal	Old-growth	Pacific silver fir, western red cedar
AB08	1055	Pacific silver fir/dull Oregongrape	Old-growth	Western hemlock, western red cedar
AV02	841	Pacific silver fir/Alaska blueberry	Old-growth	Pacific silver fir, western hemlock
AV06	1061	Pacific silver fir/Alaska blueberry	Old-growth	Pacific silver fir, western hemlock
AV14	1067	Pacific silver fir/Alaska blueberry	Old-growth	Pacific silver fir, western hemlock
CCNF	1250	Pacific silver fir/coolwort foamflower	Old-growth	Noble fir, western hemlock
SRNF	1506	Pacific silver fir/coolwort foamflower	Mature	Noble fir, Douglas-fir
AO03	866	Pacific silver fir/devil's club	Old-growth	Pacific silver fir, western red cedar
AX15	1024	Pacific silver fir/beargrass	Mature	Douglas-fir, western hemlock
AE10	1451	Pacific silver fir/avalanche lily	Old-growth	Pacific silver fir, Alaska yellow cedar
AR19	1615	Pacific silver fir/dwarf bramble	Mature	Subalpine fir, Pacific silver fir
AM16	1183	Pacific silver fir/fool's huckleberry	Old-growth	Alaska yellow cedar, mountain hemlock
AR07	1451	Pacific silver fir/white rhododendron	Old-growth	Pacific silver fir, mountain hemlock

lasiococcus), Pacific silver fir/fool's huckleberry (*A. amabilis*/*Menziesia ferruginea*), and Pacific silver fir/white rhododendron (*A. amabilis*/ *Rhododendron albiflorum*). Dominant tree species in the plots are Pacific silver fir, Alaska yellow cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), and subalpine fir (*Abies lasiocarpa*).

Common names for plants follow Hitchcock and Cronquist (1973).

Methods

Most of the plots consisted of 1-ha, slope-corrected squares within which all trees ≥15 cm dbh (diameter at breast height, 1.37 m) are tagged and mapped. Within the 1-ha plots, trees between 5 and 15 cm dbh were tagged and mapped on selected 0.0625 ha subplots. Three of the permanent plots (CCNF, SRNF, and AR19 in Table 1), consisted of five, 0.1 ha circular subplots systematically spaced along linear transects. Perimeters of these circular subplots were not corrected for the effects of slope and in some cases the collective projected area was less than 0.5 ha. All results are reported on a horizontal-area basis.

At establishment between 1976 and 1978, and every five years thereafter, dbh was measured on all tagged trees. The relative position of each tree's crown was recorded as lower stratum (i.e., suppressed or intermediate), or upper stratum (i.e., codominant or dominant) (Avery and Burkhart 1994). Trees that died since the last measurement were noted and conditions (e.g., position of tree bole, presence of pathogens) and possible causes of tree mortality were recorded. At each measurement, trees that had grown large enough to meet the minimum size requirement became part of the tree population, and were tagged, mapped, and measured. Due to a staggered schedule of measurements, the interval between the first and last measurements of individual plots ranged from 16 to 20 yr.

To assess changes in structure associated with old-growth forest habitat, we compared the earliest and most recent measurement of each plot to definitions of young and old forest structure (Spies and Franklin 1991, Fierst et al. 1993). Following Acker et al. (1998b), we computed an index of old-growth structure, I_{og}, by comparing various structural variables to values used to define young and old forest (Table 2). For the western hemlock zone (i.e., plots TB13, TA01, TO04, TO11), Spies and Franklin (1991) found four variables that were most efficient at distinguishing old from young forests (standard deviation of tree dbh, density of

TABLE 2. Structural variables used to define similarity to typical old-growth forest.

Variable	Young forest value	Old-growth forest value
Western hemlock zone (four variables)		
Standard deviation of tree dbh	12	32
Douglas-fir trees > 100 cm dbh per ha	0.5	19
Mean tree dbh (cm)	21	31
Trees per ha	935	448
Pacific silver fir zone (two variables)[1]		
Standard deviation of tree dbh	17	31
Quadratic mean tree dbh (cm)	40	54

[1] Values averaged across all site classes reported by Fierst et al. (1993).

Douglas-firs > 100 cm dbh, mean tree dbh, and tree density). For the Pacific silver fir zone (i.e., all other plots except PP17), Fierst et al. (1993) identified two variables that were consistently different between young and old stands (standard deviation of tree dbh and quadratic mean tree dbh). I_{og} ranges from 0 for stand structure typical of young forest, to 100 for stand structure typical of old forest (Acker et al. 1998b). Plot PP17 was excluded from the analysis of change in old-growth structure. This plot represents an azonal forest type at Mt. Rainier National Park that occurs on unproductive substrates and apparently does not develop into closed-canopy forest (Franklin et al. 1988). Old-growth characteristics have not been defined for this type of forest.

Results

Forest composition and structure changed little over the two decades of observation. The rank order of tree species in relative basal area was unchanged in 16 of the 18 plots, and changes in the other two plots were not dramatic. In plot AX15, Douglas-fir and western hemlock traded places as the first and second dominant species with Douglas-fir basal area dropping from 52% to 44% and western hemlock basal area rising from 41% to 48%. In AR07, Pacific silver fir and mountain hemlock traded places as leading species, though both species accounted for ~40% of basal area in both the first and last measurements.

Changes in total basal area were also generally subtle (Figure 1). Total basal area increased on 14 of the 18 plots, but most changes were less than 10%. The one exception was plot PP17, an open stand on a rocky, river-terrace site dominated by Douglas-fir and lodgepole pine (*Pinus contorta*). Basal area in this plot increased by 26% (Figure 1), though it was still less than 35% of the mean basal area of the 18 plots (25.5 m²/ha for PP17; mean of 79.1 m²/ha for all plots).

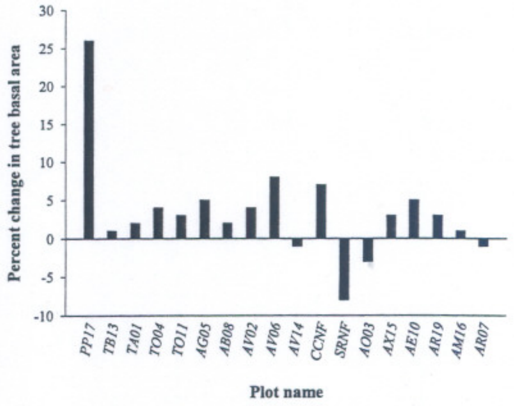

Figure 1. Percent change in total tree basal area on permanent plots at Mount Rainier National Park. Plots are ordered from warm and dry to cold and wet using the plant association classification of Franklin et al. (1988).

More change occurred in stem density, with 10 of the 18 plots changing by ≥ 10% (Figure 2). Of the three plots that decreased by at least 10%, two are mature stands that appeared to be undergoing competitive thinning, as would be expected (Franklin et al. 2002). In both plots TB13 and AX15, over 80% of the dying trees

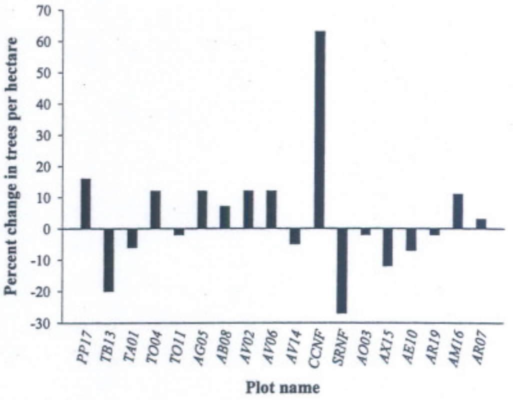

Figure 2. Percent change in total stem density (trees per hectare) on permanent plots at Mount Rainier National Park. Plots are ordered from warm and dry to cold and wet using the plant association classification of Franklin et al. (1988).

were from lower canopy strata and nearly 80% of dying trees were found standing. This mortality process is responsible for the ascendancy of western hemlock over Douglas-fir at plot AX15 as noted above. In plot TB13, competitive thinning did not result in notable changes in tree species composition.

Competitive thinning does not appear to be the cause of the relatively large decline in stem density at plot SRNF. There, nearly 30% of dying trees were from upper canopy strata and total basal area of the stand declined by >5% (Figure 1). The mean annual mortality rate was ~2%, about twice published rates for similar-age stands in the region (Franklin et al. 1987; Edmonds et al. 1993). Over 80% of dying trees were of a single species (noble fir). Nearly 90% of dying trees were standing, suggesting some biotic agent (e.g., insects or pathogen) as the cause of mortality, or possibly drought.

On seven of the plots, stem density increased by ≥ 10%. Recruitment was primarily shade-tolerant western hemlock and Pacific silver fir in all cases except plot PP17. Plots with significant recruitment of shade-tolerant species include moist (TO04, CCNF), modal (AV02, AV06), dry (AG05), and cold (AM16) types.

High turnover of stems in the lower canopy stratum occurred in most plots (Table 3). In 17 of the 18 plots, mortality in the lower stratum, recruitment, or both was equivalent to at least 10% of the initial stem density. Shade-tolerant species accounted for nearly all recruitment, with the exception of plot PP17. In contrast to trees lower in the canopy, there was little mortality of trees in the upper canopy stratum in most plots. With the exception of plot SRNF, upper stratum mortality ranged from 0 to 24 trees per ha. Mortality of shade-tolerants in the upper stratum ranged from 0 to 20 trees per ha.

There was no relationship between recruitment of shade-tolerant trees and mortality of shade-tolerants in the upper canopy stratum (Figure 3). High amounts of recruitment occurred across almost the entire range of upper canopy mortality. In addition, in some plots relatively high mortality of upper canopy shade-tolerants coincided with relatively little recruitment of shade-tolerant trees.

In general, the degree of development of habitat characteristics associated with old-growth forest

TABLE 3. Initial tree density, mortality, recruitment, and final tree density of shade-tolerant (Tol) and shade-intolerant (Intol) species. Plots are ordered from warm and dry to cold and wet using the plant association classification of Franklin et al. (1988). All values are in trees per ha.

		Mortality by canopy stratum						
	Initial	Lower		Upper		Recruitment		Final
Plot	density	Tol	Intol	Tol	Intol	Tol	Intol	density
PP17	815	18	48	0	13	53	206	947
TB13	572	95	5	9	4	4	0	455
TA01	399	15	3	1	9	4	0	375
TO04	423	83	1	11	3	197	1	471
TO11	249	46	1	4	0	45	0	243
AG05	870	122	0	18	0	285	0	975
AB08	422	6	0	7	2	58	0	453
AV02	1034	91	0	18	1	228	0	1153
AV06	1188	126	2	11	0	385	0	1326
AV14	491	61	0	13	0	66	0	465
CCNF	423	44	2	0	2	300	16	691
SRNF	776	13	162	0	67	31	0	565
AO03	381	42	0	20	0	53	0	372
AX15	925	64	49	0	20	28	0	818
AE10	781	91	1	4	0	42	0	724
AR19	756	0	86	0	24	62	34	744
AM16	841	17	0	7	0	146	0	936
AR07	487	35	0	15	0	64	0	498

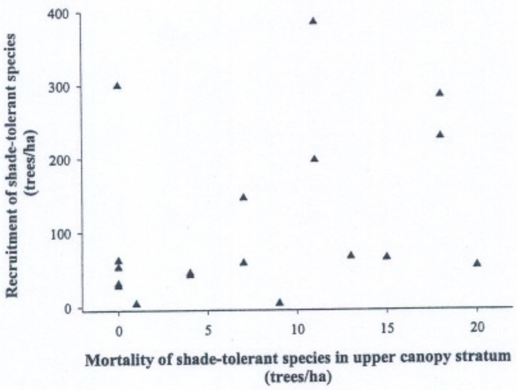

Figure 3. Recruitment of shade-tolerant stems (trees per hectare) on permanent plots at Mount Rainier National Park versus mortality of shade-tolerant stems in the upper canopy stratum.

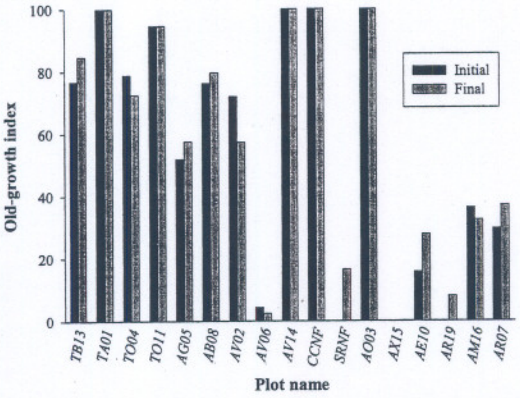

Figure 4. Old-growth index (I_{og}) for permanent plots at Mount Rainier National Park, at beginning and end of study. Plots are ordered from warm and dry to cold and wet using the plant association classification of Franklin et al. (1988).

changed only slightly over the two decades of observation (Figure 4). In 14 of the 17 plots analyzed, I_{og} changed 10 points or less out of a possible 100 points. The three stands with greater change in old-growth characteristics include an old-growth stand in which I_{og} declined (AV02), a mature stand in which I_{og} increased (SRNF), and an old-growth stand in which I_{og} increased (AE10). At AV02, recruitment and, to a lesser extent, upper canopy mortality (Table 3), shifted the diameter distribution to smaller sizes and reduced the heterogeneity of tree sizes (i.e., decreased standard deviation of tree dbh). At SRNF, mortality occurred among trees of all sizes, but was somewhat concentrated among smaller trees (Table 3), shifting the diameter distribution to larger trees. At AE10, mortality in the lower stratum exceeded recruitment (Table 3), shifting the diameter distribution to larger trees and increasing the heterogeneity of tree sizes.

Four stands classified as old-growth based on stand age were structurally more similar to young forest than old growth (i.e., I_{og} <50; AV06, AE10, AM16, AR07). Three of these four stands occupied the coldest and wettest forest habitats in the Park (Franklin et al. 1988), and all were above 1060 m elevation.

Discussion

The set of permanent plots of Mount Rainier National Park is not a statistical sample of the Park's forests, so direct inferences to overall forest conditions are not possible. However, the plots do span the elevational, geographic, and compositional range of forest in the Park and so should be broadly representative of trends in forest dynamics. The forests do not appear to be undergoing rapid decline, as has been observed in permanent plots elsewhere (Keane and Arno 1993, Vacek and Leps 1996). Similar to lower-elevation old-growth forests in the Pacific Northwest, little change has occurred in species composition or stand structure, even as a relatively large number of individual stems have died and been replaced (Franklin and DeBell 1988, Edmonds et al. 1993). Habitat conditions associated with old-growth forest have generally persisted, though continuation of present trends, including recruitment of trees of shade-tolerant species, could result in decreased similarity to typical old-growth structure.

Some of these results confirm and some run counter to previous generalizations about Pacific Northwest old-growth forest. As previously shown for lower-elevation old-growth forests, the overall stability in stand structure and composition over two decades is deceptive, because many stems died (mostly lower in the canopy) and were replaced on most plots (Franklin and DeBell 1988). It is necessary to track individual trees to understand overall stand dynamics and population processes in old-growth forests (Franklin and DeBell 1988).

Recruitment was primarily of shade-tolerant species (Table 3), as others have found in the region (Huff 1995, Edmonds et al. 1993, Moeur 1992, Franklin and DeBell 1988, Stewart 1986, 1989, DeBell and Franklin 1987). However, in contrast to some previous studies (Stewart 1986, 1989), recruitment of shade-tolerant trees was not restricted to plots with marked attrition of shade-tolerant individuals in the upper canopy. There is, no doubt, an upper limit on the potential stocking of these stands, so that at some point competition-induced mortality will decrease the density of recruits or upper canopy trees, or both.

Though the degree of similarity to typical old-growth structure was constant or nearly constant on most plots, the exceptions point to processes that both generate and remove old-growth structure. The most marked increase in similarity to old-growth structure occurred in the mature noble fir stand represented by plot SRNF. This was also the plot with the largest tree mortality, in terms of percentage of the original cohort (Figure 2). This stand appears to have undergone a brief spike in tree mortality in the mid-1990s, due to the combined effects of drought, the pathogenic fungus *Armillaria* sp., and the bark beetle *Scolytus ventralis* (David C. Shaw, Oregon State University, personal communication). Franklin et al. (2002) reported that density-independent or non-competitive mortality agents such as bark beetles and root rots play important roles in development of old-growth characteristics in mature stands of Douglas-fir, which also appears to be the case in mature noble fir stands at higher elevations. Plot AV02 illustrates the potential longer-term implications of recruitment of large numbers of shade-tolerant trees (and upper stratum mortality): a shift to a tree-size distribution dominated by smaller trees, less heterogeneity of tree sizes, and as a consequence, habitat characteristics more akin to young forests.

In the Pacific Northwest, most efforts to develop quantitative definitions of old-growth forests have been devoted to more widespread, lower-elevation forests where Douglas-fir is a dominant species (Marcot et al. 1991). The consistently low similarity to typical old-growth structure we found for several old-growth plots in the Pacific silver fir zone may reflect the lack of knowledge of variation of old-growth structure along environmental gradients within that zone. Three of these four plots represented the coldest, wettest forested environments at Mount Rainier National Park (Franklin et al. 1988). It may be that the typical patterns of development and resulting old-growth structure are fundamentally different in the cold and wet extremes of upper slope forests in the Pacific Northwest. If so, land managers seeking to promote old-growth structure will need to adopt different approaches for sites representing different positions along key environmental gradients within the Pacific silver fir zone.

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Literature Cited

Acker, S. A., W. A. McKee, M. E. Harmon, and J. F. Franklin. 1998a. Long-term research on forest dynamics in the Pacific Northwest: a network of permanent plots. Pages 93-106 *In* F. Dallmeier and J.A. Comiskey (editors), Forest Biodiversity in North, Central and South America, and the Caribbean: Research and Monitoring. UNESCO, Paris.

Acker, S. A., T. E. Sabin, L. M. Ganio, and W. A. McKee 1998b. Development of old-growth structure and timber volume growth trends in maturing Douglas-fir stands. Forest Ecology and Management 104:265-280.

Avery, T. E., and H. E. Burkhart. 1994. Forest Measurements. 4th edition. McGraw-Hill, New York.

Barbour, M., E. Kelley, P. Maloney, D. Rizzo, E. Royce, and J. Fites-Kaufman. 2002. Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada, US. Journal of Vegetation Science 13:461-472.

Bolsinger, C. L., and K. L. Waddell. 1993. Area of Old-growth Forests in California, Oregon, and Washington. USDA Forest Service Resource Bulletin PNW-RB-197. Pacific Northwest Research Station, Portland, Oregon.

DeBell, D. S., and J. F. Franklin. 1987. Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. Western Journal of Applied Forestry 2: 111-114.

Dyrness, T., and S. Acker. 2000. Permanent Plots in the Mount Rainier National Park. Permanent Plots of the Pacific Northwest. H. J. Andrews Experimental Forest Long-Term Ecological Research Site, Corvallis, Oregon. Available online at http://www.fsl.orst.edu/lter/pubs/webdocs/reports/permplot.cfm.

Edmonds, R. L., T. B. Thomas, and K. P. Maybury. 1993. Tree population dynamics, growth, and mortality in old-growth forests in the western Olympic Mountains, Washington. Canadian Journal of Forest Research 23: 512-519.

Fierst, J., D. White, J. Allen, T. High, and S. Greene. 1992. Region 6 Interim Old Growth Definition for Pacific Silver Fir Series. USDA Forest Service, Timber Management Group. Portland, Oregon.

Forest Ecosystem Management Assessment Team. 1993. Forest Ecosystem Management: an Ecological, Economic, and Social Assessment. U.S. Government. Printing Office, Washington, D. C.

Franklin, J. F. 1989. Importance and justification of long-term studies in ecology. Pages 3-19 *In* G. E. Likens (editor), Long-term Studies in Ecology. Springer-Verlag, New York.

Franklin, J. F., and D. S. DeBell 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. Canadian Journal of Forest Research 18:633-639.

Franklin, J. F., and C. B. Halpern. 2000. Pacific Northwest forests. Pages 123-159 *In* M. G. Barbour and W. D. Billings (editors), North American Terrestrial Vegetation. 2nd Edition. Cambridge University Press, Cambridge, UK.

Franklin, J. F., W. H. Moir, M. A. Hemstrom, S. E. Greene, and B. G. Smith. 1988. The Forest Communities of Mount Rainier National Park. Scientific Monograph Series No. 19, USDI National Park Service, Washington, D.C.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. BioScience 37:550-556.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399-423.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, Washington.

Huff, M. H. 1995. Forest age structure and development following wildfires in the western Olympic Mountains, Washington. Ecological Applications 5:471-483.

Janisch, J. E., and M. E. Harmon. 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. Tree Physiology 22:77-89.

Keane, R. E. and S. F. Arno. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. Western Journal of Applied Forestry 8:44-47.

Marcot, B. G., R. S. Holthausen, J. Teply, and W. D. Carrier. 1991. Old-growth inventories: status definitions, and visions for the future. Pages 47-60 *In* L. Ruggiero, (editor), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. General Technical Report PNW-GTR-285. USDA Pacific Northwest Research Station, Portland, Oregon.

Moeur, M. 1992. Baseline demographics of late successional western hemlock/western redcedar stands in northern Idaho Research Natural Areas. Research Paper INT-456. USDA Forest Service Intermountain Research Station, Ogden, Utah.

Moeur, M., T.A. Spies, M. Hemstrom, J. Martin, J. Alegria, J. Browning, J. Cissel, W.B. Cohen, T.E. Demeo, S. Healey, and R. Warbington. 2005. Northwest Forest Plan-The First 10 Years (1994-2003): Status and Trend of Late-successional and Old-growth Forest. General Technical Report PNW-GTR-646. USDA Pacific Northwest Research Station, Portland, Oregon.

Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91-110 *In* L. Ruggiero, (editor), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. General Technical Report PNW-GTR-285. USDA Pacific Northwest Research Station, Portland, Oregon.

Spies, T. A., and J. F. Franklin. 1996. The diversity and maintenance of old growth forests. Pages 296-314 *In* R.C. Szaro and D.W. Johnston (editors), Biodiversity in Managed Landscapes: Theory and Practice. Oxford University Press, New York.

Stewart, G. H. 1986. Population dynamics of a montane conifer forest, western Cascade Range, Oregon, USA. Ecology 67:534-544.

Stewart, G. H. 1989. The dynamics of old-growth *Pseudotsuga* forests in the western Cascade Range, Oregon, USA. Vegetatio 82:79-94.

Thomas, J. W. 1997. Foreward. Pages ix-xii *In* K. A. Kohm and J. F. Franklin (editors), Creating a Forestry for the 21st Century. Island Press, Washington, D. C.

Vacek, S., and J. Leps. 1996. Spatial dynamics of forest decline: the role of neighboring trees. Journal of Vegetation Science 7:789-798.

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