LONG-TERM PATTERNS OF DOUGLAS-FIR AND WESTERN HEMLOCK MORTALITY IN THE WESTERN CASCADE MOUNTAINS OF WASHINGTON AND OREGON

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ABSTRACT

LONG-TERM PATTERNS OF DOUGLAS-FIR AND WESTERN HEMLOCK MORTALITY IN THE WESTERN CASCADE MOUNTAINS OF WASHINGTON AND OREGON

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Change in temporal patterns of mortality rates, tree population structure (size and density), biomass accumulation, input of coarse woody debris, and causes of mortality of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sargent) were investigated in nine stands spanning the young (45–80 yr), mature (81–200 yr), and old-growth (>200 yr) stages of forest development using long-term records (12 to 84 yr) in permanent plots in the Cascade Mountains of western Washington and Oregon. High average annual mortality rates for Douglas-fir (1.1-2.9%) occurred in young stands which was driven by the mortality of small, suppressed trees (≤25 cm DBH). In old growth, mortality rates were substantially lower (0.5-0.7%) and causes were from density-independent agents notably root and stem decay. In young and mature stands, the high rates of mortality of small Douglas-fir had little negative effect on the accumulation of biomass which increased steadily (~4.8 Mg ha^{-1} yr^{-1}). However, in old growth, due to minimal recruitment, slow growth, and continued mortality, Douglas-fir biomass accumulation rates were mostly negative and standing stocks decreased. Average annual input of Douglas-fir woody debris was similar among all stand ages (~2.1 Mg ha^{-1} yr^{-1}). Western hemlock average annual mortality rates were low in young (0.0%) and mature (0.1%) stands, but, in old growth, rates were greater (0.3-0.5%) due to a combination of suppression, snow loading and physical damage from falling trees. Western hemlock contribution to biomass was minimal as the majority of individuals were small. Mortality was also composed mostly of small trees and input to woody debris was light (0.2-0.8 Mg ha^{-1} yr^{-1}). Many of the patterns that emerge from these records support previous assumptions about mortality, although these are among the first data to confirm these trends. The larger perspective provided by these data sets allow for some new inferences about relationships of tree mortality to forest stand development and ecosystem processes.

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INTRODUCTION

Tree mortality is an important process in the development of forest ecosystems. The transfer of biomass to debris, the release of resources, and the creation of wildlife habitat are all set in motion by tree death (Sollins 1981, Harmon et al. 1986, Franklin et al. 1987, Maser et al. 1988, Castello et al. 1995, Hennon 1995, Wells et al. 1998, Van Pelt and Franklin 2000). At times mortality may even be the dominant process that influences tree population structure (size and density) and community composition (Peet and Christensen 1980).

Yet as fundamental to forest development as tree mortality appears to be, foresters and ecologists have amassed limited knowledge of the overall process. The majority of published information on mortality represents the study of single-species, single cohort stands. Considerably less is known about causal agents of mortality and concomitant effects on ecosystem structure, composition, and function in more complex and older forests (Franklin and DeBell 1988, Milton et al. 1994). This is a major limitation to forest science: for example, Ryan et al. (1996) cited the general lack of information on tree mortality as a constraint to predicting forest response to global climate. Goudriaan et al. (1999) concluded that mortality was difficult to represent in models of forest dynamics because there are few data on tree mortality rates.

The longevity of tree species and the temporal and spatial variability of mortality make it difficult to study the process. Empirical data, from long-term observations (20 or more years) at a large spatial scale, are critical for accurate analysis of trends and variations in patterns of tree mortality (Franklin 1989, Pickett 1991). Fortunately, appropriate data sets are beginning to emerge from various forested regions (e.g., Franklin and Van Pelt 1990, Condit 1998).

This study is a detailed examination of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sargent) mortality in advancing stages of forest structural development from young (45–80 yr), to mature (81–200 yr), and old growth (>200 yr). Results were drawn from nine forested study areas located along the western Cascade Mountains in Oregon and Washington. These study areas ranged in age from 45 to 460 yr at the time of permanent plot installation and have long records (12 to 84 yr) of repeated observations. My primary objectives were to investigate (1) changes in temporal patterns of mortality rates, (2) effects of mortality on tree population structure (density and sizes), (3) changes in patterns of biomass accumulation rates and stocks and inputs of woody debris, and (4) causes of mortality.

METHODS

STUDY SPECIES

The primary species of interest are Douglas-fir and western hemlock of the western Cascadian Province of the Western Hemlock Zone in Washington and Oregon. Douglas-fir is a long-lived, shade-intolerant species that often dominates low- to mid-elevation forests west of the crest of the Cascades Range. It regenerates well following wildfires that eliminate the overstory canopy and expose mineral soil seedbeds. Establishment of Douglas-fir with canopy closure (45–80 yr) and the redevelopment of deep soil organic layers and low available soil moisture (Isaac 1943, Spies and Franklin 1988, Spies 1997). Those individuals that survive canopy closure can live more than 750 yr attaining heights of 70–80 m at the mature stage (81–200 yr) of forest structural development and 150–220 cm in diameter at breast height (DBH) in the old-growth stage (>200 yr) (Franklin and Waring 1980, Spies and Franklin 1988, Spies 1997). In the absence of recruitment, Douglas-fir gradually declines in abundance and is replaced by shade-tolerant conifers, particularly western hemlock (Franklin et al. 2001).

Western hemlock is a long-lived, shade-tolerant species that can also establish after a major disturbance in the region, but large numbers of trees are more typical in the later stages of forest development (Franklin and Hemstrom 1981, Spies 1997). It regenerates well in shaded understory conditions, particularly as a Douglas-fir dominated stand undergoes maturation (Franklin et al. 2001). Individual western hemlock can live for centuries and grow to 50–60 m in height and 90–120 cm in DBH (Franklin and Waring 1980, Franklin and Hemstrom 1981). In the absence of another major disturbance, western hemlock gradually increases its importance in the stand (Munger 1930, Munger 1940).

Several other conifer species inhabit the Western Hemlock Zone, but Douglas-fir or western hemlock or both typically dominate composition throughout the entire course of forest development. Associated coniferous species include Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), grand fir (*Abies grandis* (Dougl.) Lindl.), noble fir (*Abies procera* Rehd.), incense-cedar (*Calocedrus decurrens* Torr.), western white pine (*Pinus monticola* Dougl. Ex D. Don.), Pacific yew (*Taxus brevifolia* Nutt.), and western red-cedar (*Thuja plicata* Donn.).

STUDY AREAS

Long-term observations are necessary for an accurate identification of trends as well as rare or subtle variations in patterns of tree mortality. Fortunately long-term data are continually being acquired and made available by the Permanent Sample Plot (PSP) program, a partnership among the Forest Science Data Bank (FSDB), the Department of Forest Science at Oregon State University, the U.S. Forest Service Pacific Northwest Research Station, and the National Science Foundation's Long-Term Ecological Research Program (NSF-LTER). PSP datasets contain information on plant association, tree sizes (DBH and tree heights), and mortality. Data are collected from tagged trees on permanent plots. Minimum DBH for inclusion into datasets is 5 cm.

Nine forested study areas were selected from the PSP database to construct a sequence spanning the young (45–80 yr), mature (81–200 yr), and old-growth (>200 yr) stages of forest development: three were young-mature (45–137 yr), two mature (90–148 yr), and four old growth (270–472 yr). The nine study areas range in elevation from 300 to 1000 meters and distributed from Mount Rainier National Park in Washington to near the middle fork of the Willamette River in central Oregon (Figure 1, Table 1). Details on climate, soils, geology and plant composition in the Western Hemlock Zone are provided in Franklin and Waring (1980) and Franklin and Dyrness (Franklin and Dyrness 1988).

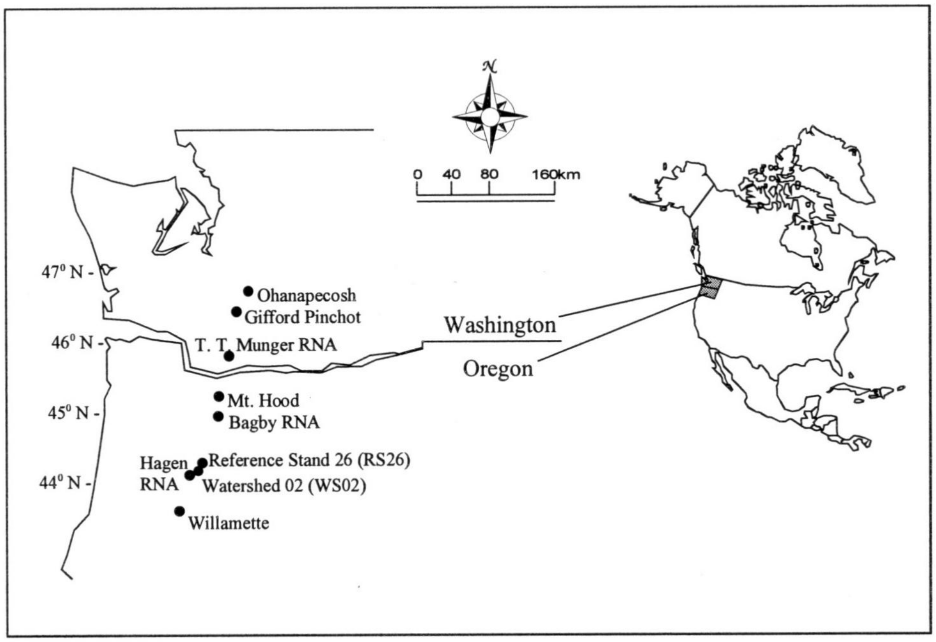

Figure 1. Location of the nine study areas in Washington and Oregon.

Table 1. Forest age, length of data record, and total plot area for the nine study areas.

Study area	— Forest age at —		Data record (yr)	Plot area (ha)	Lat. Long. (elev. m)
	plot establishment	last remeasurement			
Mt. Hood	45	109	64	1.2	45.32°N 121.91°W (600)
Gifford Pinchot	50	117	67	1.2	46.46°N 121.86°W (475)
Willamette	55	137	82	1.2	43.82°N 122.62°W (400)
Hagen RNA	90	~102	12	9.6	44.0°N 122.0°W (485-1000)
RS26	130	~148	18	1	44.15°N 121.7°W (1000)
Bagby RNA	~270	~288	18	1	45.0°N 121.7°W (780)
Ohanapecosh	~270	~288	18	1	46.7°N 121.5°W (640)
T. T. Munger RNA	~400	~450	50	40.8	45.7°N 121.9°W (310-660)
WS02	~460	~472	12	6.6	44.15°N 121.7°W (560-1050)

YOUNG-MATURE STANDS (AGES 45–137 YR)

Between 1910 and 1930, the USDA Forest Service Pacific Northwest Forest and Range Experiment Station installed several permanent plots (Williamson 1963). The objective was to observe growth and yield of Douglas-fir in densely stocked, single-species, single-cohort stands. Of the extant plot systems in the Cascade Range, plots on Mt. Hood, Gifford Pinchot, and Willamette National Forests were chosen for this study. Plots on these three forests had minimal or no impact from adjacent management activities. At the time of plot installation, each site supported young forests with newly formed, closed canopies. Data cover development from young to mature stands. Plot layout consists of three closely spaced, one-acre (~0.4 ha) square plots (Figure 2).

The Mt. Hood plots (45.31° N 121.91° W, elev. 600 m) were installed in 1930 in a 45-yr-old forest that regenerated after fire in the 1880s. The plots lie on a moderately steep hillslope (~25° slope) with a north-facing aspect. Plant association is western hemlock/swordfern (*Polystichum munitum* (Kaulf.) Presl). At the time of plot installation, there was approximately 920.8 conifer trees per hectare (TPH) composed of 92.0% Douglas-fir and 4.0% western hemlock. Plots were remeasured in 1934, '39, '45, '52, '65, '71, '83, '89 and '94. At the last remeasurement (forest age 109 yr), density of conifers had diminished to 545.8 TPH with 56.0% Douglas-fir and 40.5% western hemlock (Table 2).

The Gifford Pinchot plots (46.46° N 121.86° W, elev. 475 m) were installed in 1927 in a 50-yr-old forest that regenerated after fire in the 1870s. Plots lie in a valley bottom on flat topography. Plant association is western hemlock/devilsclub (*Oplopanax horridum* (J. E. Smith.) Miq.). At the time of plot installation, Douglas-fir comprised 100% of density at 556.7 TPH. Western hemlock first appeared in the data after the 1989 remeasurement (forest age 112 yr) at a density of 237.2 TPH with several >15 cm DBH;

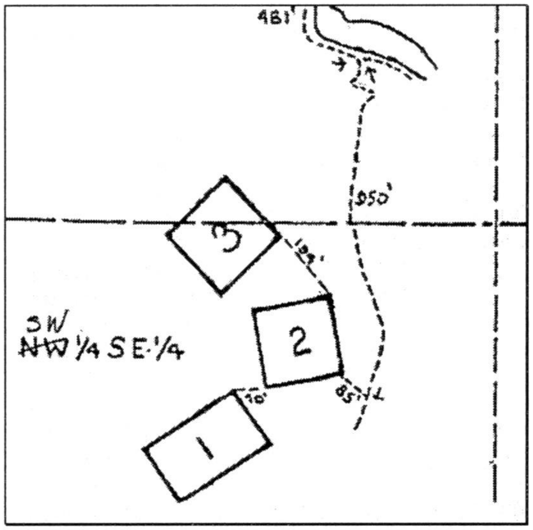

Figure 2. Example of the layout of the 0.4 ha plot triplets: Mt. Hood study area.

it had apparently been excluded until 1989 and probably did exist at that time of plot establishment. Plots were remeasured in 1932, ‘37, ‘43, ‘52, ‘57, ‘83, ‘89 and ‘94. At the last remeasurement (forest age 117 yr), density of conifer trees had decreased to 417.7 TPH with western hemlock as the dominant at 55% and Douglas-fir at 43% (Table 2).

The Willamette plots (43.82° N 122.62° W, elev. 400 m) were installed in 1910 in a 55-yr-old forest that regenerated after fire in the 1850s. Plots occupy flat, upland topography. Plant association is western hemlock/salal (*Gaultheria shallon* Pursh). At the time of plot installation, density of conifers was 490.0 TPH composed of 99.8% Douglas-fir and 0.2% western hemlock. Plots were remeasured in 1915, ‘20, ‘25, ‘30, ‘34, ‘39, ‘45, ’50, ’55, ’70 and ‘92. At the last remeasurement (forest age 137), Douglas-fir comprised 81.7% of the 255.0 TPH and western hemlock 17.6% (Table 2).

Table 2. Basic statistics at plot installation and last remeasurement for the Mt. Hood, Gifford Pinchot, Willamette young-mature and Hagen RNA, RS26 mature study areas: TPH=trees per hectare, BA=basal area (m^2 ha^{-1}), Biomass=above-ground stem wood and bark only (Mg ha^{-1}).

Mt. Hood	TPH	BA	Biomass
45 yr (1930)			
Douglas-fir	846.7	46.9	198.2
Western hemlock	36.7	0.4	0.0
Western white pine	32.5	1.0	3.7
Western red-cedar	5.0	0.1	0.0
Total	920.8	48.4	201.9
109 yr (1994)			
Douglas-fir	305.8	63.0	422.7
Western hemlock	220.8	4.1	8.9
Western red-cedar	19.2	0.5	1.1
Western white pine	0.0	0.0	0.0
Total	545.8	67.6	432.7
Gifford Pinchot			
50 yr (1927)			
Douglas-fir	556.7	56.3	364.2
117 yr (1994)			
Western hemlock	230.8	0.7	5.2
Douglas-fir	180.8	64.7	567.7
True fir	6.0	0.0	0.0
Total	417.7	65.4	572.9
Willamette			
55 yr (1910)			
Douglas-fir	489.2	46.4	292.3
Western hemlock	0.8	0.0	0.0
Total	490.0	46.4	292.3
137 yr (1994)			
Douglas-fir	208.3	78.0	681.7
Western hemlock	45.0	1.7	6.7
Western red-cedar	1.7	0.0	0.0
Total	255.0	79.7	688.4

Hagen RNA	TPH	BA	Biomass
90 yr (1982)			
Douglas-fir	284.4	50.9	344.1
Western hemlock	8.0	0.2	0.1
Pacific yew	0.8	0.0	0.0
Total	293.2	51.1	344.2
102 yr (1994)			
Douglas-fir	245.8	55.6	393.2
Western hemlock	12.8	0.4	1.3
Pacific yew	0.7	0.0	0.0
Total	259.3	56.0	394.5
RS26			
130 yr (1977)			
Douglas-fir	385.0	87.4	702.7
Western hemlock	327.0	0.0	7.4
True fir	10.0	0.1	0.1
Western red-cedar	1.0	0.0	0.0
Total	723.0	87.5	710.2
148 yr (1994)			
Douglas-fir	335.0	93.9	788.4
Western hemlock	414.0	0.4	12.6
True fir	8.0	0.1	0.1
Western red-cedar	2.0	0.0	0.0
Total	759.0	94.4	801.1

MATURE STANDS (AGES 90–148 YR)

In 1981, a systematic grid of permanent plots was established at the Hagen Research Natural Area (RNA) (44.0° N 122.0° W, elev. 485–1000 m) to sample the 470-ha watershed of North Fork Hagen Creek (Klopsch 1985). Topography is deeply dissected (30-40° slope) presenting multiple aspects and slope positions. Plant associations range from western hemlock/devilsclub and western hemlock/sword fern on moist sites, to western hemlock/salal and western hemlock/Oregongrape (*Berberis nervosa* Pursh) on drier sites, and western hemlock/ocean spray (*Holodiscus discolor* (Pursh) Maxim.) and western hemlock/bear grass (*Xerophyllum tenax* (Pursh) Nutt.) on more xeric sites. Klopsch (1985) identified at least two distinct stand-establishing fire events at the Hagen RNA that resulted in two age classes of 90 and 130 yr (*ca.* 1840s and 1890s). The plot system consists of 96, 0.10-ha circular plots spaced at 100 m intervals along eight parallel transects that are separated by 400 m; plots are located primarily within the 90-yr-old forest (Figure 3). At the time of plot installation, conifer density was 293.2 TPH composed of 97.0% Douglas-fir and 2.7% western hemlock. Plots were remeasured in 1988 and 1994. At the last remeasurement, Douglas-fir composed 94.8% of the 259.3 TPH and western hemlock 5.1% (Table 2).

Reference Stand 26 (RS26) is a square, 1-ha plot installed in 1977 in an approximately 130-yr-old, fire-regenerated forest (*ca.* 1840s). The stand lies near the gently sloping crest of Blue River Ridge on the H. J. Andrews Experimental Forest (44.15° N 121.7° W elev. 1000 m). Plant association is western hemlock/Pacific rhododendron (*Rhododendron macrophyllum* G. Don)-Oregongrape. At the time of plot installation, conifer density was 723.0 TPH composed of 53.3% Douglas-fir and 45.2% western hemlock. The plot was remeasured in 1983, '88 and '94. At the last remeasurement, Douglas-fir represented 44.1% of the 759.0 TPH and western hemlock 54.5% (Table 2).

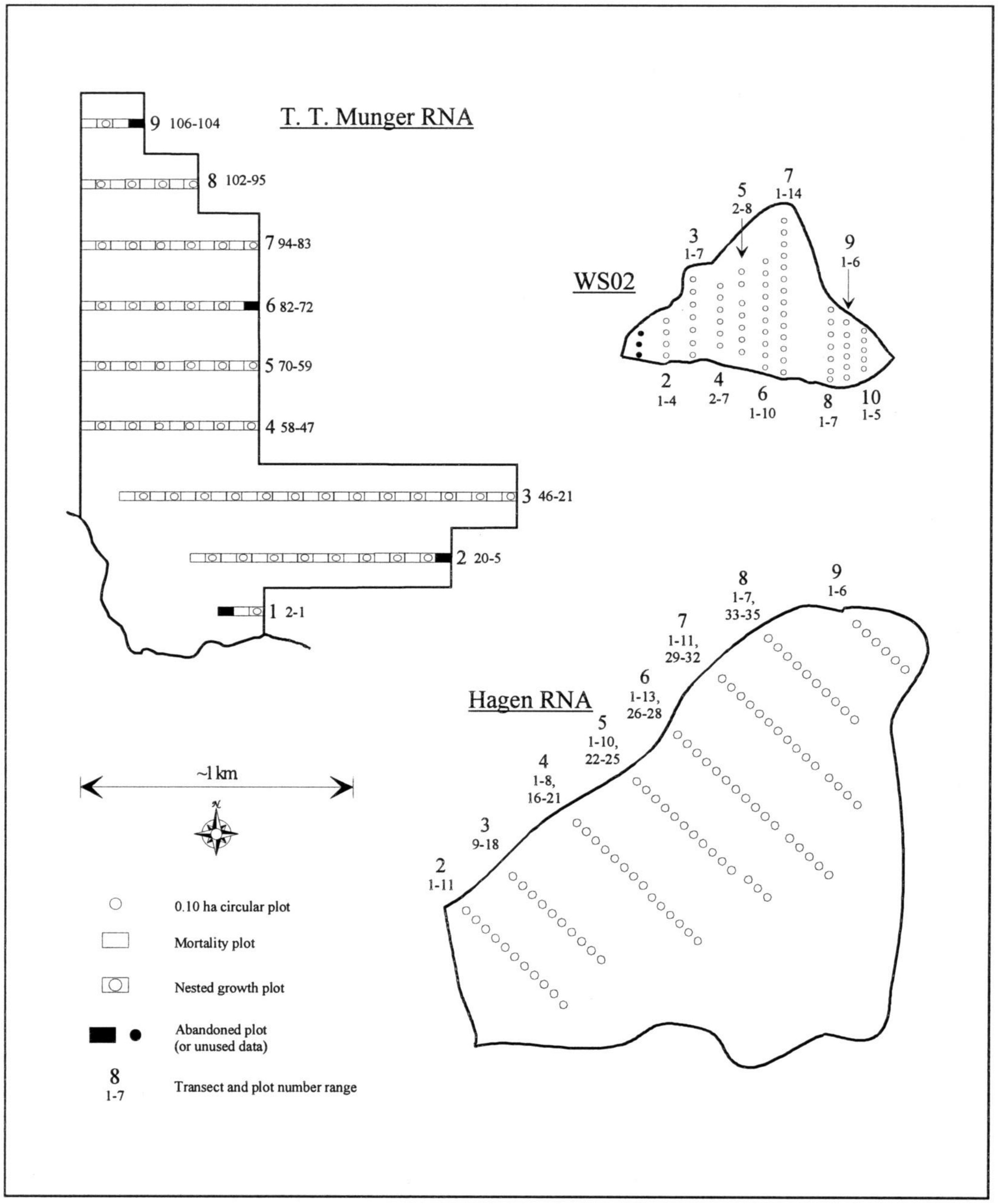

Figure 3. Plot layout for the Hagen RNA, T. T. Munger RNA and WS02 study areas.

OLD-GROWTH STANDS (AGES 270–472 YR)

Two study areas, Bagby RNA and Ohanapecosh, were chosen to represent an early stage of old-growth forest development (between 200 and 350 yr), when vertical elaboration of the canopy is the dominant process (Spies 1997, Franklin et al. 2001). In 1977, 1-ha plots were installed in the Bagby RNA (45.0° N 121.7° W, elev. 780 m) and near Ohanapecosh Campground in Mt. Rainier National Park (46.7° N 121.5° W, elev. 640 m). At the time of plot installation, both stands were approximately 270 yr old and had originated after fire. Both plots are situated at the foot of tall ridgelines. Plant association at Bagby RNA is western hemlock/bunchberry dogwood (*Cornus canadensis* L.)-cutleaf goldenthread (*Coptis laciniata* Gray). Plant association at Ohanapecosh is western hemlock/vanilla leaf (*Achlys triphylla* (Smith) DC). At the time of plot installation, conifer density at Ohanapecosh was 398.0 TPH consisting of 34.7% Douglas-fir and 58.3% western hemlock. At Bagby RNA, a density of 406.0 TPH was composed of 31.3% Douglas-fir and 64.0% western hemlock. Both plots were remeasured in 1982, '89 and '95. At the last remeasurement composition had changed little: of a density of 373.0 TPH, 33.8% were Douglas-fir and 59.8% western hemlock at Ohanapecosh; and of 380.0 TPH, 27.4% were Douglas-fir and 67.1% western hemlock at Bagby RNA (Table 3).

Two study areas, T. T. Munger RNA and Watershed 02, were chosen to represent an advanced stage of old-growth development (>400 yr) when both vertical and horizontal structure are well developed (Spies 1997, Franklin et al. 2001). In 1947, plots were installed in the T. T. Munger RNA (originally the Wind River Natural Area; 45.7° N 121.9° W, elev. 310–660 m) an approximately 400-yr-old forest. Topography is flat to gently sloping (slope <10%). The major plant associations are western hemlock/Oregongrape-salal at lower elevations (<600 m) in the eastern portion of the RNA, and Pacific silver fir/salal higher elevations in the western portion. A total of 102, 0.4-ha rectangular (40 x 100 m) mortality plots lie contiguous along nine parallel transects; 50, 0.02- and 0.08-ha concentric circular growth plots are nested in each odd-

Table 3. Basic statistics at plot installation and last remeasurement for the Ohanapecosh, Bagby RNA, T. T. Munger RNA, and WS02 old-growth study areas: TPH=trees per hectare, BA=basal area ($m^2 ha^{-1}$), Biomass=above-ground stem wood and bark only ($Mg ha^{-1}$).

Ohanapecosh	TPH	BA	Biomass
270 yr (1977)			
Western hemlock	232.0	18.7	206.7
Douglas-fir	138.0	85.7	847.2
Pacific yew	14.0	0.4	0.1
True fir	12.0	11.0	1.1
Western red-cedar	2.0	0.0	0.0
Total	398.0	115.8	1055.1
288 yr (1995)			
Western hemlock	223.0	20.0	221.6
Douglas-fir	126.0	86.1	865.1
True fir	12.0	12.0	1.2
Pacific yew	10.0	0.3	0.1
Western red-cedar	2.0	0.0	0.0
Total	373.0	118.4	1088.0
Bagby RNA			
270 yr (1977)			
Western hemlock	260.0	17.0	92.3
Douglas-fir	127.0	78.4	671.2
Western red-cedar	16.0	18.0	5.6
True fir	2.0	0.0	0.0
Pacific yew	1.0	0.0	0.0
Total	406.0	113.4	769.1
288 yr (1995)			
Western hemlock	255.0	16.3	101.9
Douglas-fir	104.0	73.3	643.3
Western red-cedar	17.0	21.2	6.0
True fir	3.0	0.0	0.0
Pacific yew	1.0	0.0	0.0
Total	380.0	110.8	751.2

T. T. Munger RNA	TPH	BA	Biomass
400 yr (1947)			
Western hemlock	213.0	20.4	146.8
True fir	104.8	3.7	23.6
Pacific yew	57.2	1.0	3.8
Douglas-fir	52.8	36.7	295.6
Western red-cedar	12.6	3.5	13.2
Western white pine	4.1	1.7	12.2
Total	444.5	67.0	495.2
450 yr (1998)			
Western hemlock	208.1	24.4	174.8
True fir	109.8	3.9	26.6
Pacific yew	50.2	1.0	4.6
Douglas-fir	38.1	32.1	267.4
Western red-cedar	14.8	3.9	14.8
Western white pine	0.5	0.3	2.2
Total	421.5	65.6	490.4
WS02			
460 yr (1982)			
Western hemlock	221.5	12.9	64.8
Douglas-fir	89.1	42.3	348.7
Pacific yew	49.4	0.7	2.2
Western red-cedar	18.6	1.3	3.5
Incense-cedar	0.5	0.0	0.0
Sugar pine	0.3	0.0	0.0
Western white pine	0.2	0.0	0.0
Total	379.6	57.2	419.2
472 yr (1994)			
Western hemlock	210.8	14.9	78.0
Douglas-fir	81.5	40.4	332.9
Pacific yew	46.1	0.7	2.4
Western red-cedar	19.1	1.5	4.1
Incense-cedar	0.5	0.0	0.0
Sugar pine	0.3	0.0	0.0
Western white pine	0.2	0.0	0.0
Total	358.5	57.5	417.4

numbered mortality plot (Figure 3). Trees in growth plots were tagged in 1947 (DBH of ≥5.0 and <25.4 cm in the 0.02-ha plots and ≥25.4 cm in the 0.08-ha plots). Prior to 1991 mortality plots were cruised for dead trees ≥25.4 cm DBH which, when found, were tallied and blazed with an axe. In 1991 all Douglas-fir ≥5.0 cm DBH in the mortality plots were tagged together with all other tree species ≥45.7 cm DBH. To reconstruct forest structure between 1947 and 1991, growth patterns for live and tallied dead trees in the mortality plots were derived from average growth rates of extant trees in the circular growth plots. At the time of plot installation, stands consisted 444.5 TPH of which 11.9% was Douglas-fir and 47.9% western hemlock. All plots were remeasured in 1953, ’59, ’65, ’71, ’77, ’83, ’91 and ’98. At the last remeasurement, composition had changed little with Douglas-fir at 9.0% and western hemlock 49.4% of 421.5 TPH (Table 3).

The permanent sample plot system in Watershed 02 (WS02) (H. J. Andrews Experimental Forest elev. 560–1050 m) was established in 1982 in a 96-ha, 460-yr-old forest. Plots lie along one long moderately steep, north-facing slope. Primary plant associations are western hemlock/salal at higher elevations and western hemlock/Oregon grape on the lower slope. The sampling design is similar to that in the Hagen RNA but with 69, 0.10-ha circular plots spaced along 10 parallel transects (Figure 3). At the time of plot installation, stands had a density 379.6 TPH composed of 23.5% Douglas-fir and 58.4% western hemlock. Plots were remeasured in 1988 and 1994. At the last remeasurement, composition was at 22.7% Douglas-fir and 58.8% western hemlock of 358.5 TPH (Table 3).

MORTALITY RATES

Average annual mortality rates, *m*, reported in percent are derived from the exponential population model:

$$N_{t+1} = N_t e^{-mt} \text{ where, } m = ((\ln(N_t) - \ln(N_{t+1}))/t) * 100 \qquad (1)$$

N_t is the number of tagged trees at the beginning of a remeasurement interval of t years with N_{t+1} representing the survivors (N_t minus the number of N_t that had died over a remeasurement interval). Means and standard errors (se) of mortality rates and regressions were calculated using SPLUS 2000 Pro R3. Regressions were performed without weights or transformations on variables; the objective being simply to elucidate pattern. Four or more data points are needed to produce a uniform distribution for the calculation of standard errors (Chernick 1999).

The compound formula is also a common method for calculating mortality rates:

$$N_{t+1} = N_t(1-m)^t \quad \text{where,} \quad m = (N_{t+1} / N_t)^{1/t} \tag{2}$$

Results from the exponential and compound methods are readily comparable, the difference being ±0.01% per 1% mortality rate (Sheil et al. 1995). Both methods were used to estimate change over time in Douglas-fir density at the Willamette plots. Each predicted exactly the same number of surviving trees counted during field remeasurements. Franklin and DeBell (1988) and Acker et al. (1996) used the compound method in studies of mortality in Pacific Northwest forests. However, I chose to use the exponential method because it is easier to program and is widely applied in studies of tree mortality in both temperate and tropical forested ecosystems (e.g., Harcombe 1986, Condit et al. 1995).

POPULATION STRUCTURE

Trees were placed in 10-cm DBH classes (5.0-15, 15.1-25, 25.1-35… but reported as 5.0-15, 25, 35, 45…). Classes were considered small enough to provide a detailed frequency distribution diagram yet large enough to include a sufficient number of stems for an accurate calculation of long-term mortality rates without the use of proportional weighting or other smoothing procedures. DBH classes with ≤5 individuals are ignored as such small numbers results in artificially high mortality rates if smoothing procedures are not applied (Rick Condit, *personal communication*).

BIOMASS AND INPUT OF COARSE WOODY DEBRIS

Biomass of above-ground stem wood and bark and mass of input of stem wood and bark coarse woody debris (Mg ha^{-1}) were calculated for all conifers at each study area. Branch and foliage components were not estimated as equations were either unavailable or not considered reliable. My primary goal is to illustrate trends in biomass accumulation and stocks and inputs of coarse woody debris, and not to provide rigorous quantification of stocks or rates. Wood and bark volumes (m^3) were calculated using DBH (cm) and tree height (m) data in optical dendrometer-based regression equations (http://www.fsl.orst.edu/) (Table 4):

$$Volume = B_0 * (DBH^2 * Height)/10000 \qquad (3)$$

Volume to density multipliers (Mg/m^3) were then applied (Mark Harmon, Oregon State University, *personal communications*) (see Table 4 for density multipliers). Equations for calculating mass of Pacific yew were adapted from Grier and Logan (Grier and Logan 1977) , where stem wood = $e^{(-2.172+2.257*\ln(DBH))/1000}$ and stem bark = $e^{(-4.373+2.258*\ln(DBH))/1000}$. Identical methods were applied to the calculation of coarse woody debris with DBH and height being taken from the previous remeasurement when the tree was last recorded as alive.

Only a sub-sample of trees on PSP plots are measured for heights. Missing tree heights in meters were estimated using a Chapman-Richards style function fitted with plot specific data (Garman et al. 1995):

$$Height = 1.37 + [b_0(1 - e^{(b_1 * DBH)})^{b^2}] \qquad (4)$$

Table 4. Volume coefficients (eqn. 3) and density multipliers for Douglas-fir and western hemlock wood and bark.

Species	(β_0)		Density multiplier (Mg/m^3)	
	Wood	Bark	Wood	Bark
True fir	0.2916	0.0257	0.570	0.400
Douglas-fir	0.2346	0.0519	0.452	0.438
Western red-cedar	0.2180	0.0128	0.312	0.333
Western hemlock	0.2961	0.0317	0.421	0.415

AGENTS OF TREE MORTALITY

Information from the PSP datasets regarding causes of Douglas-fir and western hemlock mortality range from brief comments such as "bugs" in the early US Forest Service growth and yield data to a more standardized and elaborate format created in the early 1980s for the NSF-LTER program. The LTER data have a greater degree of consistency and include structural features associated with tree death and inferences about causes. Still, there has been a tendency to generalize causes into broad categories such as "unknown" and "windthrow."

An important aspect of mortality is the factor responsible for tree death because this has important implications for ecosystem structure and function. To obtain more detailed information on agents of mortality all plots were revisited to relocate all Douglas-fir and western hemlock listed as dead and record additional information on possible causal agents. During field examination, dead Douglas-fir and western hemlock were assigned to one of eight categories of mortality agents: unknown, suppression, root and stem decay, Douglas-fir bark beetle, western hemlock dwarf mistletoe, wind or snow breakage, crushed or hit (by live or dead falling tree), or other (substrate failure, lightning, animal damage, physically removed); a probability of accurate identification was also made.

Unknown

"Unknown" was assigned as the cause of death when the following were encountered: large, standing dead trees with full crowns (branches, twigs, brown needles); or broken stems with no outward sign of pests, pathogens or extensive mechanical abrasions (wounds). Most broken stems assigned to the category exhibited a smooth and straight break. In contrast, a fracture due to wind or snow breakage is jagged and uneven resulting from tension, compression and shear forces on living tree fibers. A large portion of the "unknowns" are recorded in the original PSP data with no assigned causes of mortality; decay has resulted in a loss of information other than DBH and time of death.

Suppression

"Suppression" mortality, also referred to as competitive- or density-dependent mortality, is usually related to low available light and soil moisture (Oliver and Larson 1990, Spies 1997). Although the physiological basis of mortality is not directly observable with census-type surveys, the structure of these newly dead trees is unmistakable. They are relatively small, standing trees with intact crowns (branches, twigs, and sometimes brown needles) that are overtopped (shaded) by larger trees. In an even-aged stand it is easy to identify this mortality as it consists of individuals in the lower 1/4 to 1/3 of the diameter distribution. Field crews can accurately classify suppression-related mortality; therefore, in the PSP data if suppression was listed as cause of death, it was accepted and no attempt was made to relocate trees in the field.

Root and stem decay

Douglas-fir and western hemlock host several wood-decaying fungi which render stem and root wood in living trees structurally unsound (Boyce 1932, Childs 1970, Manion

1991, Hennon 1995) (Table 8). These fungi typically leave behind persistent fruiting bodies and setal hyphae attached to the dead tree as well as characteristic patterns of decay in wood. For example, velvet top (*Phaeolus schweinitzii* (Fr.) Pat.) is a rot that produces large (~10 x 15 cm) angular, red-brown blocks of mostly lignin after consuming cellulose in the roots, root collar, and basal area of a stem. In order to positively identify decay on tall dead trees with broken stems, the top of each tree had to be located on the ground and examined. If the top could not be found or there was no decay present then "unknown" cause or "wind" or "snow breakage" were usually assigned as the cause of mortality. Stem or root failure at the point of decay may have been triggered by wind or snow loads on the crown. These events, however, are rarely observed and can only be inferred from climatic data or anecdotal records contained in field notes. Characteristics found in the structure of dead trees provides the only direct evidence. Identification of decay in western hemlock was problematic as western hemlock are often infected with Annosus-s (*Heterobasidion annosum* (Fr.) Bref) a lignin and cellulose-consuming species that may not form a fruiting body and host wood weathers quickly. In addition, the base and upper stem of western hemlock are often colonized by red belt fungus (*Fomitopsis pinicola*), which consumes cellulose in trees that are already dead (a secondary decay) and may erase signs of mortality agents that infected living trees.

Douglas-Fir Bark Beetle

Douglas-fir bark beetles (*Dendroctonus pseudotsugae* Hopkins) construct egg and larval galleries in the cambium, disrupting conduction through phloem and xylem tissue and causing nutritional deficiency and water stress in living Douglas-fir (Furniss and Carolin 1977, Maser et al. 1988). These galleries have a distinct pattern which can be found on bark plates surrounding the base of a dead tree. Many trees in the original data were assigned bark beetles as the agent of mortality; this is common when field crews find individual or small groups of standing dead trees. During reassessments of mortality, mortality was usually reassigned to the "unknown" category if no clear evidence of bark beetles was found (e.g., galleries in bark plates, ingress/egress holes).

Hemlock dwarf mistletoe

Hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G. N. Jones) is a vascular parasite that taps into branches of western hemlock via a modified root system and robs the tree of moisture and carbohydrates (Mathiasen 1996). Mistletoe has a profound effect on crown architecture creating a ragged, tangle of dead braches with matted clumps of brown foliage, known as brooms. To assign mistletoe as a cause of mortality, however, existence of flower and(or) fruits of mistletoe had to be present. These are easily seen on smaller trees and with the aid of binoculars are usually visible even on larger trees (Shaw et al. 2000).

Wind or snow breakage

Wind or snow loading can add substantial weight to tree crowns and produce torque that results in breakage (Sathers et al. 1994). This category was assigned to trees that were leaning (>45 lean) but still rooted, had broken stems, or were prostrate but had little or no decay in roots or stems and no outward signs of pests, pathogens, or mechanical abrasions. Wind is more likely a factor in tall, dominant and co-dominant trees, while snow is more likely for small trees in the understory. Broken stem fractures due to wind or snow breakage are jagged and uneven resulting from tension, compression, and shear forces on living tree fibers.

Crushed or Hit

Small trees (especially shade-tolerant species in the understory of a structurally diverse forest) are often crushed by falling large trees or snags (standing dead trees). Large trees also may be mortally wounded or completely toppled in the same manner. When a tree has been crushed the cause of mortality is obvious, but it is less clear when a tree has been wounded and remains standing. A determination of mortal wounding is subjective but can be inferred by examining the extent and the severity of wound. If the tree that caused the wound was also tagged, then it is possible to date the wound.

Other

Although "other" is a miscellaneous category of mortality agents, relatively few trees were assigned to this group. Substrate failure is usually encountered in mountainous terrain were soils are thin or near stream channels where erosion undercuts rooting substrate, forcing the entire tree to fall. Lightning kills are distinguished by long strips of wood blasted out from the stem along the grounding line when moisture in the tree is converted to steam by the energy of the lightning bolt (Paul Durr, *personal communication*). Animal damage is usually apparent near the base of a tree where bears, deer, or beavers feed on the cambium, leaving indentation marks from teeth and rake marks from claws. At the T. T. Munger RNA, beavers constructed a dam which drowned several Douglas-fir. Trees may be physically removed from a plot either by natural (e.g., land slide) or anthropogenic (harvest, road building) agents; some remains of the tree (e.g., stump) may be present.

Edge effect

Of special interest at the T. T. Munger RNA and the WS02 study areas was the potential impact of abnormally high wind velocity associated with nearby clearcuts (Chen et al. 1992, 1993) and high mortality rates due to windthrow of Douglas-fir. To explore this, plot-level mortality rates of Douglas-fir were regressed on distance from plot center to the nearest forest edge (0-100 m, 101-200 m, 201-300 m, and >300 m) using the simple linear model:

$$m = \beta_0 \pm \beta_1(DISTANCE) \tag{5}$$

and testing whether slope was significantly different from zero using a t test (Zar 1984)

RESULTS

TEMPORAL PATTERNS OF MORTALITY RATES

Douglas-fir mean annual mortality rates and variability in rates declined with stand age (Table 5). Mean and standard error in overall mortality rates were highest (2.0 ± 0.9%) in the young stage. In mature stands overall mean and range (1.0 ± 0.4%) were one-half the values calculated for the young stage. In old growth mean and range (0.7 ± 0.2%) in overall rate were lower than for mature stands; however, the magnitude of the difference was less than between young and mature stands. Plotting mortality rates from all remeasurements at each of the nine study areas produced a generalized Douglas-fir mortality curve. Such curves are useful when comparing life-history traits, in this case mortality rates, among different species (Harcombe 1987). Douglas-fir mortality declined with a negative exponential function (Figure 4):

$$m = 0.6593 + 8.8769e^{(-0.0310 * age)} \quad \text{(residual se = 0.51)} \tag{6}$$

Average annual mortality rates for western hemlock increased with stand age. Overall average and range in mortality rate was negligible in the young (0.0%) and mature (0.1 ± 0.0%) stands; however, rates in old growth were considerably higher (0.4 ± 0.1%) (Table 6). Western hemlock mortality rates increased linearly (Figure 4):

$$m = -0.1645 + 0.0019 * age \quad \text{(residual se = 0.21)} \tag{7}$$

Table 5. Douglas-fir average annual mortality rates (%) and standard errors by study area and young, mature, and old-growth stages of forest development.

Study area	Douglas-fir annual mortality rates (%) Young mean (se)	Mature mean (se)	Old growth mean (se)
Mt. Hood	2.0 (1.0)	1.3 (0.2)	
Gifford Pinchot	2.2 (0.9)	0.7 (0.4)	
Willamette	1.9 (0.8)	1.1 (0.5)	
Hagen RNA		1.2 (0.6)	
RS26		0.8 (0.2)	
Bagby RNA			0.6 (0.3)
Ohanapecosh			0.6 (0.3)
T. T. Munger RNA			0.7 (0.2)
WS02			1.0 (0.1)
Overall	2.0 (0.9)	1.0 (0.4)	0.7 (0.2)

Table 6. Western hemlock annual mortality rates (%) and standard errors by study area and young, mature and old-growth stages of forest development.

Study area	Western hemlock annual mortality rates (%) Young mean (se)	Mature mean (se)	Old growth mean (se)
Mt. Hood	0.0 (0.0)	0.0 (0.0)	
Gifford Pinchot	0.0 (0.0)	0.0 (0.0)	
Willamette	0.0 (0.0)	0.1 (0.0)	
Hagen RNA		0.1 (0.0)	
RS26		0.1 (0.0)	
Bagby RNA			0.4 (0.1)
Ohanapecosh			0.2 (0.1)
T. T. Munger RNA			0.6 (0.2)
WS02			0.5 (0.1)
Overall	0.0 (0.0)	0.1 (0.0)	0.4 (0.1)

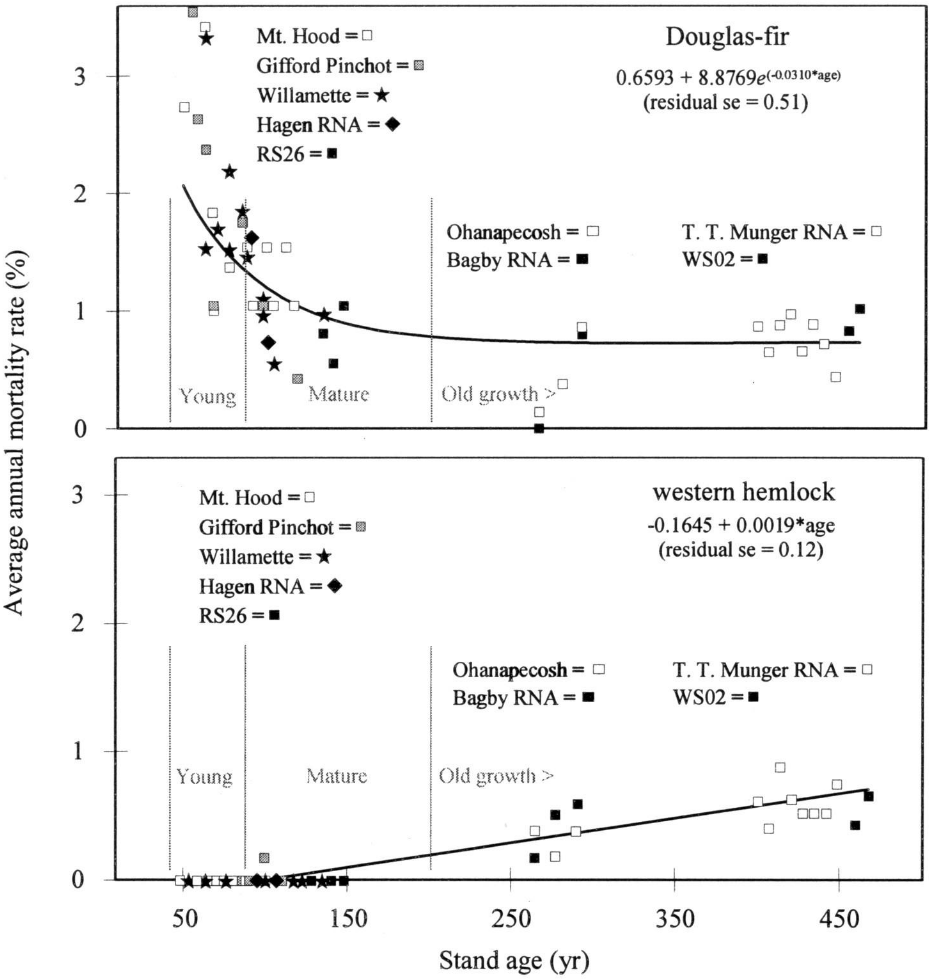

Figure 4. Average annual mortality rates for Douglas-fir. Composite long-term trends are represented by solid line and respective function.

CHANGE IN POPULATION STRUCTURE

DOUGLAS-FIR

Because of the lack of recruitment, mortality and growth were the dominant processes shaping Douglas-fir population structure. Density of Douglas-fir at all study areas declined with time (Figure 5). During the young stage (40-55 yr after permanent plot installation) the Mt. Hood, Gifford Pinchot, and Willamette study areas had lost an average of 44% of their Douglas-fir. Low mortality rates in old growth translated into a slow decline in density of trees. The T. T. Munger RNA, for example, lost only 27% of its Douglas-fir over a 50-yr period.

In the young stage, high average annual mortality rates and rapid decline in density were correlated with initial high densities of small diameter trees at the Mt. Hood, Gifford Pinchot, and Willamette study areas. Mortality rates in the 5–25 cm DBH classes (7.8–12.6%) were higher than rates in larger size classes (≤2.0%) (Figure 6). At maturity, DBH-class mortality rates at these three study areas were generally lower, but highest rates were still concentrated in the smaller diameter classes (~4.0% for DBH ≤35 cm) with the exception of Gifford Pinchot as Douglas-fir bark beetle killed several large trees (Figure 7). A similar pattern of high mortality rates in small diameter classes (~4.0% for DBH ≤35 cm) was also evident at the Hagen RNA and RS26 mature study areas (Figure 8). Mortality rates by diameter class at all old-growth study areas were generally low (<2.0%) and revealed no consistent pattern related to diameter (Figure 9). Over the 50-yr period of observation at the T. T. Munger RNA, mean DBH of dead trees varied: 1953 = 95.6 cm, 1959 = 75.7 cm, 1965 = 72.3 cm, 1971 = 85.3 cm, 1977 = 90.1 cm, 1983 = 81.0 cm, 1991 = 79.5 cm, and 1998 = 96.2 cm. The overall change in Douglas-fir population structure from young to mature stands was one of a large decrease in density of small trees (Figures 10 and 11). In old-growth stands, overall density was still in decline, but there were substantially larger trees in the population (Figure 12, Table 7).

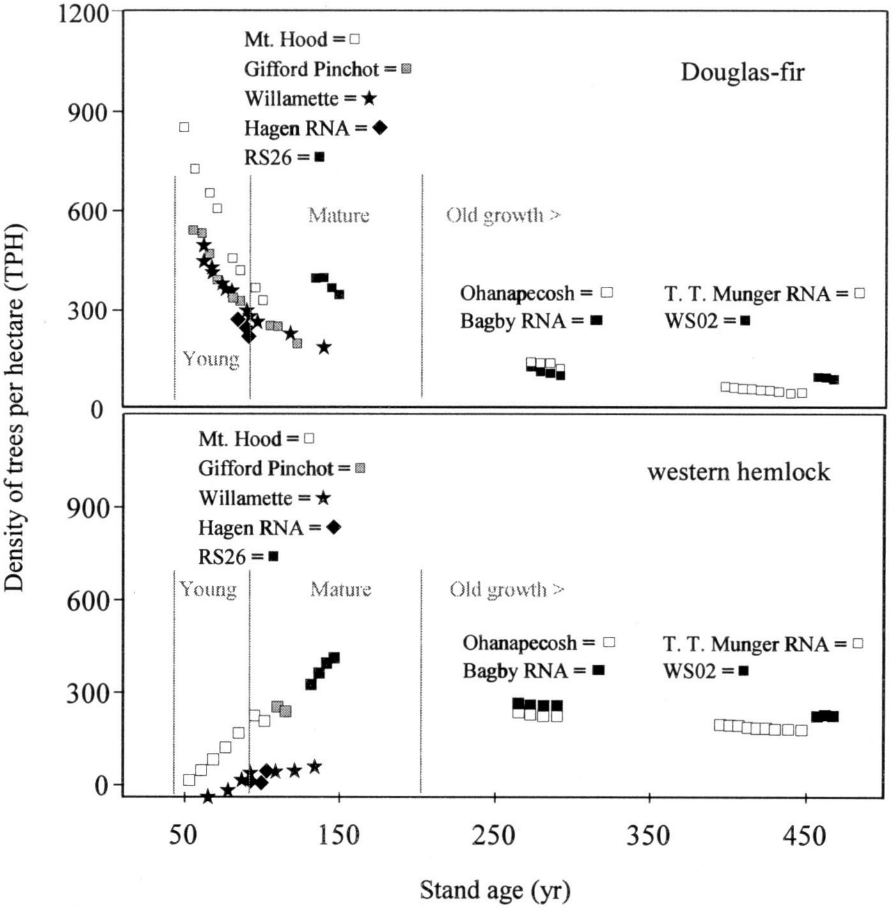

Figure 5. Long-term changes in density (TPH: trees per hectare) of Douglas-fir and western hemlock.

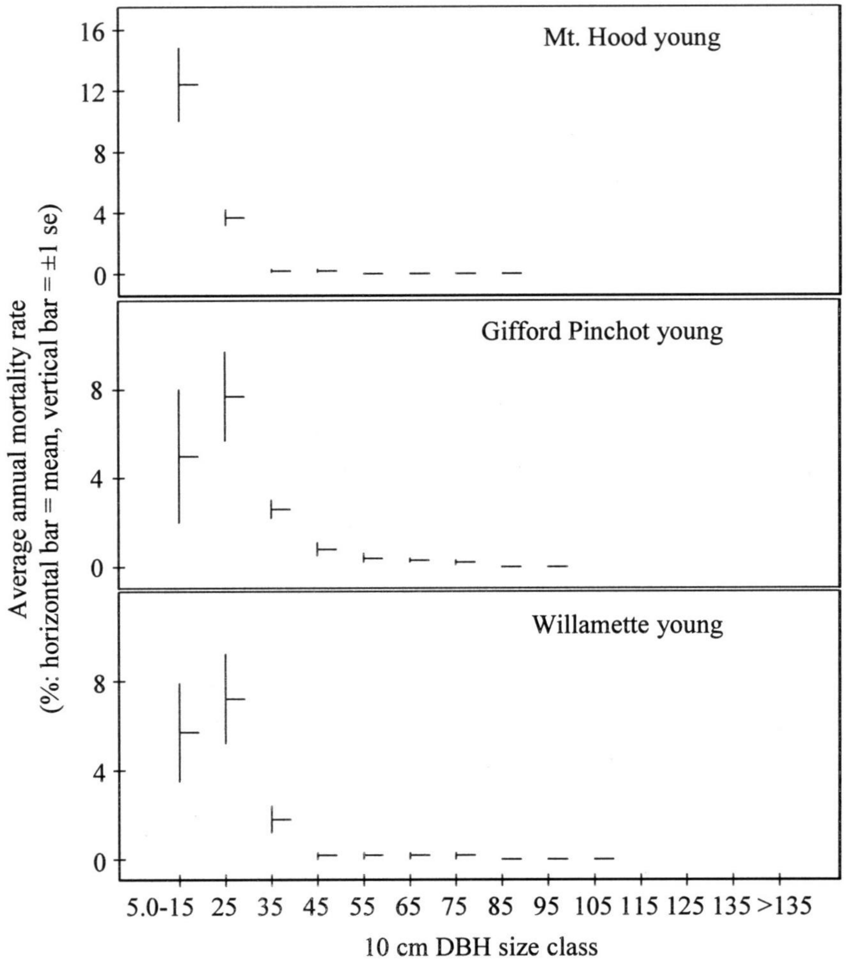

Figure 6. Douglas-fir average annual mortality rates (%) by 10 cm DBH class: Mt. Hood, Gifford Pinchot and Willamette young study areas in the young stage (45-80 yr).

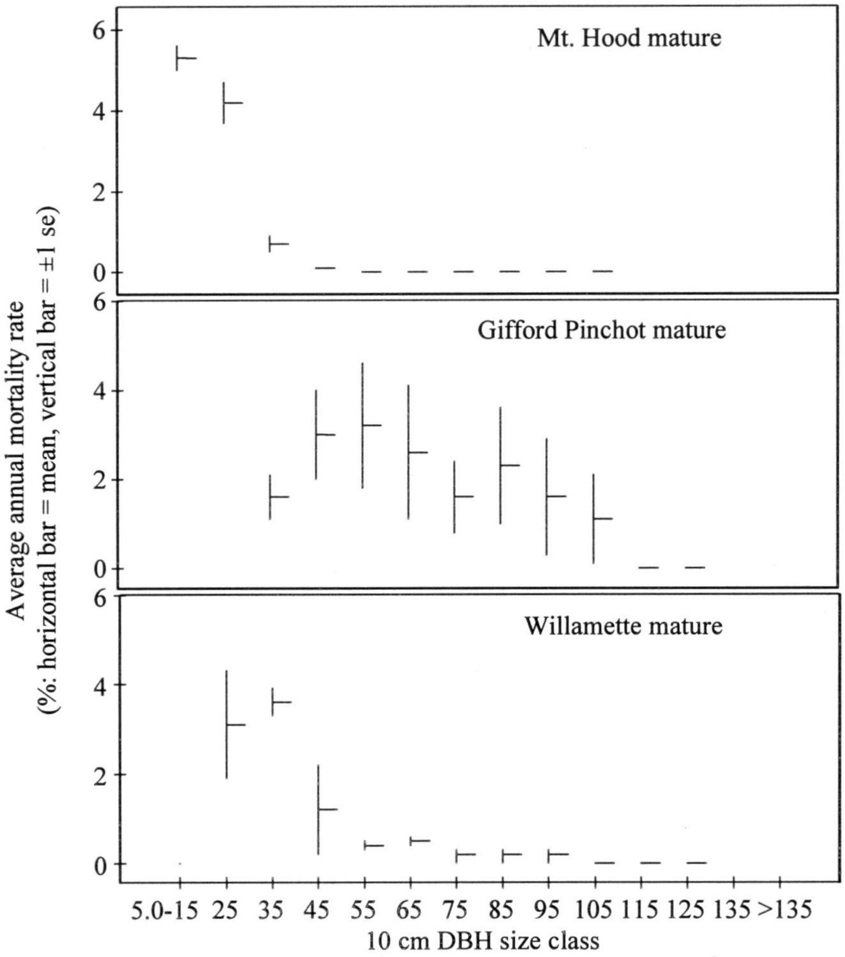

Figure 7. Douglas-fir average annual mortality rates (%) by 10 cm DBH class: Mt. Hood, Gifford Pinchot and Willamette in the mature stage (81–137 yr).

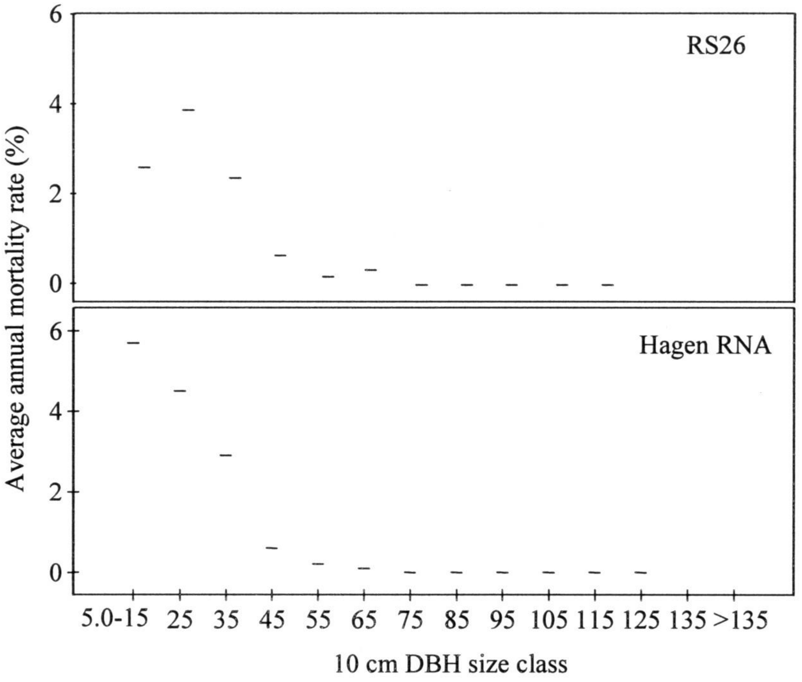

Figure 8. Douglas-fir average annual mortality rates (%) by 10 cm DBH class: RS26 and Hagen RNA mature study areas. Standard errors are not calculated due to small number of remeasurements.

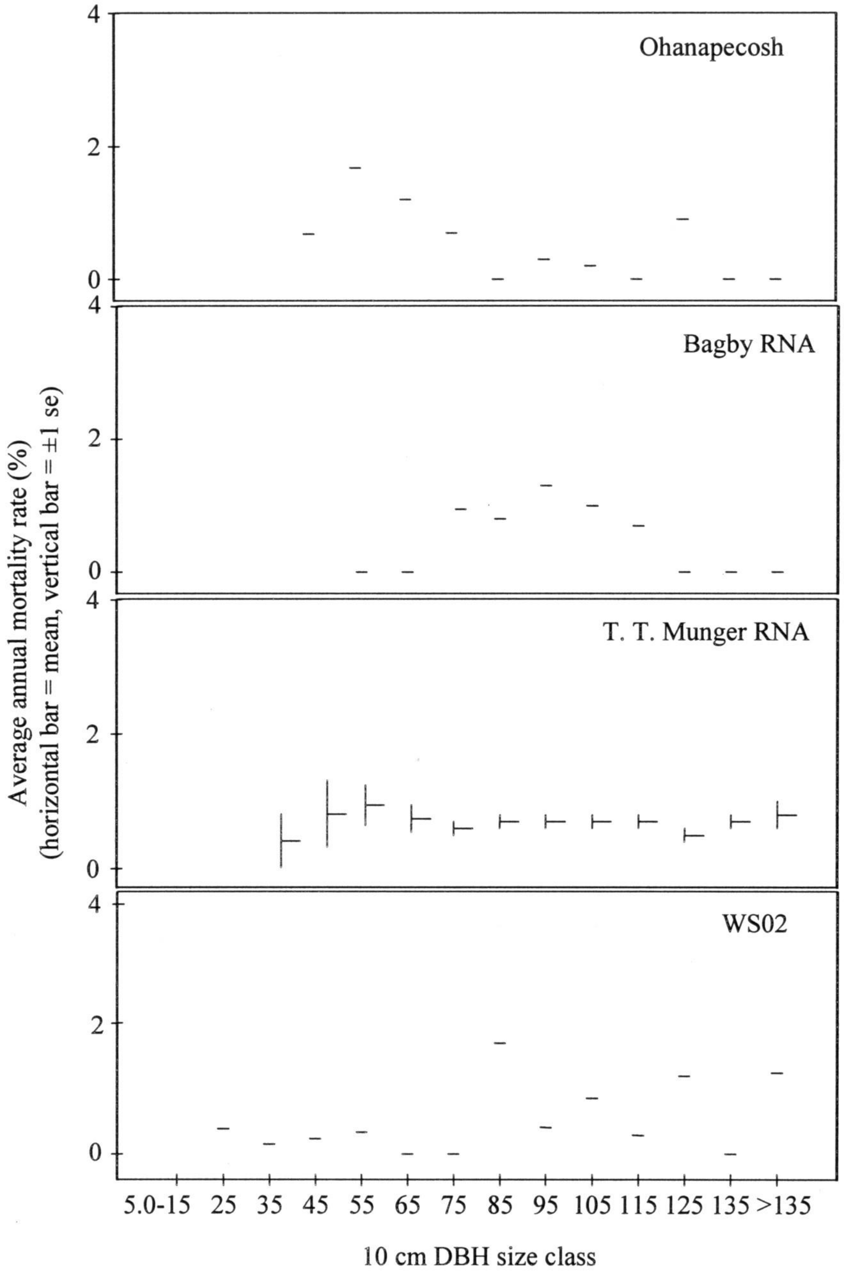

Figure 9. Douglas-fir average annual mortality rates (%) by 10 cm DBH class: Ohanapecosh, Bagby RNA, T. T. Munger RNA and WS02 old-growth study areas. Standard errors were not calculated for Ohanapecosh, Bagby RNA or WS02 due to small number of remeasurements.

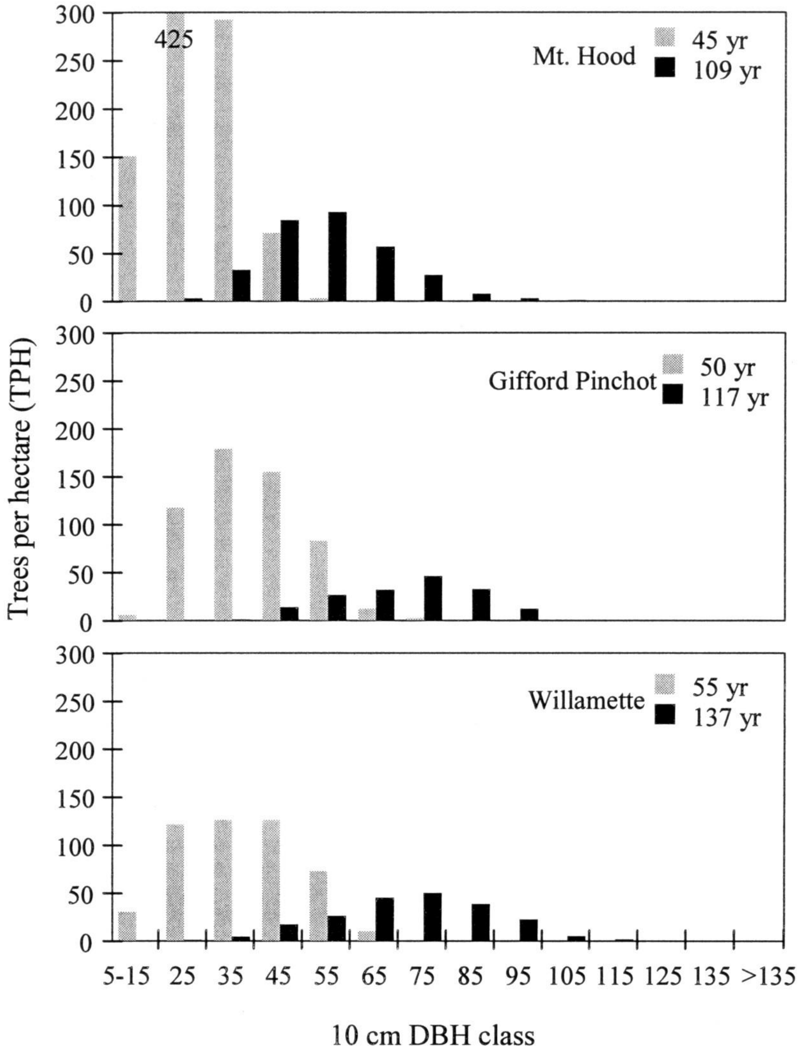

Figure 10. Change in density (TPH) and DBH distribution of Douglas-fir at the Mt. Hood, Gifford Pinchot and Willamette young-mature study areas at the beginning and end of each study.

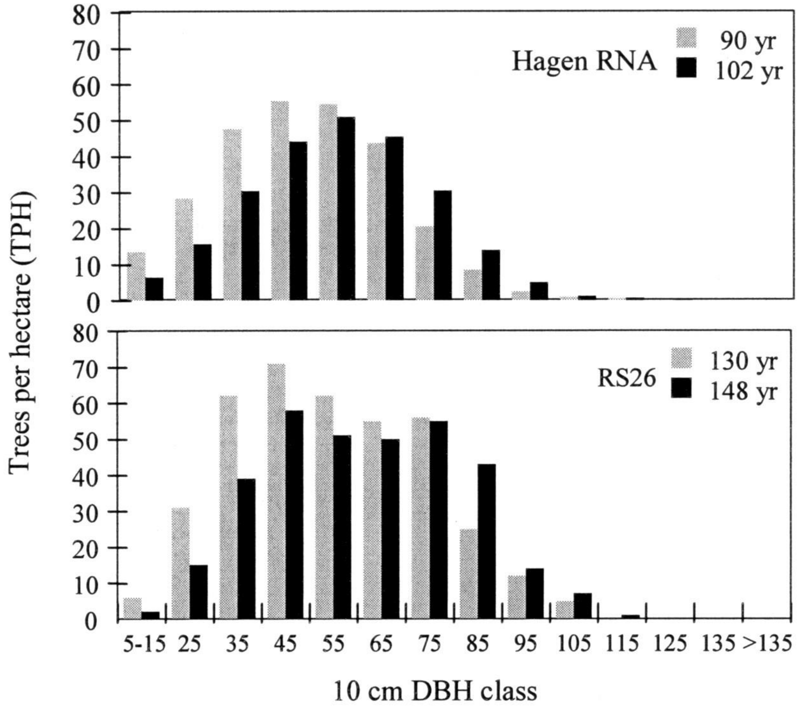

Figure 11. Change in density (TPH) and DBH distribution of Douglas-fir at the Hagen RNA and RS26 mature study areas at the beginning and end of each study.

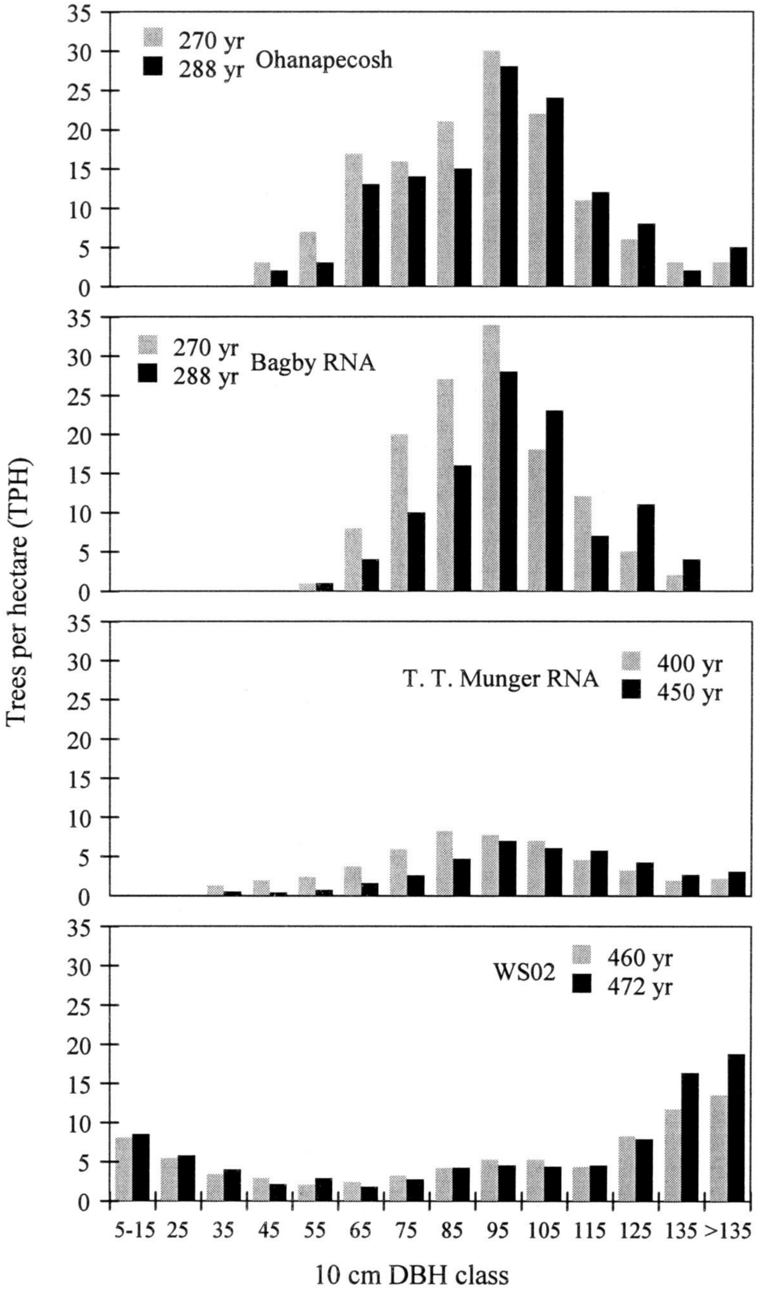

Figure 12. Change in density (TPH) and DBH distribution of Douglas-fir at the Ohanapecosh, Bagby RNA, T. T. Munger RNA and WS02 old-growth study areas at the beginning and end of each study.

Table 7. Arithmetic average and maximum DBH (cm) and height (m) for Douglas-fir and western hemlock. Beginning (plot installation) and ending (last) remeasurement for all nine study areas in their respective stages of forest development.

	Douglas-fir							
Study area	Average DBH		Maximum DBH		Average height		Maximum height	
	beginning	ending	beginning	ending	beginning	ending	beginning	ending
young								
Mt. Hood	23.2	40.2	51.8	85.3	23.9	33.8	39.6	51.1
Gifford Pinchot	34.3	51.2	73.4	90.9	35.9	44.5	53.7	59.3
Willamette	32.6	45.9	63.0	77.5	33.7	41.0	49.1	54.6
mature								
Mt. Hood		49.7		99.5		38.2		54.6
Gifford Pinchot		64.9		112.3		49.7		64.9
Willamette		67.0		106.5		50.2		63.7
Hagen RNA	44.2	50.3	114.3	121.0	35.6	38.2	54.1	54.8
RS26	50.1	56.2	102.8	109.5	42.7	45.5	62.9	64.8
old growth								
Ohanapecosh	85.9	90.7	144.6	148.6	57.4	58.7	68.6	69.0
Bagby RNA	87.3	93.2	127.8	133.6	50.8	52.2	58.1	58.8
T. T. Munger RNA	86.8	96.1	172.0	190.0	44.7	46.7	57.8	58.7
WS02	59.6	61.6	181.0	182.9	29.8	30.8	59.8	60.0
	western hemlock							
young								
Mt. Hood	10.0	11.8	25.7	44.2	7.0	8.4	16.2	17.1
Gifford Pinchot		0.0		0.0		0.0		0.0
Willamette	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
mature								
Mt. Hood		13.2		54.7		9.1		17.8
Gifford Pinchot		10.5		31.3		7.7		17.1
Willamette		19.1		41.0		13.8		31.2
Hagen RNA	15.0	15.9	44.3	47.1	6.3	11.1	10.6	34.7
RS26	10.4	11.7	38.8	58.4	7.4	8.4	17.6	17.8
old growth								
Ohanapecosh	25.4	27.2	97.2	103.1	43.7	45.5	73.4	73.8
Bagby RNA	23.8	24.2	101.8	105.6	17.1	17.8	48.1	48.4
T. T. Munger RNA	53.5	64.1	150.3	169.9	34.9	39.1	50.0	50.2
WS02	21.8	23.2	110.5	112.9	16.6	34.8	49.7	50.2

WESTERN HEMLOCK

Recruitment as well as growth and mortality of western hemlock occurred at each study area. By a forest age of 100 yr density of western hemlock (300 TPH) nearly equaled density of Douglas-fir at the Mt. Hood and Gifford Pinchot study areas (Figure 5). At RS26 at a forest age of 137 yr, western hemlock (414 TPH) had outnumbered Douglas-fir (335 TPH). However, at the Willamette and Hagen RNA study areas numbers of western hemlock were less dense than in the other mature stands, but densities were increasing. At the four old-growth study areas, numbers of western hemlock had declined slightly.

Western hemlock mortality rates in the young-mature and mature study areas were near zero and density of trees increased. At all old-growth sites mortality rates were much higher, particularly for small diameter trees (0.6–0.7% for trees ≤35 cm). At the T. T. Munger RNA, a high mortality rate was also found in the largest DBH class (0.7% for trees >85 cm); however, no patterns of mortality in relation to larger diameter classes were evident at the other three old-growth study areas (Figure 13).

The overall change in western hemlock population structure in young-mature and mature stands was one of a large increase in the density of small trees (Figures 14 and 15). In old-growth stands density of small trees was still high but there were increasingly larger trees in the population (Figure 16). Maximum DBH and tree height in mature stands were well below values for old growth. On average, maximum DBH in old-growth was 76.4 cm larger than in mature stands. Change in maximum DBH averaged 0.7 cm yr^{-1} and 0.3 cm yr^{-1} in mature and old-growth stands, respectively. Maximum tree height in old-growth stands averaged 32 m taller than in mature study areas. In mature stands, change in maximum tree height was erratic: Hagen RNA averaged 2 m yr^{-1} while western hemlock in RS26 had not changed. At all old-growth sites change in maximum tree heights had ceased (Table 7).

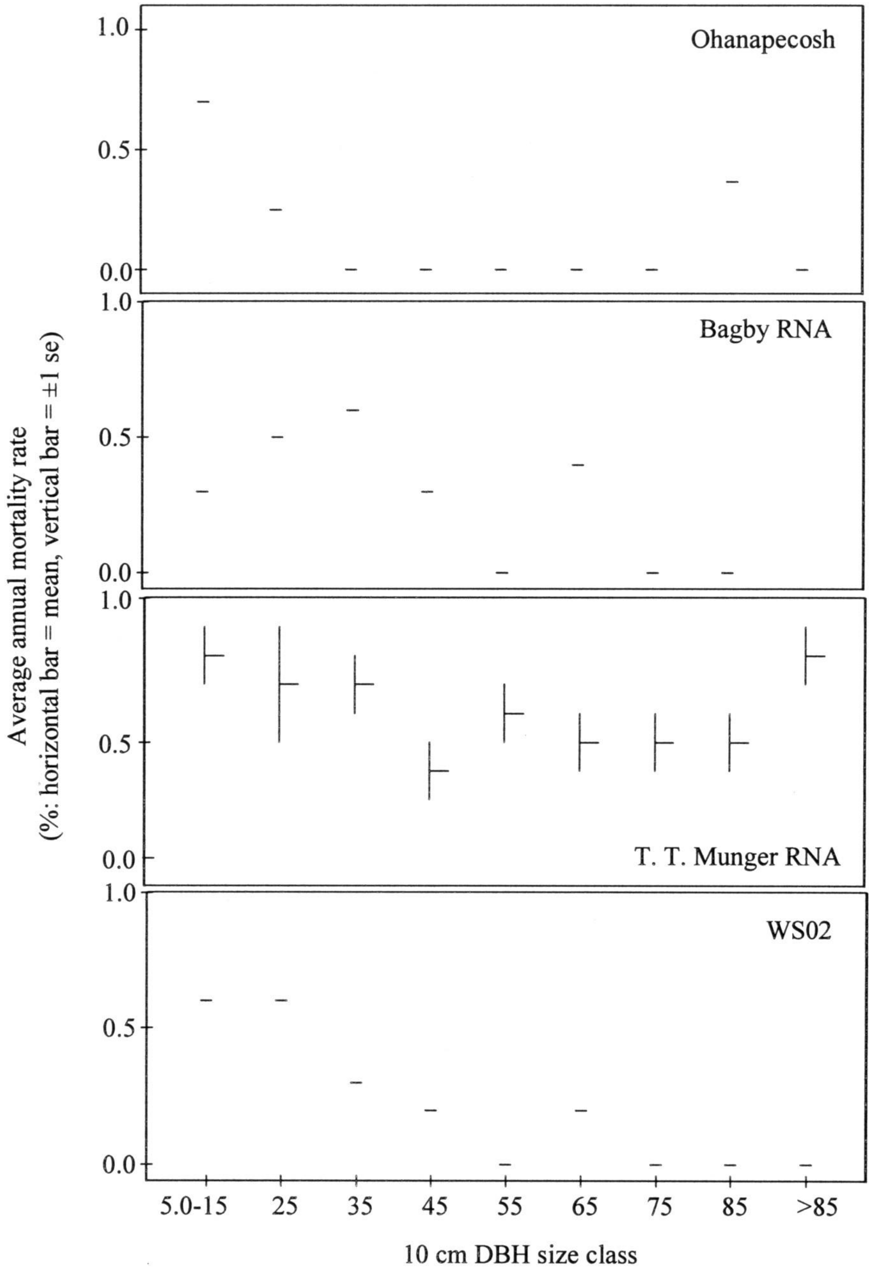

Figure 13. Western hemlock average annual mortality rates (%) by 10 cm DBH class: Ohanapecosh, Bagby RNA, T. T. Munger RNA and WS02 old-growth study areas. Standard errors were not calculated for Ohanapecosh, Bagby RNA or WS02 due to small number of remeasurements.

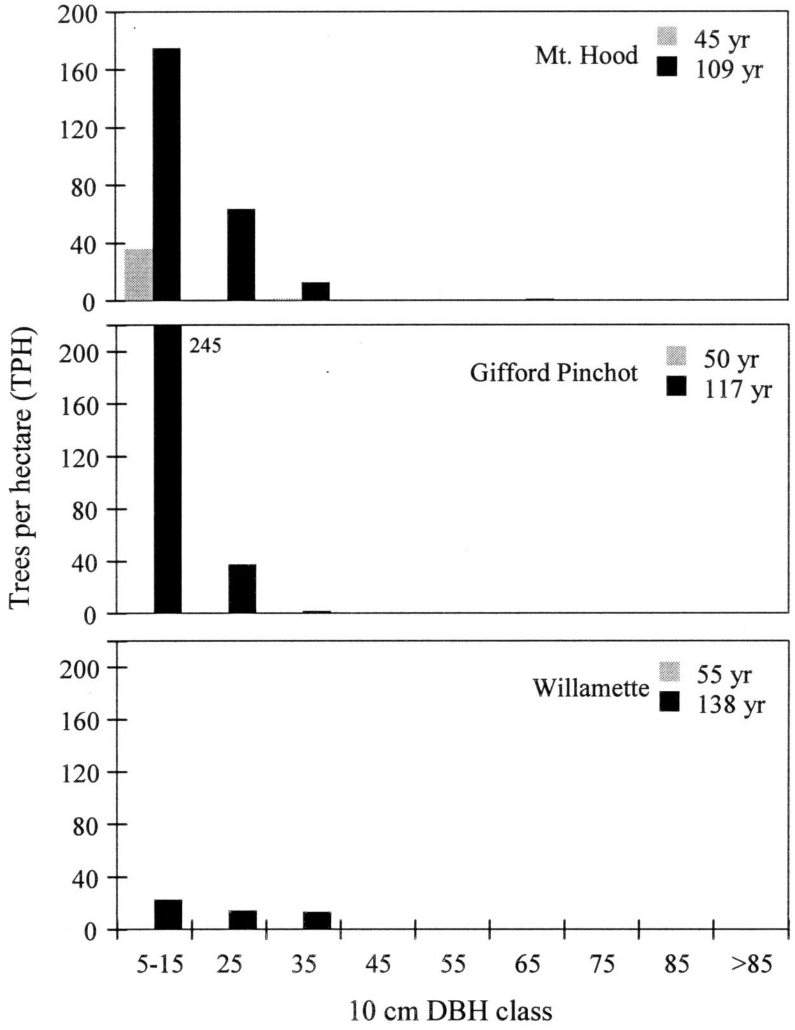

Figure 14. Change in density (TPH) and DBH distribution of western hemlock at the Mt. Hood, Gifford Pinchot and Willamette young-mature study areas at the beginning and end of each study.

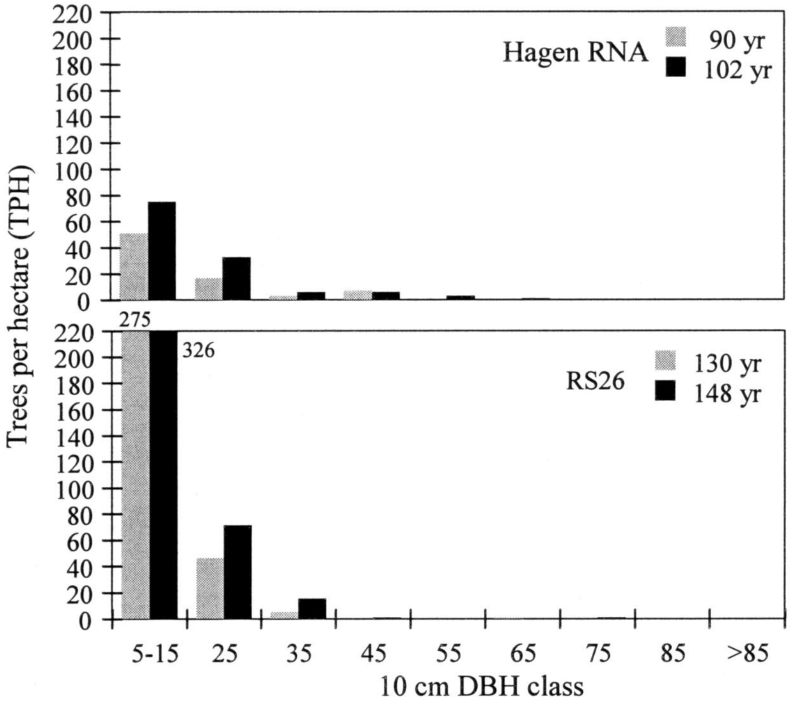

Figure 15. Change in density (TPH) and DBH distribution of western hemlock at the Hagen RNA and RS26 mature study areas at the beginning and end of each study.

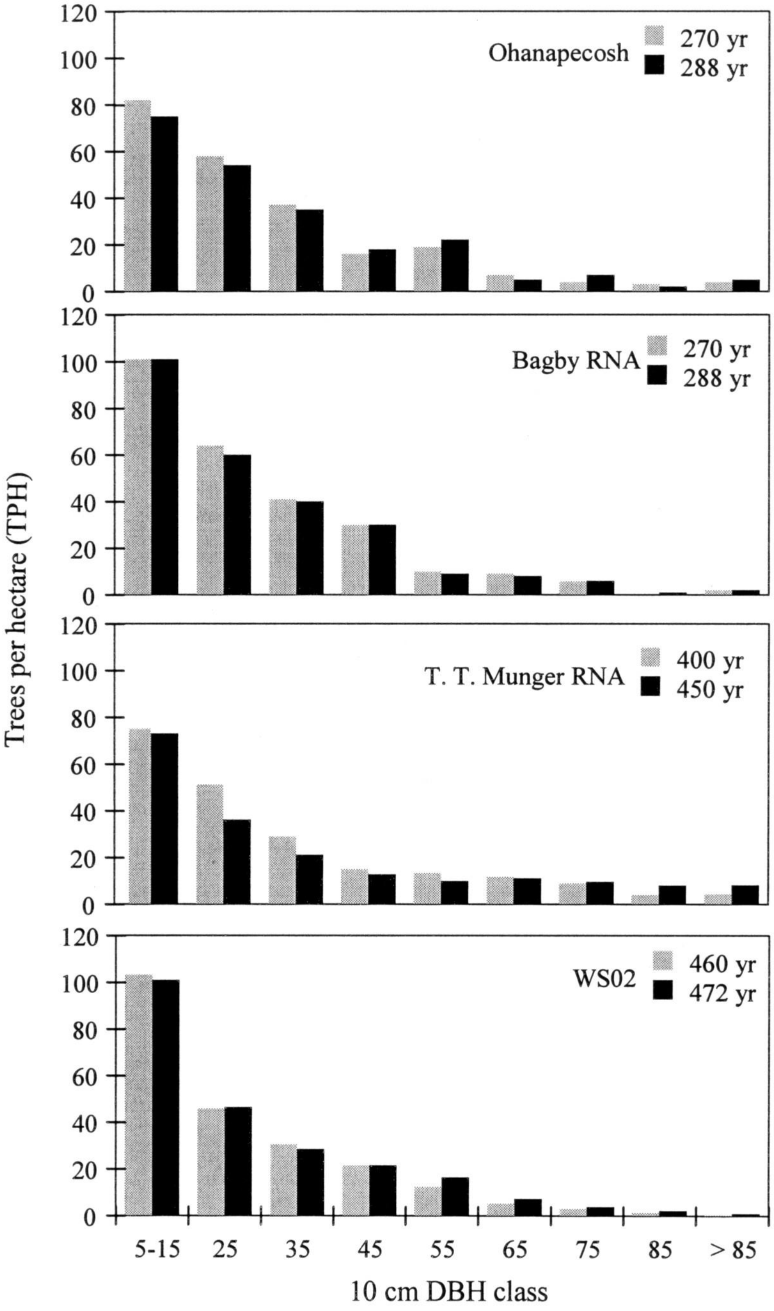

Figure 16. Change in density (TPH) and DBH distribution of western hemlock at the Ohanapecosh, Bagby RNA, T. T. Munger RNA and WS02 old-growth study areas at the beginning and end of each study.

BIOMASS ACCUMULATION AND INPUT OF COARSE WOODY DEBRIS

RATES

Annual accumulations of Douglas-fir stem wood and bark biomass in the young-mature and mature study areas averaged 4.8 Mg ha^{-1} yr^{-1}; while input of stem wood and bark coarse woody debris averaged 1.8 Mg ha^{-1} yr^{-1} (Figure 17). In young stands, average DBH of input of debris was 24.7 cm, and in mature stands, 33.1 cm. Both the Ohanapecosh and Bagby RNA early old-growth stands experienced constant decline in Douglas-fir biomass accumulation, and negative values were recorded at the last remeasurement of each plot. At the T. T. Munger RNA and WS02 advanced old-growth sites, biomass accumulation averaged -0.7 Mg ha^{-1} yr^{-1}. Input of stem wood and bark debris at all four old-growth study areas averaged 2.1 Mg ha^{-1} yr^{-1} which was only slightly higher than the average for the five younger stands. Average DBH of input of debris in old-growth forests was 80.3 cm.

Accumulation of western hemlock stem wood and bark biomass in the young-mature and mature stands averaged 0.2 Mg ha^{-1} yr^{-1} while input of coarse woody debris was minimal (<0.1 Mg ha^{-1} yr^{-1}) (Figure 18). Average DBH of debris was <5 cm. Biomass accumulations were higher at all four old-growth stands and averaged 0.8 Mg ha^{-1} yr^{-1}. Input of debris at the T. T. Munger RNA (0.8 Mg ha^{-1} yr^{-1}) exceeded the average accumulation of western hemlock biomass at the site (0.5 Mg ha^{-1} yr^{-1}). Average DBH of western hemlock input of debris at the T. T. Munger RNA equaled 67.8 cm. Input of debris at the three other old-growth sites ranged from a trace to 0.2 Mg ha^{-1} yr^{-1}, and the average DBH equaled 13.1 cm.

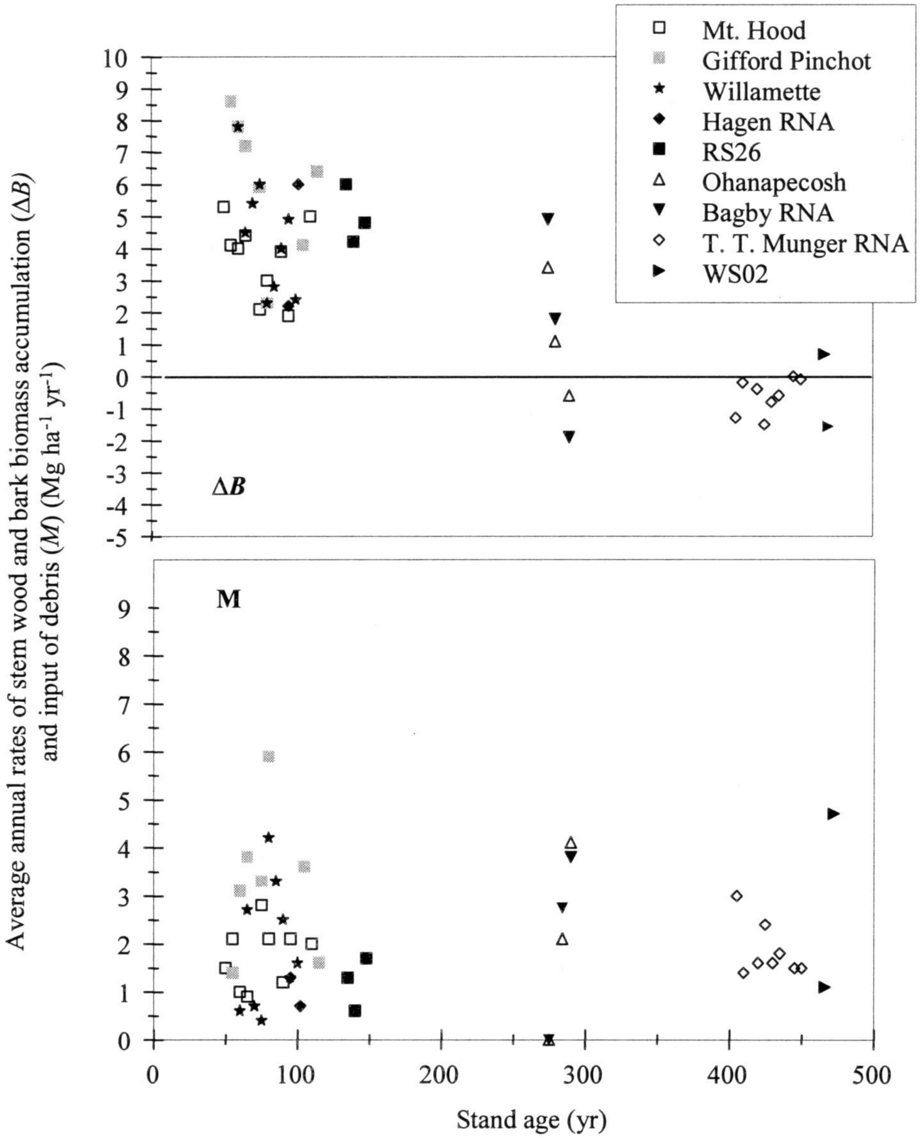

Figure 17. Douglas-fir average annual rate of stem wood and bark biomass accumulation and input of stem wood and bark debris.

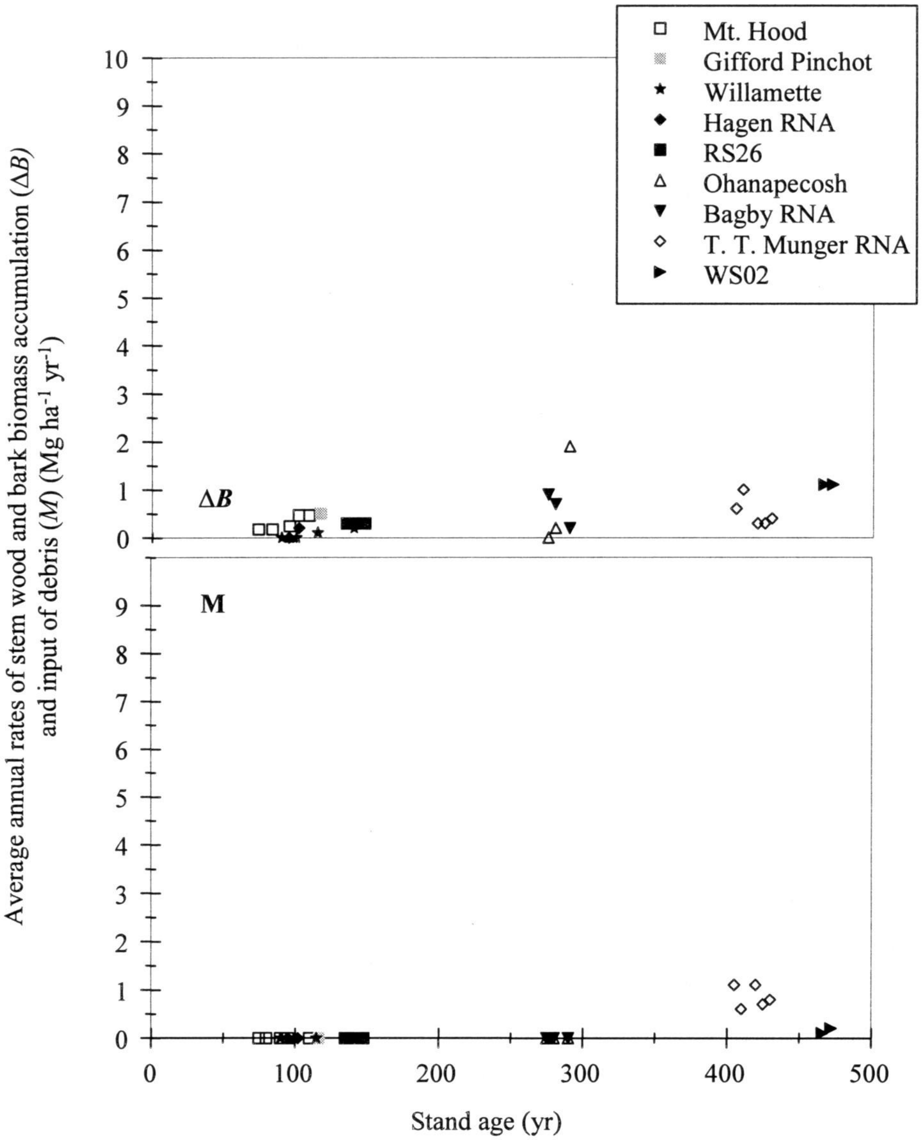

Figure 18. Western hemlock average annual rate of stem wood and bark biomass accumulation and input of stem wood and bark debris.

BIOMASS STOCKS

Stocks of Douglas-fir biomass increased in young-mature, mature, and early old growth stands (Figure 19). Stocks were highest in the early old-growth plots (Ohanapecosh had the maximum at 865.1 Mg ha^{-1}). In the advanced old-growth stands stocks were considerably lower and in decline: T. T. Munger RNA dropped from 297.3 to 267.8 Mg ha^{-1} and WS02 from 348.7 to 332.9 Mg ha^{-1}.

Western hemlock biomass stocks were minimal at the young-mature and mature stands. Stocks were higher and increasing at the four old-growth plots: T. T. Munger RNA increased from 106.2 to 167.4 Mg ha^{-1} and WS02 increased from 64.8 to 78.0 Mg ha^{-1} (Figure 19).

The pattern in stem wood and bark biomass accumulations for all conifer species from young to old-growth stands was driven by Douglas-fir biomass which rose rapidly in the early stages of forest development and dropped in the latter stages. At the two advanced old-growth study areas there had been little change in total conifer stem wood and bark biomass stocks: T. T. Munger RNA averaged 485.6 Mg ha^{-1}, WS02 418.3 Mg ha^{-1} signifying that the continued loss of Douglas-fir was no longer an important factor in change of biomass stocks (Figure 20).

Average biomass per conifer tree increased at all sites even though there was a continuous decline in total density of all conifers. Decline in density was driven by the loss of Douglas-fir, and the increase in average biomass was the result of recruitment and growth of shade-tolerant species especially western hemlock (Tables 2 and 3). The pattern followed a negative exponential trend (Figure 21):

$$AvgBiomass = 329.1570xTPH^{-0.9035} \quad \text{(residual se = 0.53)} \qquad (8)$$

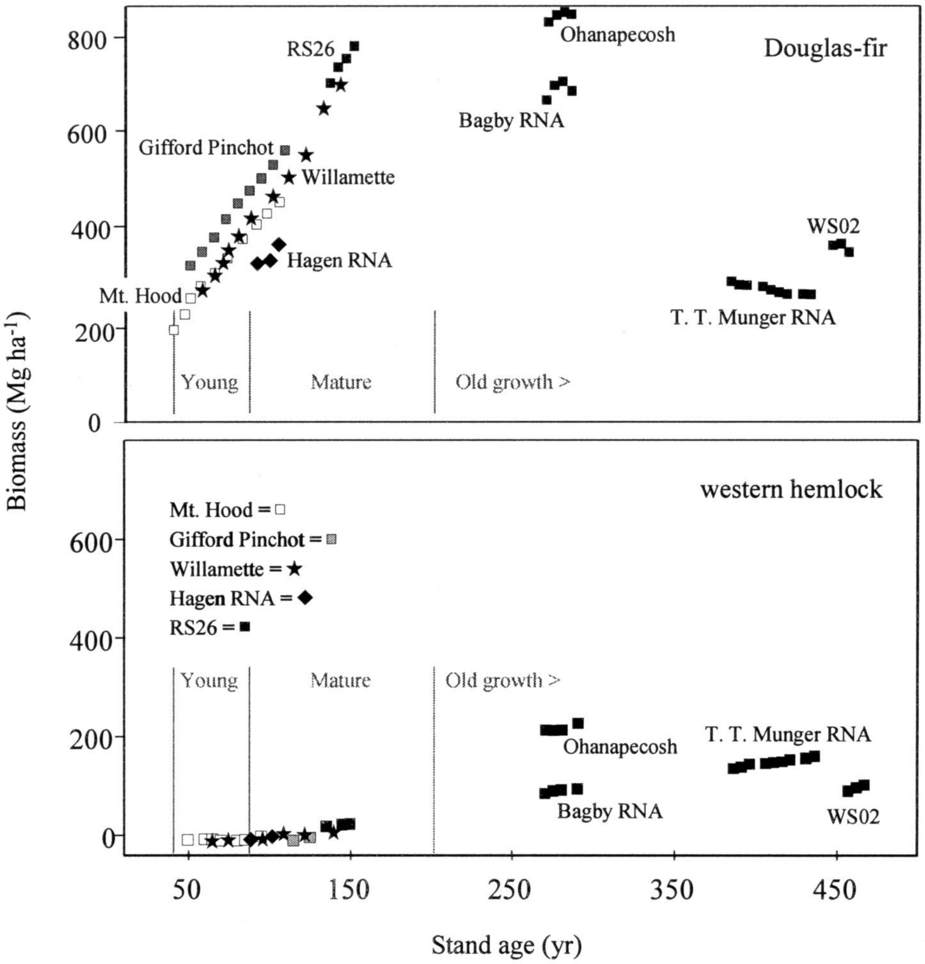

Figure 19. Long-term trends in Douglas-fir and western hemlock biomass stocks at each of the nine study areas.

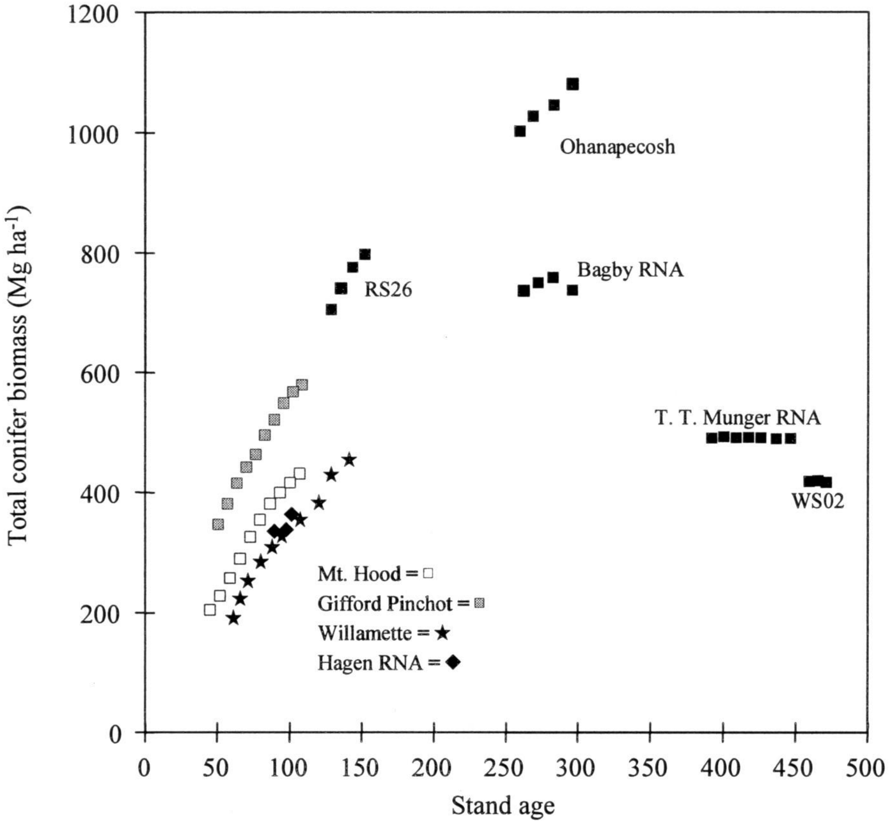

Figure 20. Long-term trends in total conifer biomass stocks at the nine study areas.

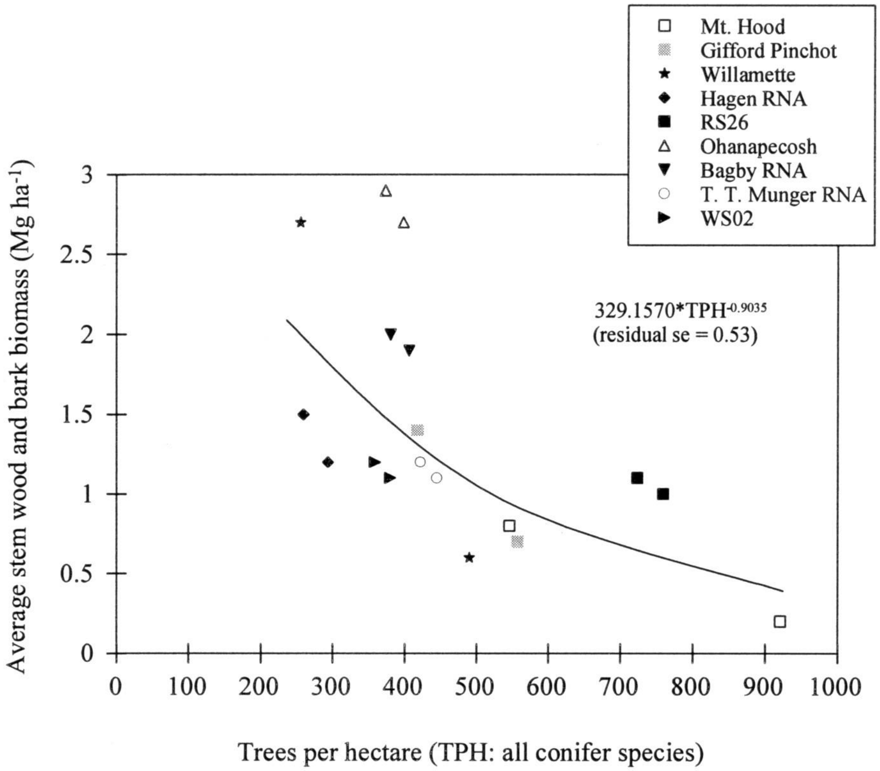

Figure 21. The relationship between long-term average biomass of stem wood and bark per tree for all conifer species over change in density of all conifer species.

When density is measured in trees per hectare the intercept coefficient (329.1570) represents the number of trees per hectare that should result in a theoretical maximum average biomass per tree (White and Harper 1970, White 1981). Only the Willamette and Hagen RNA study areas dropped below this theoretical density as both stands had relatively few western hemlock; if density of shade-tolerant species were to increase then there should be a move toward the theoretically optimal stocking of 329 TPH.

AGENTS OF MORTALITY

Most of the larger (>65 cm DBH) Douglas-fir and western hemlock listed as dead at the nine study areas were successfully relocated. Smaller trees (<65 cm DBH) were generally already decayed and often could not be found; thus no new information could be gathered beyond that provided by the Permanent Sample Plot program. The unknown category is composed mostly of such small trees plus many broken stems with tops that had decayed and could not relocated.

YOUNG-MATURE AND MATURE STUDY AREAS

Sixty-four years after installation of plots at the Mt. Hood study area 765 Douglas-fir (67.6% of the original stand) and 24 western hemlock had died (Table 8). Suppression was the leading cause of Douglas-fir mortality (490 individuals). Most of these suppressed trees were small averaging 20.4 cm DBH and 22.3 m tall placing them at least 11.5 m below the average height for Douglas-fir at the end of the young stage (Table 7). A majority were recorded as dead in the 1934 and 1939 remeasurements (forest ages of 49 and 54 yr, respectively). Wind or snow was the second ranked identifiable cause of Douglas-fir mortality (60 trees). Williamson (1963) stated that there had been, "severe wind damage to plot 1 which lies on an exposed slope," but mortality rates for this cause at plot 1 were comparable to plots 2 and 3 at all remeasurements. Douglas-fir bark beetle claimed only 17 trees over the entire data record; however, beetles were still active on the site. Several living Douglas-fir have fire scars at their base on the uphill side indicating that a ground fire had occurred at least once after stand reestablished. Such scars are access points for wood decay fungi; however, no decay-related deaths were confirmed. Mortality of western hemlock was low. The dominant cause of mortality for this species was being crushed by another larger tree (18 of the 24 dead trees).

Table 8. Total number of dead Douglas-fir and western hemlock by agent of mortality in the young-mature and mature study areas.

Douglas-fir	Mt. Hood	Gifford Pinchot	Willamette	Hagen RNA	RS26	Total
Unknown	197	161	110	131	13	612
Suppression	490	177	196	203	34	1100
Root & stem decay		2	1	1		4
Bark beetle	17	82		6		105
Wind or snow	60	35	19	17	3	134
Crushed or hit	1	1	2	13		17
Other		3	9	12		24
Total	765	461	337	383	50	1996
Western hemlock	Mt. Hood	Gifford Pinchot	Willamette	Hagen RNA	RS26	Total
Unknown		1	4	2	3	10
Suppression	4				6	10
Root & stem decay						
Mistletoe						
Wind or snow	2	1			2	5
Crushed or hit	18	2	1			21
Other		3				3
Total	24	7	5	2	11	49

Sixty-seven years after installation of the Gifford Pinchot plots 461 Douglas-fir (67.6% of the original stand) and seven western hemlock had been recorded as dead (Table 8). Suppression was again the leading assigned cause of mortality of Douglas-fir (177 trees). High rates of mortality for these trees were recorded as in the 1937 and 1943 remeasurements (forest age 60 and 66 yr, respectively). Again these were mostly small trees averaging ≤27.3 cm DBH and ≤32.2 m tall placing them 12.3 m below the average height for Douglas-fir at the end of the young stage (Table 7). Douglas-fir bark beetles were assigned as the mortality agent for 82 trees, the highest density of all nine study areas, and most deaths occurred during the most recent remeasurements. Earlier in the history of the study area a minor landslide sent debris into the stand wounding several trees; beetles apparently have attacked these weakened individuals. Wind or snow breakage was also common accounting for 35 individuals. Honey mushroom (*Armillaria* spp.) was found on two prostrate Douglas-fir. Mortality of western hemlock was low.

Eighty-two years after plot installation, 337 Douglas-fir (57.4% of the original stand) and five western hemlock had died at the Willamette study area (Table 8). Suppression, also the leading cause of Douglas-fir mortality, accounted for 196 individuals. Mortality rates for these trees were highest at the 1934 and 1939 remeasurements (forest age 79 and 84 yr, respectively). Average size of these trees was ≤23.0 cm DBH and ≤28.3 m tall placing them at least 11.8 m below the average height for Douglas-fir at the end of the young stage (Table 7). Wind or snow break claimed 29 individuals; this was an important cause of mortality at the 1920 remeasurement (forest age 65 yr). At this remeasurement, T. T. Munger (Munger 1946) reported, "extraordinary loss from snowbreak..." as the chief cause of mortality. He also stated that when the forest was 40 yr old a ground fire swept though the stand creating, “bad basal scars which are... undoubtedly harboring basal rot.” However, fire scars are no longer obvious and velvet top was found on only one felled Douglas-fir, although fruiting bodies of this fungus were found on a few live trees within the study area. Mortality of western hemlock at the Willamette study area was low.

Twelve years after installation of plots at the Hagen RNA, 383 Douglas-fir (14.0% of the original population) and two western hemlock had died (Table 8). Suppression-related mortality was judged responsible for the death of 203 Douglas-fir. Again these were relatively small trees averaging 26.0 cm DBH and 27.1 m in height placing them 8.5 m below the average height for Douglas-fir at the time of plot establishment (Table 7). A majority of the suppressed trees had died by the first remeasurement in 1988 (forest age 96 yr). Several trees had broken stems, but red ring (*Phellinus pini* (Thore.:Fr.) Pilat) was identified on only one tree the rest were attributed to wind or snow breakage. Bark beetle activity was minimal. Reexamination of 29 trees listed in the original PSP data as wind-related mortality revealed that 18 had existed in close proximity to creek channels or on steep slopes; undercutting of rooting substrate by water and thin soils plus being hit by large trees that were falling due to substrate failure was considered to be the actual cause of mortality. Western hemlock is rare at the Hagen RNA and only two deaths of unknown cause were recorded.

Eighteen years after installation of Reference Stand No. 26, 50 Douglas-fir (13.0% of the original population) and 11 western hemlock had been recorded as dead (Table 8). Suppression was again considered the leading cause of death (34 individuals). All were standing dead with crowns present and averaged 27.5 cm DBH and 31.5 m tall placing them 14.0 m below the average height for Douglas-fir at the final remeasurement. Wind or snow breakage had also taken 3 trees. RS26 has a dense population of western hemlock, but only 11 had died with, suppression as the dominant cause of mortality assigned to six individuals.

OLD-GROWTH STUDY AREAS

Eighteen years after plot installation at the Ohanapecosh study area only 12 Douglas-fir (5.2% of the original population) and nine western hemlock had died (Table 9). Two Douglas-fir were in an intermediate canopy position and were assigned to suppression-related mortality. Two Douglas-fir had roots completely decayed by velvet top and were associated with fruiting bodies which were also found around living trees. Wind or snow snapped two additional Douglas-fir and evidence of bark beetles was found on one tree. As with all young and mature study areas western hemlock mortality was low. Out of nine total dead western hemlock, six were smaller trees, which had died of suppression, and three were crushed under a single fallen tree.

Eighteen years after plot installation in the Bagby RNA 23 Douglas-fir (18.1% of the original population) and 21 western hemlock had been recorded as dead (Table 9). Douglas-fir bark beetle had claimed 17 Douglas-fir. Beetle-related mortality was found in two small groups of three-four trees. Wind or snow had toppled two Douglas-fir, and laminated root rot (*Phellinus weirii* (Murr.) Gilb.) was found on one downed tree.

Table 9. Total number of dead Douglas-fir and western hemlock by agent of mortality in the old-growth study areas.

Douglas-fir	Ohanapecosh	Bagby RNA	T. T. Munger RNA	WS02	Total
Unknown	5	3	892	9	909
Suppression	2				2
Root & stem decay	2	1	247	13	263
Bark beetle	1	17	113	7	138
Wind or snow	2	2	18	14	36
Crushed or hit					
Other			16		
Total	12	23	1286	43	1364
Western hemlock	Ohanapecosh	Bagby RNA	T. T. Munger RNA	WS02	Total
Unknown		2	353	30	385
Suppression	6	9	221	86	322
Root & stem decay			40		40
Mistletoe			48		48
Wind or snow	3	8	281	32	324
Crushed or hit		2	10	14	26
Other				2	2
Total	9	21	953	164	1147

Although density of western hemlock was similar to density at Ohanapecosh, mortality was greater at the Bagby RNA plot. Suppression was the dominant cause of western hemlock mortality claiming nine of the 21 individuals. Eight small trees (≤45 cm DBH) were found lying on the ground and were assumed to have been flattened by snow.

After 50 years of measurement at the T. T. Munger RNA, 1281 Douglas-fir (62.9% of the original population) and 953 western hemlock had been recorded as dead (Table 9). Unfortunately, many Douglas-fir (892) and western hemlock (353) mortality records had had no previous mortality agent assigned and remained in the unknown category. Many of these trees had broken stems with tops that could not be located. A total of 247 Douglas-fir deaths were attributed to root and stem decay: 100 were associated with velvet-top and 55 with laminated root rot, 60 broken stems were associated with quinine conk (*Fomitopsis officinalis* (Vill.:Fr.) Bond and Sing.), and 32 with red ring. Twenty-seven prostrate western hemlock had Annosus-s decay at their base. On 13 broken western hemlock stems red ring was found in the fracture zone. Bark beetles were assigned a cause of death for 113 Douglas-fir. Hemlock dwarf mistletoe was wide-spread at the RNA and related to 48 western hemlock deaths. Wind or snow breakage had killed 281 relatively small (≤45 cm DBH) western hemlock. Suppression was not identified as a significant agent of mortality for Douglas-fir but was assigned as the cause of death for 221 western hemlock. Ten small western hemlock were also crushed by falling trees. Other causes of mortality included: three lightning kills, seven toppled by erosion adjacent to ephemeral streams, and six drowned by a beaver pond.

At the T. T. Munger RNA, Douglas-fir and western hemlock average annual mortality rates were relatively high (0.9% and 0.8%, respectively, Tables 5 and 6) during the six-yr interval between 1947 and 1953 (forest age ~400 to 406 yr). Greater than 60% of all mortality assigned to Douglas-fir bark beetle occurred during this one interval and affected mostly large trees on only two adjacent plots (80 and 81) which also had had substantial root and stem decay. For western hemlock wind or snow breakage and root and stem decay were the chief causes of mortality affecting several trees of various sizes on several plots. Unusually strong winter winds were reported from 1949 to 1951 (Steele and Worthington 1955). January to February in 1950, 79 m of snow fell at the NOAA Wind River meteorological station, which was the heaviest snow on record for the station. Douglas-fir and western hemlock mortality rates were again high (0.9% and 0.8%, respectively) during the third remeasurement interval between 1959 and 1965. During this interval 89% of western hemlock mortality was categorized as wind or snow breakage and 71% of Douglas-fir mortality was categorized as related to root and stem decay both affecting one or two trees on many plots. However, no unusual climatic conditions (heavy snow or rain) were recorded at the NOAA Wind River meteorological station over this six-yr period.

Twelve years after permanent plot system installation at the WS02 study area 43 Douglas-fir (7.3% of the original population) and 164 western hemlock were listed as dead. Suppression was the leading cause of mortality for western hemlock followed by wind or snow breakage (Table 9). Western hemlock mortality rates were similar over both remeasurement intervals. Douglas-fir mortality was attributed mostly to root and stem decay (primarily velvet top and rosy-brown top rot (*Fomitopsis cajanderi* (Karsten) Kotlaba and Pouzar)) and wind and snow breakage. Seven Douglas-fir were killed by bark beetles during the six-yr interval ending in 1994 (forest age 472 yr). This event was sufficient to raise Douglas-fir annual average mortality rates to their highest recorded value (0.9%).

Both the T. T. Munger RNA and WS02 are adjacent to managed forests (Figure 22). However, it was determined that proximity of T. T. Munger RNA and WS02 plots to an edge of a managed stand had not been a significant factor in Douglas-fir mortality rates. Slope coefficients of simple linear regression of mortality rate by plot over distance to managed edge were not significantly different from zero: T. T. Munger RNA β_1, $t = 1.37519$, 99 d.f.; WS02 β_1, $t = 0.5336$, 59 d.f. (Figure 23).

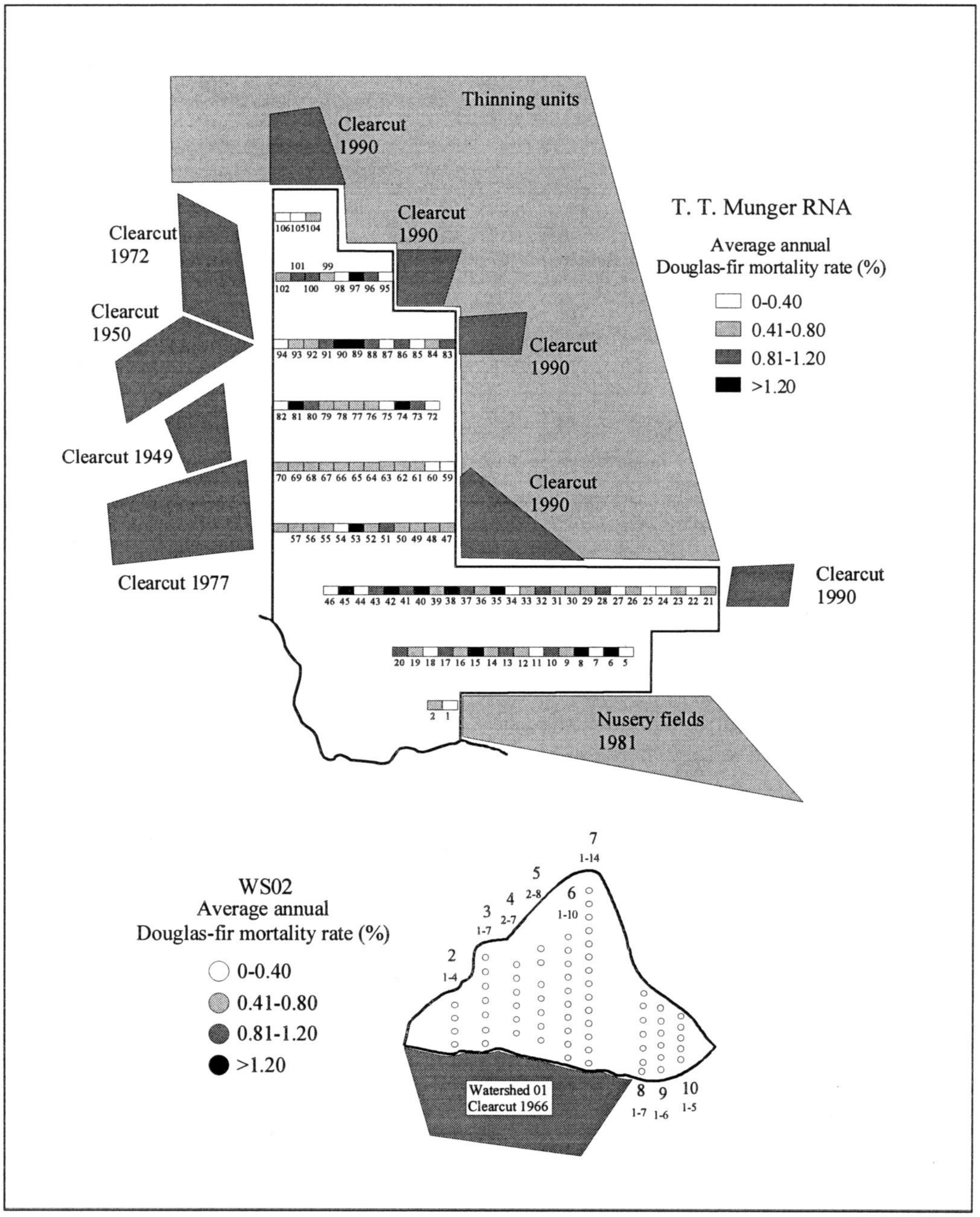

Figure 22. Layout of T. T. Munger RNA and WS02 plot systems, plot-level Douglas-fir mortality rates (trees >65 cm DBH), and adjacent management areas.

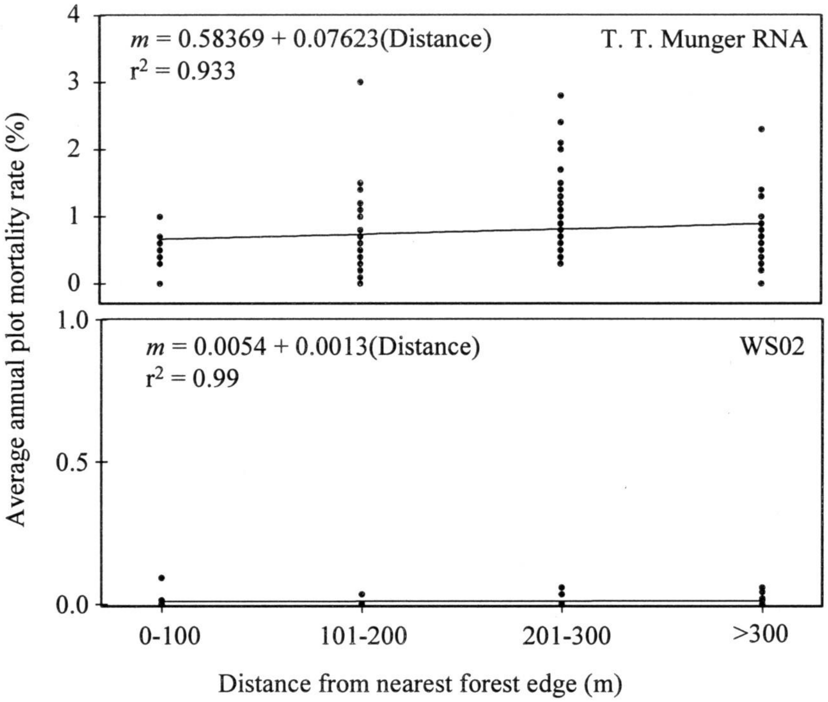

Figure 23. Linear regression models for plot specific Douglas-fir mortality rates (trees >65 cm DBH) and distance to the nearest forest edge for the T. T. Munger RNA and WS02 old-growth study areas.

DISCUSSION

The permanent sample plot data reported here provide a long-term perspective on rates and causes of mortality for the two primary tree species in the low-elevation forests of the Cascade Mountains of western Washington and Oregon. Although the plots represent a classic chronosequence, they also provide long-term records for individual stands, including the transition from stand youth to maturity. Many of the patterns that emerge from these records support previous assumptions about mortality, although these are among the first data to confirm these trends. The larger perspective provided by these data sets allow for some new inferences about relationships of tree mortality to forest stand development and ecosystem processes.

RATES OF MORTALITY

DOUGLAS-FIR

Mortality rates of Douglas-fir show a regular decline with forest age. This general pattern of declining mortality fits with conventional wisdom (McArdle et al. 1949, Staebler 1953) regarding Douglas-fir stand development, although most of this knowledge is based on observations in stands <160 years of age. A continuing decline in rates of mortality for older Douglas-fir has been hypothesized (Franklin and Hemstrom 1981), but empirical data have been limited (Franklin and DeBell 1988).

The high rates of survival for large, old Douglas-fir trees are an important life history attribute of the species. The potential for increased survival—as opposed to increased mortality—is typically not incorporated into traditional forest planning. More specifically, formulas for predicting mortality in many successional models assume increased rates of mortality as trees approach maximum ages and sizes (Botkin 1992, Shugart et al. 1992). However, Franklin et al. (unpublished data) did report a negative relationship between size class of Douglas-fir and rate of mortality.

The pattern of increased rates of survival for older trees is a conspicuous life-history characteristic of at least some tree species in tropical forests, as well. Clark and Clark (992) reported a decreasing probability of mortality with increasing size for several tree species in Costa Rica. In Panama higher rates of mortality in smaller individuals were found in the 50 ha Barro Colorado Island plot (BCI) (Condit et al. 1995). Milton et al. (1994) also recorded lower mortality rates in large, canopy level trees at BCI.

WESTERN HEMLOCK

The low rates of mortality for western hemlock in young and mature stands in this study are surprising since the population consists mostly of small understory trees identified as belonging to the "suppressed" crown class. Favorable environmental (including light) conditions in the understory of these Douglas-fir stands as they make the transition from the developmental stage of competitive exclusion to the maturation stage (Franklin et al. 2001) are almost certainly important factors in the high rate of hemlock survival. In pure western hemlock stands and coastal Sitka spruce (*Picea sitchensis* (Bong.) Carr.)-western hemlock forests developing after catastrophic windthrow or fire, western hemlock as a dominant component undergoes similar patterns of mortality (Harcombe 1986, Harcombe et al. 1990, Acker et al. 2000) to those reported for Douglas-fir stands in my study.

Mortality rates for western hemlock in old-growth stands are at levels comparable to those of Douglas-fir and are generally distributed across all size classes, including small trees. These results are consistent with those reported earlier from the T. T. Munger RNA (Franklin and DeBell 1988). Franklin and Hemstrom (1981) hypothesized that mortality rates would increase with diameter based partially on the notion that western hemlock would exhibit increasing susceptibility to diseases and insects. In fact, there was no consistent relationship between western hemlock diameter and mortality rate in the four old-growth data sets utilized in this study, except for a drop in rates for tree diameters >35 cm DBH. The long-term pattern in western hemlock mortality rates from my data were best fit with a linear function (eqn 7); however, it is most certain that mortality rates will not continued to rise in forest older than 450 yr. A more realistic formula would be one of a logistic nature with an upper asymptote of 4-5% reached by age 450 yr. More data are required before a good fit to a logistic function can be obtained.

A high mortality rate for western hemlock >85 cm DBH at T. T. Munger Research Natural Area is one exception to the general pattern observed in this study (Figure 13). Several factors may have contributed to this increase, including a high level of infection by hemlock dwarf mistletoe. At the three other old-growth sites, which lacked similar mistletoe infections, there was no consistent pattern in mortality of older trees. However, the length of observation period at these other sites was much shorter than at T. T. Munger and, perhaps, it was too short to capture the dynamics of this long-lived, late-seral species. In the early old-growth plots at Bagby and Ohanapecosh, western hemlock was only beginning to reach co-dominant canopy positions and larger sizes.

In old growth, high rates of mortality do occur in smaller western hemlock trees. These are partially a result of poor environmental conditions (low available moisture and light) in the understory as has been revealed in mortality rates of seedlings (Christy 1986). Also, like other trees low in the canopy, they are subject to additional hazards, such as crushing by snow and by falling trees. For example, small Pacific silver fir were observed to have high rates of mortality due to falling noble fir dominants in one subalpine forest stand (Acker et al. 1996).

COMPARISONS OF OBSERVED MORTALITY RATES WITH YIELD MODEL PREDICTIONS

Stand yield tables represent early attempts to describe patterns in forest development. Yield tables are constructed from density, diameter, and height data collected from trees in natural or managed stands and are used to predict timber volumes over time. These documents are often referred to in contemporary publications and the concepts used in their design have been incorporated in many mortality subroutines in stand and ecosystem development models (White and Harper 1970, Monserud 1976, White 1981, Peet and Christensen 1987, Clutter et al. 1988, Oliver and Larson 1990, Botkin 1992, Shugart et al. 1992, Jack and Long 1996, Waring and Running 1998, Cramer et al. 1999, Goudriaan et al. 1999). Two sets of yield tables widely distributed by the U. S. Department of Agriculture are McArdle et al. (1949) for natural Douglas-fir stands and Barnes (1962) for natural western hemlock stands.

McArdle et al. (1949) constructed yield tables for Douglas-fir (>5 cm DBH) in the Pacific Northwest based on data from a chronosequence of 2049 temporary sample plots. These were mostly small (<0.4 ha) plots in natural 20 to 160 yr-old stands. A few plots became permanent plots including the Mt. Hood, Gifford Pinchot, and Willamette study areas. In their Table II, McArdle et al. included several matrices of changes in tree density by stand age (20-yr increments) and site productivity index where site productivity was measured as an estimate of maximum height attained by dominant and codominant trees at a stand age of 100 yr. Douglas-fir average annual mortality rates derived from Table II site productivity indices I (high) through IV (low) were at the top of the range of rates calculated with Equation 6 and individual stands of equivalent ages used in my research (Tables 5 and 10). Predictions from their yield tables would, therefore, have a substantially steeper decline in average density of Douglas-fir early in forest development than was observed in my study. This divergence was probably due to assumptions by McArdle et al. (1949) of continuous decline in density that conforms to a maximum -1.5 power function (White and Harper 1970, White 1981). However, from data used in this study, a more accurate maximum power function would be on the order of –1.25.

Table 10. Comparison of Douglas-fir average annual mortality rates (%) for forest ages 60 to 140 yr calculated with Equation 6 (Results section) and derived from McArdle et al. (1949) Table II for site productivity indices I (high) to IV (low). Based on maximum tree heights at 100 yr, the nine study areas used in this research fall into the site index II and III categories for Douglas-fir.

Age	Eqn. 6	McArdle I	McArdle II	McArdle III	McArdle IV
60	2.0	2.8	2.6	2.8	3.1
80	1.4	1.8	1.8	1.9	1.9
100	1.1	1.3	1.3	1.2	1.2
120	0.9	1.0	1.0	1.0	1.0
140	0.7	0.7	0.7	0.7	0.7

Barnes's (1962) yield tables for western hemlock (>3.8 cm DBH) were created from a large pool of data collected by a previous researcher from small temporary plots in natural, Sitka spruce-western hemlock stands in coastal Alaska, Oregon and Washington (Meyer 1937) that had at least 40% of their basal area in western hemlock. Of the 294 plots in Oregon and Washington, only 2% were in forests greater than 100 yr with the maximum being 173 yr. Although data came from stands near the coast, Barnes stated that his tables probably could be applied to Cascadian forests. In his Table 3, Barnes presents a matrix of changes in density of western hemlock over time by site productivity from plots located in Oregon and Washington. Unlike McArdle et al.'s Table II, mortality rates cannot be calculated from Barnes's Table 3 as it includes recruitment; it is in fact a table only of expected net changes in population density (recruitment minus mortality). Harcombe (1986), made the mistake of using this table for validation of his analysis of western hemlock mortality rates at Cascade Head Experimental Forest on the coast of Oregon. Barnes presents in Table 3 a series of populations with constantly decreasing density at all ages and site productivity indices (Table 11). This would mean that mortality always exceeds recruitment. This was not the case in the young-mature and mature stands used in my research; however, it might be understandable in coastal forests where western

Table 11. Western hemlock average annual changes in population density (%) for forest ages 60 to 300 yr derived from Barnes (1962) Table 3 for site productivity indices I (high) to IV (low). Based on maximum tree heights at 100 yr, the nine study areas used in this research fall into the site index III and IV categories for western hemlock.

Age	Barnes I (200)	Barnes II (170)	Barnes III (140)	Barnes IV (110)
60	-4.4	-4.4	-4.3	-4.3
80	-2.0	-1.9	-1.9	-2.0
100	-1.3	-1.4	-1.4	-1.4
120	-1.0	-0.9	-0.9	-1.0
140	-0.8	-0.8	-0.6	-0.8
160	-0.6	-0.6	-0.7	-0.5
180	-0.5	-0.4	-0.5	-0.5
200	-0.3	-0.3	-0.4	-0.3
250	-0.7	-0.7	-0.7	-0.8

hemlock populations are generally dense at an early age thus density-dependant mortality could also be high in young stands. In effect, the population dynamics of western hemlock emulate Douglas-fir, but rates of change in stand density in the 60-yr age class as predicted in Barnes's Table 3 are higher than average annual mortality rates calculated for Douglas-fir. If recruitment is taking place in these stands, which it most probably is, then turnover of stems as predicted by Barnes would be extraordinarily high. Barnes's predictions for rate of decline in population density of 250-yr-old stands (-0.7%), an extrapolation, is also probably unrealistically high as it is in excess of rates observed at the two early old-growth study areas (0.0 to -0.5%) used in this research.

Even though McArdle et al. (1949) and Barnes (1962) did incorporate large numbers of samples into the construction of their respective yield table, rates of population change can only be approximated from chronosequence data. It is only through long-term observations from permanent plots with tagged trees that trends and variations in rates can be accurately measured (Franklin 1989, Magnuson 1990, Pickett 1991). Mortality though was not considered as an important process; McArdle et al. (1949) mentioned mortality only briefly in an appendix. Stand yield tables are also limited for exploring changes in tree sizes as a result of mortality. Built into yield tables, as is done in other single-species volume tables, site index curves, and "self-thinning" rules (e.g., Clutter et al. 1988, Oliver and Larson 1990, Waring and Running 1998), are predefined and constant diameter frequency distributions. When mortality rates are imposed on fixed distributions the result will be a change in tree density but there will be no change in diameter distribution. The underlying assumption is that the sizes of trees that are dying are proportionally identical to those that survive (White 1981).

McArdle at al. (1949) normalized Douglas-fir diameter distributions. This dictated a bell-shaped distribution through time with the peak being set to the average tree diameter (determined as the tree diameter that corresponded to the average basal area; arithmetic averages, as in Table 7 are ~1 size smaller). This form of frequency distribution is theoretically valid for many shade-intolerant species (Peet and Christensen 1987); however, it cannot account for variability in DBH-class mortality rates. Douglas-fir DBH distributions at last remeasurement of the Mt. Hood, Willamette, and Hagen RNA study areas did appear normal as would be expected by McArdle at al. (Figures 10 and 11); however, at the Gifford Pinchot study area the distribution had low numbers of trees in the 55 cm and 65 cm DBH classes due to mortality caused by Douglas-fir beetle (Figure 11). At the Bagby RNA study area, the 288-yr diameter distribution had fewer trees in the 115 cm DBH class than would be predicted under the normality rule due also to Douglas-fir beetle mortality (Figure 12). Ohanapecosh had fewer trees in smaller diameters from the continued effect of suppression (Figure 12). These may seem like minor discrepancies, but one must also consider that Douglas-fir DBH distributions may never resemble normality. At WS02 there are high numbers of trees in the smaller and larger diameter classes (Figure 12). The majority of the smaller stems are within 300 m of the border with Watershed 01 (Figure 22) and exist because of the altered microclimate from that adjacent clearcut. The multitude of larger stems are scattered throughout the study area and are individuals, or "biological legacies" (Foster et al. 1998), that survived the disturbance which occurred over 400 years ago and cleared the way for the establishment of this stand. Douglas-fir diameter distribution at the RS26 study area is of a somewhat truncated form (Figure 11). The lack of a distinct peak in the frequency distribution in this plot is probably a result of competition with western hemlock that also established early and prevented Douglas-fir from dominating composition early in stand development.

Barnes (1962) modeled diameter distributions of western hemlock on a reverse J-shape curve (negative slope logarithm function of density over size class) typical of shade-tolerant species that are increasing in density with numerous individuals in the smaller DBH classes (Condit et al. 1998). However, there can be noticeable departures from this distribution. For example, at the Ohanapecosh and Bagby RNA study areas there is a substantial drop in number of trees in diameters >45 cm and >55 cm DBH, respectively (Figure 16). It is unclear what mechanism(s) underlie this pattern as it developed at both sites before the time of plot establishment. However, there may have been a low-intensity ground fire from which density in the <55 cm DBH classes has since recovered, but larger DBH classes are composed of trees that survived the event.

DBH distributions for all tree species should be recognized as dynamic, and that mortality as well as other factors will change the shape of a distribution. For shade-intolerant species this change in DBH distribution is permanent; there will be no recruitment to refill the gaps made by mortality. Platt et al. (1988) working with long-leaf pine (*Pinus palustris* Mill.), a shade-intolerant, long-lived conifer, concluded that mortality created significant instability in diameter frequency and prediction of future demographic states based on a pre-determined distribution was unreliable. Condit (1998) also concluded that fixed distributions were overly simplistic and would under or overestimate actual numbers of trees in relatively small or large diameter classes depending on species under consideration because mortality rates are not in fact constant over all sizes.

CAUSES OF MORTALITY

Accurately identifying causes of tree death is often challenging and sometimes impossible. Mortality is frequently a product of numerous factors that have been operating and interacting, often for long periods of time prior to the final death of the tree (Franklin et al. 1987). Apparent or proximate causes of death are often not the primary agent of mortality, such as where wind or snow bring down trees that have been mechanically weakened by root or stem decays. Nevertheless, it is important to try to understand the relative importance, mechanisms, and interactions of various agents of mortality during stand development.

In this study, it is important to acknowledge that "unknown" was the largest single category recorded under causes of mortality. Some of these deaths are probably due to pathogens of various types and others are probably due to some form of competitive pressure. Nonetheless, subsequent discussions about the stand-level consequences of mortality must be tempered with knowledge of this large pool of mortality of unknown cause.

SUPPRESSION

Suppression was the dominant cause of mortality of Douglas-fir identified in the young and mature stands, affecting primarily smaller trees. Crown position relative to the stand and intact, standing dead trees were taken as evidence of suppression mortality. Episodes of higher than average mortality in suppressed trees can be observed in the data sets used in this study. In other studies such elevated rates have been associated with climatic events. For example, Condit et al. (1995) associated high rates of mortality in small, suppressed trees with El Nino-related drought events at BCI.

Suppression was the dominant agent of western hemlock mortality in nearly all stands; however, episodes of significantly higher than average rates were not observed. At the T. T. Munger Research Natural Area, for example, numerous, mostly small western hemlock died of suppression over the 50 year study period but mortality rates varied little. The same pattern of suppression mortality was observed in western hemlock in WS02 at the H. J. Andrews Experimental Forest.

DOUGLAS-FIR BARK BEETLES

Mortality caused by Douglas-fir bark beetles is relatively easy to identify because of the readily observed galleries and its occurrence as small patches of trees. Most beetle mortality occurs as a result of infrequent outbreaks, which can result in brief (1-3 yr) elevated mortality rates. A ten-year study of mortality in a large tract of 180-year-old Douglas-fir in the Coos Bay region provides an excellent example (Wright and Lauterbach 1958). There were large fluctuations in annual rates as a consequence of a Douglas-fir bark beetle epidemic in 1951 and 1952, which followed major windstorms in the winter of 1949-50 and December 1951 corresponded to a range in average annual mortality rate from 0.11 to 3.5%. Similarly, 14.5 percent of trees were lost to bark beetle and wind during a ten-year period (1948 to 1957) in a 250-year-old stand at Tar Creek on the Mount Hood National Forest located near the Bagby RNA stand used in my study.

Bark beetle mortality occurred in almost all plots in my study at one time or another, but episodic events of relatively high mortality occurred infrequently. On the Gifford Pinchot young-mature plots, bark beetle mortality was essentially confined to a single remeasurement interval over the 67 years of record. On the Willamette plots bark beetle-related mortality occurred only once during the 82 years of record. At the T. T. Munger RNA bark beetle-related mortality occurred primarily during the six-year interval between 1947 and 1953 during 50 years of observation.

Bark beetles are believed to primarily attack trees that have already been weakened in some way although if beetle populations increase, such as in recently windthrown trees, they can successfully attack trees that are believed to be healthy (Furniss and Carolin 1977, Maser et al. 1988). At T. T. Munger, bark beetle mortality occurred on only two plots, which were also plots where there was extensive root and stem decay; the presence of several down and broken trees killed by fungi, may have contributed to the buildup in bark beetle populations and the successful attacks on living trees. On the Gifford Pinchot and Bagby Research Natural Area plots bark beetle attacks were also associated with trees weakened by either mechanical abrasion or disease.

Bark beetle mortality is typically spatially aggregated and typically kill trees in clusters of from three to four trees to larger patches of 15-20 or more creating canopy gaps. Douglas-fir bark beetles also kill trees across the full range of diameters, including some of the largest trees in the stand. In young and mature forests this will mean larger inputs of coarse woody debris.

ROOT AND STEM DECAY

Root and stem decays are dominant agents of mortality in old-growth Douglas-fir but can be difficult to identify. For example, much of the mortality that was actually due to mechanical failure associated with root, basal or stem decays has been described as "windthrow" or "windbreak." Perhaps the most important single mortality agent in old-growth Douglas-fir is velvet-top fungus; but infected trees, which suffer mechanical failure due to the rot, often appear to the untrained observer to have been uprooted or broken. Fortunately, root and basal rots are quite easy to identify with modest training and evidence is usually present on the ground (which may not be the case with stem rots). Hence, a major contribution of this study was to revisit and correctly identify the root and basal rots as mortality agents for old-growth Douglas-fir.

Host trees may be infected with decay fungi at a variety of ages and from a variety of causes. In young stands, ground fires, mechanical abrasions that expose the inner bark and phloem, and natural death and breakage of branches provide entry points (Manion 1991). Root and basal rot fungi can spread through direct contact between root systems, presumably at any age. High rates of growth in young stands may enable the tree to maintain much of its mechanical strength despite the presence of the decay fungus; trees also have at least some capacity to isolate wounds and decay pockets by impregnating adjacent tissue with resins (Manion 1991). In old-growth, small increments in wood growth may eventually be overtaken by decay and the potential for loss of structural integrity increases. One can hypothesize, for example, that velvet top is a fungus that develops relatively slowly, taking one to several centuries before it eventually weakens to the tree to the point of failure (Jerry Franklin, *personal communication*).

Wood decaying fungi are generally associated with heartwood in the center of roots and stems, the primary structural support for trees. Cambial and sapwood tissue may also be decayed by some fungi that possess powerful digestive enzymes (Eslyn and Highley 1976, Montgomery 1979). Hence the potential exists that some of the decay fungi may have a direct physiological as well as mechanical impact on the vigor of a tree. Boyce (Boyce and Wagg 1953) hypothesized that red ring fungus could destroy cambial tissue in Douglas-fir creating physiological stress which ultimately was manifested in dead tree tops and trees susceptible to bark beetle attack.

WIND OR SNOW AND CRUSHED OR HIT

Wind and snow breakage and crushing were second only to suppression as the cause of mortality for western hemlock in nearly all stands. These agents of mortality are generally relatively easy to assign although the death may not be immediate. A majority of the western hemlock are small trees that occur in the understory; hence, the heavy wet snows (characteristic of the Cascade Range) dropping from the crowns of the overstory trees can bend or break the entire stem or wrench it from the ground. These small understory trees are also commonly crushed by falling trees or snags. In the T. T. Munger RNA one heavy snow event was associated with high mortality in understory western hemlock. Trees are resilient organisms so that individuals that have been mortally wounded by snow or stem crushing may live for several years afterward (Everham III 1995); as a consequence cause and effect are displaced in time.

EDGE EFFECT

However, an edge-effect was evident at both study areas. At the T. T. Munger RNA a 80 m buffer strip was mandated for the western border. Today this buffer is almost gone having been leveled by westerly winds. Without this protection it is expected that mortality due to wind will increase inside the western border of the RNA in the near future. At WS02 plots were small and although there are several areas with windthrown Douglas-fir none were in close proximity to the permanent sample plots.

CONSEQUENCES OF SHIFTS IN MORTALITY AGENTS FOR STAND AND ECOSYSTEM DEVELOPMENT

There is a major shift in causes of mortality as stands progress from a young to old, which has major consequences for structural development and ecosystem processes. Early stages are dominated by density-dependent mortality, which tends to be manifested uniformly where initial densities are high; later stages are characterized by density-independent processes such as disease, insects, and wind. Mortality in young stands is related primarily to competition among small trees hence identification with "competitive exclusion" (Franklin et al. 2001) or "stem exclusion" (Oliver and Larson 1990) stage of stand development. Mortality in old stands affects all sizes of trees. Mature stands represent an intermediate or transitional condition between dominance of these two forms of mortality based upon the data from this study. Substantial competitive mortality is still occurring but pathogens and wind are beginning to become significant causes of mortality.

The shift in these two patterns of mortality have profound consequences for stand structural development. In a fully stocked young stand, the process of competitive mortality contributes little to development of stand structural complexity; its primary contributions are to increase growth rates of the surviving trees and, ultimately, provide for increased light in the understory. In contrast, the mix of disease, insect, and wind-related mortality in old-growth stands contributes strongly to the development of spatial heterogeneity within the stand in the form of canopy gaps as well as providing a greater diversity (i.e., sizes, decay states, and positions) of dead tree structures. Thus, the high levels of structural complexity that define of old-growth forest structure (Spies and Franklin 1988, Spies and Franklin 1991, Franklin et al. 2001) derive in part from a shift in causes of mortality during stand development.

EFFECTS OF MORTALITY ON ACCUMULATION OF BIOMASS AND COARSE WOODY DEBRIS INPUTS

Total biomass of conifers increased continuously in the young-mature and mature stands. In this aggrading stage, live biomass increment exceeds biomass loss to mortality (Peet 1981, Acker et al. 2000) (Figures 17 and 18). Highest biomass was found in the Ohanapecosh and Bagby RNA early old-growth stands (forest age of ~288 yr). However, Douglas-fir biomass rate of increase were in decline and eventually recorded as negative in these two stands (Figure 17). As Douglas-fir biomass constituted 80% to 86% of total conifer biomass, decline in the rate of Douglas-fir accumulations signals that a peak in total conifer stem wood and bark biomass accumulation is in the process of forming in these stands. This compares well with Franklin and Waring (1980) who predicted that biomass in Douglas-fir-western hemlock forests would peak at around 300 to 400 yr.

Several theories have been proposed on the factors that may ultimately limit biomass accumulations (Peet 1981, Harcombe et al. 1990, Ryan and Yoder 1997). In forests dominated by a large, shade-intolerant species, like Douglas-fir, the peak corresponds to the greatly reduced growth but continued mortality of the pioneer species (cf. Paré and Bergeron 1995). At the Bagby RNA and Ohanapecosh early old-growth plots, Douglas-fir heights were nearly unchanged and DBH increment had diminished resulting in a decrease in overall stem growth. Stem wood and bark mass of a single Douglas-fir of 92.0 cm DBH and 55.5 m in height (mean size for the early old-growth plots) averages

6.0 Mg; therefore, death of a single tree this size per year would completely negate all gains in Douglas-fir average annual biomass accumulations at either the Ohanapecosh or Bagby RNA; this is exactly what happened. Given no recruitment and current growth and mortality rates for Douglas-fir at these two sites, total conifer biomass could drop to values found at the advanced old-growth sites within a century. This is the first study to show a rapid drop in total conifer biomass accumulations after a peak in production. This is of course based on data from various plot systems; however, if the pattern holds in further studies of plots of varying productivity, it will certainly replace the previous (and theoretical) view of a smooth decline in biomass accumulations after a peak down to levels sustained by shade-tolerant species.

Eventually, the decline in total biomass after a peak in Douglas-fir will partially be compensated for by growth of western hemlock, as well as other shade-tolerant tree species. At the T. T. Munger RNA and WS02 advanced old-growth study areas decline in Douglas-fir biomass increment was balanced by an increase in western hemlock biomass (net gain 0.1 Mg ha^{-1} yr^{-1}). As in Douglas-fir, height growth in large old-growth western hemlock had ceased and DBH increment was slowing, yet growth was steadily increasing biomass stocks (Table 3). Presumably these larger western hemlock are taking advantage of growing space released by death of Douglas-fir.

To illustrate potential future change in biomass composition at the T. T. Munger RNA, a transition matrix was constructed using the 50-yr record of change in the Douglas-fir population (Table 12). The matrix provides a distribution-free method for describing average changes in the proportion of trees that remain in the same DBH class, grow into the next DBH class, or die (Hartshorn 1975, Harcombe 1987, Platt et al. 1988, Condit et al. 1998). Assuming that transition probabilities remain the same as the historic 50-yr pattern, the estimated Douglas-fir density at a stand age of 700 yr will be 5 TPH with an estimated biomass of approximately 73.1 Mg ha^{-1} (Figure 24). At a stand age of

Table 12. Transition matrix for Douglas-fir at the T. T. Munger RNA study area. Matrix contains proportional values of change in numbers of trees that remained in a 20 cm DBH class, grew into the next class, or died over a 50-yr period.

Douglas-fir	1947 DBH				
1998 DBH	45.1-65	65.1-85	85.1-105	105.1-125	>125
45.1-65	0.325				
65.1-85	0.375	0.296			
85.1-105		0.455	0.351		
105.1-125			0.401	0.367	
>125				0.334	0.699
mortality	0.300	0.249	0.248	0.299	0.301

Remained in size class

Grew into next size class

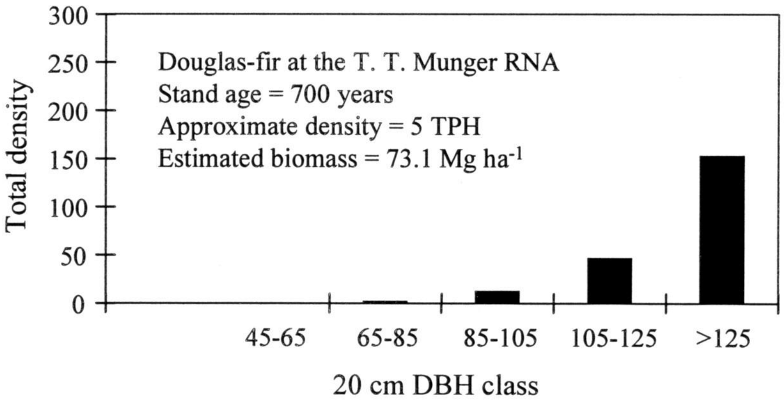

Figure 24. Size distribution at 700 years for Douglas-fir at the T. T. Munger RNA as extrapolated from transition matrix in Table 12.

900 yr, density of Douglas-fir is estimated to be ~1 TPH. If the theoretical optimal stocking in old-growth is approximately 329 TPH (eqn. 8) then western hemlock biomass will probably continue to increase at the T. T. Munger RNA as total conifer stocking declines from 421.5 TPH as recorded in 1998. Total conifer biomass declined 5.2% since permanent plot installation and over the 50-yr period western hemlock biomass increased by 19.1%. If this trend holds then at a stand age of 700 yr its biomass would increase to 418.8 Mg ha^{-1}. It is unlikely, however, that western hemlock will occupy all the growing space released by Douglas-fir. Western hemlock and other shade-intolerant species (i.e., Pacific silver fir and western red-cedar) in the RNA have maximum tree heights that are below the mid and lower crowns of Douglas-fir and thus they compete mostly with each other (Van Pelt and North 1996). Therefore, a change in canopy architecture due to the deaths of Douglas-fir over the next 250 yr will probably not benefit all western hemlock. There are other potential constraints as well: for example, a dwindling supply of large Douglas-fir nurse logs suitable for western hemlock regeneration (Harmon and Franklin 1989). Assuming, however, an additional reduction in total conifer density allows growth of western hemlock to increase at half the rate at which it had over the past 50-yr history (9.5%) then projected biomass at a stand age of 700 yr could be 275.2 Mg ha^{-1}. Assuming that biomass stocks of conifers other than Douglas-fir and western hemlock do not change and barring a catastrophic disturbance to the stand, at a stand age of 700 yr total conifer biomass at the T. T. Munger RNA could average somewhere between 396.5 and 540.1 Mg ha^{-1} a range of difference from the 1998 remeasurement of –93.9 to +49.7 Mg ha^{-1}; these are relatively small changes over a 250-yr period.

Input of Douglas-fir stem wood and bark debris changed little with stage of forest development. Apparently the high rate of mortality of mostly small trees in young forests produces nearly the same amount of woody debris as low mortality rates of larger trees in older forests. However, the quality of woody debris is significantly different. Small trees, with high surface to volume ratios, decay more quickly and residence time is short; large snags and logs, as found in mature and old-growth stands, have low surface to volume ratios and decompose much more slowly. Large logs therefore will function longer as plant and animal habitat, as a store of moisture and nutrients, and as source of soil organic matter (Harmon et al. 1986). Harmon et al. (1986) predicted that input of woody debris would decline as shade-tolerant species with reversed J-shaped diameter distribution patterns begin to dominate stand structure. This scenario fits the current trend in the two advanced old-growth study areas where input of western hemlock stem wood and bark debris is roughly half that for Douglas-fir (Figure 18 vs. Figure 17). If this is indeed the case, in advanced old growth accumulations of above-ground organic matter will be weighted toward biomass rather than woody debris.

CONCLUSIONS

In this study I analyzed the most complete set of mortality data to date for Douglas-fir-western hemlock-dominated forests in the western Cascade Mountains. In these relatively brief records several new aspects of mortality have been charted. Douglas-fir experience high mortality from young to mature stages of forest development, largely driven by death of suppressed trees. In old-growth stands, mortality rates are substantially lower and causes of mortality are composed of density-independent agents most notably root and stem decays. From young to mature stands, western hemlock mortality rates are low. In old growth, however, rates increase due to a mix of agents, primarily suppression and the effect of snow load and crushing by falling trees. Mortality rates of Douglas-fir were often episodic, yet western hemlock's were not. In old growth, mortality of Douglas-fir typically involved small groups of weakened trees and bark beetles.

High rates of mortality of small Douglas-fir in young to mature stands have little negative effect on biomass increment as rates of growth are much higher and biomass stocks increase steadily throughout these stages of forest development. Function of woody debris, however, is poor as input from such small trees decays quickly and adds little to ecosystem function in the way of habitat, soil organic matter, or seedbeds. In old-growth stands growth rates of Douglas-fir decline and the death of even a few trees removes more organic matter than is produced. At this point total conifer biomass, of which Douglas-fir comprise 70 to 80%, also decline. In advanced old-growth stands as Douglas-fir becomes locally extinct, biomass stocks will consist of shade-tolerant species, especially western hemlock. However, as the majority of western hemlock in old-growth are small and produce small amounts of woody debris and as logs of Douglas-fir continue to decompose, above-ground organic matter (biomass + woody debris) in advanced old-growth stands will become composed mostly of biomass.

An accurate understanding of the spatial and temporal complexity of mortality in forests will require continuous monitoring. Long-term studies will be necessary to capture any temporally repetitive patterns from which prediction may be made. Botkin (1992) in retelling the history of the development of JABOWA (the original gap model), wrote that at the time there was very little information about tree mortality; he had expected that better information would eventually arise. Surprisingly, this has not been the case. Data gathered from long-term studies of mortality must be used to improve mortality subroutines in models of forest stand and ecosystem development. These improvements should supplant the ubiquitous concepts of density-dependant mortality derived from single-species, single cohort stands.

Causes of mortality are also important as they have implications for ecosystem structure and function. For example, whether a stem has been infected by a lignin or cellulose fungal consuming species will dictate decomposition of woody debris (Harmon et al. 1986). A focus on aspects of mortality other than loss of timber volume will become increasingly valuable as recognition of forest ecosystems as habitat and sources and sinks of carbon become more important.

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