

Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest¹

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Tree populations exhibited considerable individual plant mortality and replacement over a 36-year period in a 500-year-old *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (Douglas-fir) - *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) forest in the Cascade Range of southern Washington, U.S.A. Nearly 22% (113/ha) of the original stems died at an annual rate of 0.75%. This was balanced by recruitment (117/ha) of *Tsuga*, *Abies amabilis* Dougl. ex Forbes (Pacific silver fir), and *Taxus brevifolia* Nutt. (Pacific yew) saplings. Diameter distributions and relative species composition were nearly identical at the beginning and end of the 36 years. Compositional changes were slow despite the high turnover; extinction of *Pseudotsuga* is predicted in 755 years at its current mortality rate. Mortality was generally caused by wind (45.5%) or suppression and unknown causes (39.4%). Additional long-term studies of old-growth forests are needed to understand the direction and rate of successional change.

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Les populations d'arbres ont exhibé un taux de remplacement et une mortalité individuelle considérables durant une période de 36 ans dans une forêt âgée de 500 ans et composée de *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (sapin de Douglas) - *Tsuga heterophylla* (Raf.) Sarg. (pruche occidentale) dans les monts Cascade du sud de l'état de Washington, É.-U. Près de 22% (113 tiges/ha) du nombre initial de tiges ont déperé à un taux annuel de 0,75%. Ce processus fut équilibré par un recrû (117 tiges/ha) de semis de *Tsuga*, *Abies amabilis* Dougl. ex Forbes (sapin argenté du Pacifique) et *Taxus brevifolia* Nutt. (if du Pacifique). La distribution des diamètres ainsi que la composition relative en espèces étaient pratiquement identiques au début et à la fin de la période de 36 ans. Les modifications dans la composition en espèces ont été lentes en dépit du taux élevé de roulement; on prévoit que *Pseudotsuga* disparaîtra dans 755 ans si le taux actuel de mortalité demeure constant. La mortalité était provoquée en général par le vent (45,5%) ou par l'oppression de diverses causes inconnues (39,4%). Des études à long terme additionnelles portant sur les forêts de première venue seront nécessaires pour mieux comprendre la direction et le taux des modifications dans la succession végétale.

[Traduit par la revue]

Introduction

In the last decade, interest in the structure and behavior of plant populations has increased dramatically. Foresters have taken part in the study and manipulation of plant populations for centuries and have made many theoretical and empirical contributions to the field (Harper 1977; Kirmmins 1987). Most of this information has been developed for young to mature forests and for plantations and other cultivated stands rather than for natural forests (e.g., Ford et al. 1979). Furthermore, patterns and rates of mortality have received less study than growth in the living stand.

Overmature or old-growth forests only recently began receiving major attention from forest scientists (e.g., Franklin et al. 1981). These forests are important as habitat for animal species (e.g., Harris 1985). Population dynamics and paths and rates of compositional change in old-growth forests are of theoretical concern because these forests seem

to approximate steady-state conditions (Harris 1985). Few studies have been done to determine turnover rates by tree size and species.

A 36-year record of change in tree populations of a 500-year-old *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (Douglas-fir) - *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) stand in the Cascade Range of southern Washington is the subject of this paper. Size-class distributions, recruitment, and mortality are considered by stand and by individual species. Although our data were limited to trees exceeding 6 cm in diameter at breast height (dbh; height = 1.37 m), these are the first long-term data on dynamics of an old-growth conifer forest. Additional data on gross and net growth in wood volume in this stand are provided by DeBell and Franklin (1987).

Study area

The forest stand used in this study was the 472-ha T. T. Munger Research Natural Area (RNA) in the Wind River valley of southern Washington State. The RNA is on the lower east and southeast

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slopes of Trout Creek Hill, an inactive Quaternary shield volcano. Elevations range from 335 to 610 m. Topography is gentle, reflecting the underlying bedrock of basaltic lava flows. The loamy sand to sandy loam soils formed in relatively young deposits of volcanic tephra. Soils are typically 2 m or more to bedrock with depth tending to increase at lower elevations. Soils are well drained and belong to the Stabler series (Franklin et al. 1972); this soil is classified as an Andic Haplumbrept.

The climate of the RNA is characterized by cool, wet winters and warm, periodically dry summers. Precipitation averages nearly 250 cm/year, but less than 10% falls from June through September; winter precipitation often occurs as snow, which accumulates in a 1-to 2-m snowpack that lasts several months. Conditions are cooler and wetter than might be expected at similar elevations on the western slopes of the Cascade Range; this reflects the location of the RNA near a valley bottom and the proximity to the central Columbia River Gorge, an area climatologically more severe than the regional norm (Lawrence 1939).

Vegetation of the RNA is intermediate between the *Tsuga heterophylla* and *Abies amabilis* Dougl. ex Forbes (Pacific silver fir) zones (Franklin and Dyrness 1973). Most of the RNA is transitional between the *Tsuga heterophylla*/*Gaultheria shallon* Pursh (salal) and *Abies amabilis*/*Gaultheria shallon* habitat types (Brockway et al. 1983). Tree species consist of *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Abies amabilis*, *Thuja plicata* Donn ex D. Don (western redcedar), *Taxus brevifolia* Nutt. (Pacific yew), *Pinus monticola* Dougl. ex D. Don (western white pine), *Abies grandis* (Dougl. ex D. Don) Lindl. (grand fir), and *Abies procera* Rehd. (noble fir). A few hardwoods, mainly *Cornus nuttallii* Audubon (Pacific dogwood) and *Acer macrophyllum* Pursh (bigleaf maple), are also present. Important shrub species include *Acer circinatum* Pursh (vine maple), *Gaultheria shallon*, *Berberis nervosa* Pursh (Oregon grape), *Vaccinium parvifolium* Smith (red huckleberry), *Rhododendron macrophyllum* G. Don (Pacific rhododendron), *Corylus cornuta* var. *californica* (DC.) Sharp (California hazelnut), and *Vaccinium membranaceum* Dougl. ex Hook (big huckleberry). Herbaceous and subshrub dominants are *Achlys triphylla* (Smith) DC. (deerfoot vanillaleaf), *Vancouveria hexandra* (Hook.) Morr. & Dec. (inside-out flower), *Adenocaulon bicolor* Hook. (pathfinder), *Clintonia uniflora* (Schult.) Kunth (queencup beadlily), *Cornus canadensis* L. (bunchberry), *Polystichum munitum* (Kaulf.) Presl. (western swordfern), *Linnaea borealis* L. (western twinflower), *Pteridium aquilinum* (L.) Kuhn. (bracken fern), *Chimaphila umbellata* (L.) Bart (prince's-pine), and *Xerophyllum tenax* (Pursh) Nutt. (beargrass).

The forest is believed to have originated after a major disturbance (or disturbances) about 500 years ago, based on age-structure analyses done in clearcut tracts adjacent to the southern and western boundaries of the RNA. Ages of *Pseudotsuga* stumps from cuttings 10 to 20 years old range from 230 to 460 years. The wide range in age is characteristic of old-growth *Pseudotsuga* stands (Franklin and Waring 1979). The age range is believed to either result from slow establishment after the initial disturbance or from subsequent disturbances that created additional conditions for establishment of the shade-intolerant *Pseudotsuga* (Franklin and Waring 1979). Tree ages determined by taking increment cores from trees within the RNA match the ages counted on stumps.

Additional details on the physical and biological features of the RNA (known as the Wind River RNA before 1977) are available in Franklin et al. (1972).

Methods

Population data are from 47 systematically located, concentric, permanent plots of 0.02 and 0.08 ha. Total sample area was 0.94 and 3.76 ha for the small and large plots, respectively. All trees 6 to 24 cm dbh were tagged and measured on the 0.02-ha plots, and all trees greater than 24 cm dbh were tagged and measured on the 0.08-ha plots. Consequently, sampling included about 0.8% of the larger (>24 cm dbh) and 0.25% of the smaller

(6 to 24 cm dbh) tree populations within the RNA. Diameters were calculated to the nearest 0.25 cm.

Plots were measured, recruits were identified and tagged, and mortality was recorded at 6-year intervals after establishment in 1947. Recruitment refers to the trees that had attained the minimum dbh for inclusion in the plot; i.e., 6 cm for the 0.02-ha plots and 24 cm for the 0.08-ha plots. Only the 1947 and 1983 data are given, except for data on mortality, which was the only process that exhibited much variation between measurement periods. Recorded causes of mortality were windthrow, crushed by falling tree, breakage, bark beetles, mistletoe infestation, missing, and unknown. The value of the information on causes of mortality is limited by lack of detail and by inconsistency in collection. Twenty-two small trees recorded as windthrown were reassigned to the unknown category during analysis; losses of small understory trees to heavy loads of snow and ice were considered more probable and could easily be mistaken for windthrow.

Additional mortality data were collected on continuous cruise strips that systematically cover 10% of the RNA; however, observations were limited to locating, recording, and marking individuals that had presumably died during the most recent measurement period and were not based on a population of tagged trees. Consequently, the live-tree population that died is not known. These data were used to calculate timber growth (DeBell and Franklin 1987) and additions of coarse woody debris (Sollins 1982) for this stand.

The probability of an individual tree surviving a given year ($P(S)$) was calculated from the mortality data using the power function

$$[1] \quad P(S_t) = P(s)^t$$

where $P(S_t)$ is the cumulative probability of survival over time t . Assuming $P(S_t)$ is equal to the proportion of the original population surviving, $P(S)$ was calculated by

$$[2] \quad P(S) = P(S_t)^{1/t} \text{ or } P(S) = \sqrt[t]{P(S_t)}$$

Mortality rate expressed on a percentage basis was calculated as

$$[3] \quad P(M) = 100(1 - P(S))$$

The time for local extinction to occur (t_{ex}) was assumed to be equal to the time for 99% of the cohort to die. Extinction time was calculated using a logarithmically transformed version of eq. 1:

$$[4] \quad t_{ex} = \frac{\ln 0.01}{\ln P(S)} = \frac{-4.605}{\ln P(S)}$$

Calculated extinction values need to be interpreted with caution because they are based on constant mortality rates, and rates change with age, size, and competitive position of trees. Shaffer and Samson (1985) suggest some other reasons for caution in calculating extinction rates when using deterministic approaches.

Results

Stand density and recruitment

Forest stand density (number of stems per hectare above 6 cm dbh) declined over the 36-year period by 7.5% (Table 1). This decline was primarily the result of a 20% reduction in the smallest (6 to 11 cm) size class. Recruitment of small trees lagged behind losses to mortality and to growth into larger size classes. Density in intermediate size classes (25 to 100 cm dbh) also declined. An upward shift in the diameter distribution of most species accompanied the decrease in stand density, particularly for *Tsuga heterophylla* and *Pseudotsuga menziesii*, the stand dominants.

Reductions in densities occurred in all species except *Thuja plicata* (Table 1). Losses differed substantially among species, however, and ranged from 7.7% for *Tsugato* 18.4% for *Pseudotsuga* and 32.7% for *Abies grandis*. Shifts in relative densities of species were remarkably small. Relative density of *Tsuga heterophylla* remained constant at 46% of the stand. *Pseudotsuga* declined from 14 to 12.5% of stems.

TABLE 1. Stand density by size class and species in 1947 and 1983 for an old-growth stand in the T. T. Munger Research Natural Area, Cascade Range, Washington

Species	Year	Sample size (n)	Mean diameter (cm)	No. of stems/ha by size class (in cm)												All sizes
				6-11	12-24	25-37	38-50	51-62	63-75	76-88	89-100	101-113	114-126	127-138	>138	
<i>Tsuga heterophylla</i>	1947	463	38.8	63.8	66.0	36.2	18.9	17.6	9.6	4.8	2.9	0.3	0.5			220.5
	1983	441	43.4	50.0	64.9	24.7	19.9	16.8	14.1	8.0	3.2	1.6	0.3			203.5
<i>Pseudotsuga menziesii</i>	1947	255	90.3		1.1	1.6	2.9	3.5	9.0	14.6	13.3	9.8	8.0	2.7	2.1	67.8
	1983	208	103.2			1.1	1.1	3.7	4.8	10.1	11.4	9.0	7.4	4.0	2.6	55.3
<i>Abies amabilis</i>	1947	145	26.6	47.9	29.8	8.0	5.6	3.5	1.9	0.3						96.8
	1983	144	28.6	43.6	33.0	8.8	4.5	2.4	2.7	0.8						95.7
<i>Taxus brevifolia</i>	1947	68	17.6	28.7	27.7	3.5	0.5									60.4
	1983	71	20.0	19.1	34.0	4.8	0.8									58.8
<i>Thuja plicata</i>	1947	38	68.5	4.3	1.1	0.5	0.5	1.6	1.6	1.6	1.1	1.3	0.3	0.3		14.1
	1983	38	67.2	4.3	5.3	0.5	0.3	0.5	1.6	1.1	1.9	1.3		0.3	0.3	17.2
<i>Abies grandis</i>	1947	25	25.6	7.4	5.3	1.6	1.9									16.2
	1983	17	25.8	5.3	3.1	1.3	0.8	0.3								10.9
<i>Pinus monticola</i>	1947	7	43.9		1.1	0.3	0.5		0.3					0.5		2.7
	1983	4	72.0				0.3	0.3						0.5		1.1
<i>Abies procera</i>	1947	1	30.7			0.3										0.3
<i>Cornus nuttallii</i>	1983	0														
	1947	0														
	1983	1	8.9	1.1												1.1
All species	1947	1002	48.6	152.1	131.9	51.9	30.8	26.1	22.3	21.3	17.8	10.4	8.8	2.9	2.1	479.5
	1983	924	50.8	123.4	140.4	41.2	27.7	23.9	23.1	19.9	17.0	12.0	7.7	4.2	2.9	443.6

TABLE 2. Recruitment (ingrowth)^a of trees by size class and species between 1947 and 1983 in an old-growth stand at the T. T. Munger Research Natural Area, Cascade Range, Washington

Species	Ingrowth by diameter class (no./ha)		
	6-23 cm	≥ 24 cm	All classes
<i>Tsuga heterophylla</i>	39.7	6.4	46.0
<i>Abies amabilis</i>	35.3	3.8	39.0
<i>Taxus brevifolia</i>	18.2	1.6	19.8
<i>Abies grandis</i>	5.4	0.8	6.1
<i>Thuja plicata</i>	6.4	0	6.4
<i>Cornus nuttallii</i>	1.1	0	1.1
<i>Abies procera</i>	0	0	0
<i>Pinus monticola</i>	0	0	0
<i>Pseudotsuga menziesii</i>	0	0	0
All species	105.9	12.7	118.6

^aAbsolute number of recruits = 146.

Abies amabilis and *Thuja plicata* increased their respective representation in the stand by 1.5% (to 21.5%) and 1.0% (to 4.0%). Recruitment consisted almost entirely of shade-tolerant conifers, primarily *Tsuga* and *Abies* (Table 2).

The size-class distribution of the stand approximated the inverse J-shaped curve expected in a steady-state stand (Table 1, Fig. 1). Distributions for individual species also fit those expected for shade-tolerant and intolerant tree species. The shade-tolerant *Tsuga heterophylla*, *Abies amabilis*, and *Taxus brevifolia* had inverse J-shaped curves. *Pseudotsuga menziesii*, the only abundant shade-intolerant species, exhibited a bell-shaped diameter distribution. The flat size-class distribution of *Thuja plicata* was distinctive; this species had low rates of recruitment but high survival in all size classes.

Mortality

Mortality in the original 1002 trees averaged 0.75% per annum or nearly 22% over the 36-year period (Table 3). Rates differed substantially for different measurement periods:

Period	Rate of mortality (% per year)
1947-1953	1.05
1954-1959	0.59
1960-1965	0.51
1966-1971	0.09
1972-1976	0.98
1976-1982	0.46

These results suggest episodic mortality, at least on the scale of 5-year intervals. This variability was not the consequence of individual species mortality patterns. Rates of mortality were higher in the lower one-third of the size classes (Table 3). Trees from 6 to 50 cm died at the rate of 0.85% per annum; mortality rates in trees over 50 cm averaged 0.54% per annum.

Mortality rates differed dramatically among species (Table 3). *Abies amabilis* had the highest rate (1.05% per annum) among the major species. Mortality rates for *Pseudotsuga* and *Tsuga* were nearly identical; however, the implications for future stand development are quite dif-

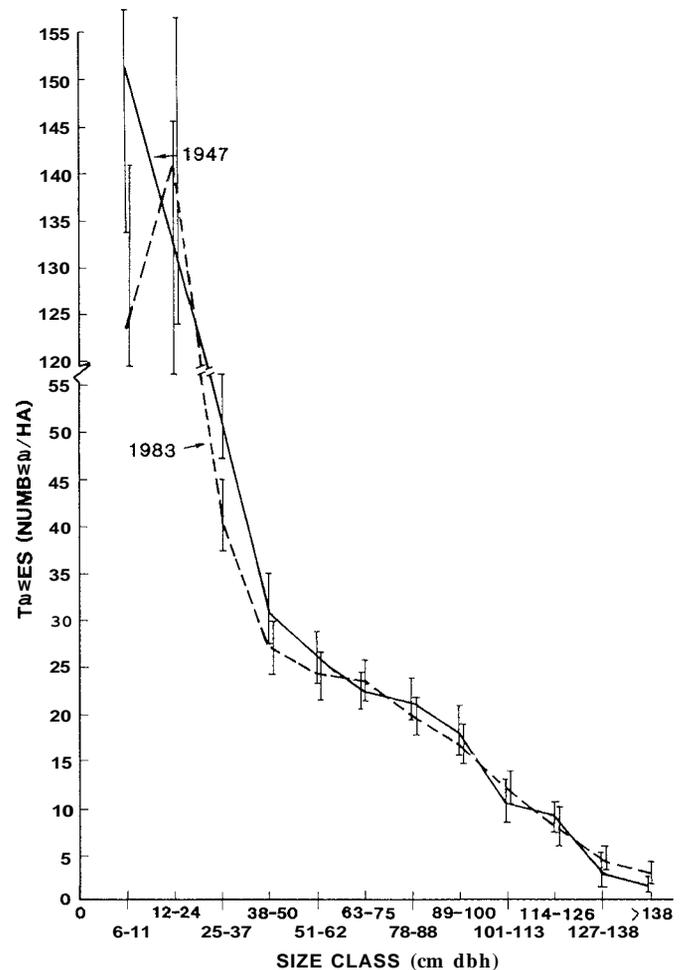


FIG. 1. Size-class distributions of forest stand (all species) in 1947 and 1983 at the T. T. Munger Research Natural Area, Washington, U.S.A. Vertical bars indicate standard deviation.

ferent. Wind and wind-related damage were the dominant causes of mortality and accounted for over 52% of the total:

Cause of tree mortality	No. of dead trees (%)
Unknown	66 (30.2)
Windthrow	51 (23.3)
Broken bole or top	47 (21.5)
Mechanical (snow)	22 (10.0)
Crushed	16 (7.3)
Insects and diseases	13 (5.9)
Miscellaneous	4 (1.8)

Suppression was probably the major cause of mortality listed as "unknown." Diseases and insects included dwarf mistletoe (*Arceuthobium campylopodum*), infections (four *Tsuga*), and bark beetles (*Dendroctonus* spp.) (six *Pseudotsuga*). Most or all the *Pseudotsuga* mortality listed as "unknown" (11 trees) may have resulted from bark beetle attacks because these dead trees were standing; if so, 37% of the *Pseudotsuga* mortality would be ascribed to beetles and the remainder to wind.

Discussion

Substantial mortality and recruitment occurred in tree populations in this old-growth forest despite limited changes in basal area, relative species abundances, and overall stand

TABLE 3. Mortality in the initial population of trees¹ by size class and species between 1947 and 1983 in an old-growth forest at the T. T. Munger Research Natural Area, Cascade Range, Washington

Species	No. of trees/ha by diameter size class (in cm)												All sizes	% original cohort	% loss per annum
	6-11	12-24	25-37	38-50	51-62	63-75	76-88	89-100	101-113	114-126	127-138	>138			
<i>Tsuga heterophylla</i>	12.8	13.9	8.4	3.2	1.1	1.4	0.3	0.8		0.5			42.4	19.3	0.59
<i>Pseudotsuga menziesii</i>		1.1	0.3	1.4	0.8	0.8	3.0	3.0	1.6	0.3	1.1	0.3	13.5	19.9	0.61
<i>Abies amabilis</i>	10.7	12.8	3.2	1.9	1.4	0.5							30.6	31.6	1.05
<i>Abies grandis</i>	4.3	2.1	1.6	1.1									9.1	56.2	2.27
<i>Taxus brevifolia</i>	8.6	5.4	0.5										14.4	23.8	0.75
<i>Thuja plicata</i>	1.1		0.3	0.3	0.3		0.3	0.3					2.4	17.0	0.52
<i>Pinus monticola</i>		1.1	0.3			0.3							1.6	59.2	2.46
<i>Abies procera</i>			0.3										0.3	100.0	
<i>Cornus nuttallii</i>													0	0	0
All species	37.5		14.9	7.9	3.6		3.6	4.1							
Total	37.4	36.4	14.8	7.8	3.5	3.0	3.5	4.0	1.6	0.8	1.1	0.3	114.3		
% original cohort	24.5	27.6	28.5	25.3	13.4	13.4	16.4	22.5	15.4	9.1	37.9	9.5	23.8		
% loss per annum	0.78	0.89	0.93	0.81	0.40	0.40	0.50	0.71	0.46	0.26	1.31	0.28	0.75		

¹Absolute number of dead trees = 219.

density. A total of 146 individuals, equivalent to 118.6/ha, were recruited into the stand. Nearly 22% (219 individuals) of the original 1002 trees died. The dynamic behavior of the stand was also reflected in high rates of timber growth and mortality reported for the T. T. Munger stand (DeBell and Franklin 1987); gross growth and mortality as measured in wood volume averaged 6.58 and 6.02 $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, respectively.

The lack of major shifts in the relative abundance of the various species was surprising in view of the high rate of turnover in the stand, but this was mainly a consequence of the decline in absolute densities of all species. Greater shifts in relative importance would have occurred had stand density remained constant during the study period. Shifts in the relative contribution of various species to stand basal area were similar to changes in their relative contribution to density:

Species	1947 (m^2/ha)	1983 (m^2/ha)
<i>Tsuga heterophylla</i>	26.06	30.09
<i>Pseudotsuga menziesii</i>	43.40	46.23
<i>Abies arnabilis</i>	5.38	6.14
<i>Thuja plicata</i>	5.19	6.10
<i>Taxus brevifolia</i>	1.47	1.85
Others	1.26	1.02
Stand total	82.76	91.43

Total stand basal area is up by 10.5% over the 36-year period; the contribution of *Pseudotsuga menziesii* has declined from 52.4 to 50.6%.

Larger shifts in dominance and lower stand growth were calculated for the T. T. Munger RNA stand by using mortality data from the strips and growth data from the permanent sample plots. Mortality was much higher on the mortality strips than on the growth plots (DeBell and Franklin 1987; Sollins 1982). Calculated per hectare wood bole volumes of *Pseudotsuga menziesii* and *Pinus monticola* actually declined during the 36 years in the combined data set (DeBell and Franklin 1987); negative net-growth values for these species balanced the positive net growth in *Tsuga*, *Abies* spp., and *Thuja*, the result was little change in wood volumes for the stand. The mortality data from the strips doubtless gave a more accurate estimate of this highly variable process for the RNA as a whole than did the data from the much smaller plot sample; however, densities of live trees on the strips were not measured, so there were no data for a population analysis.

Mortality rates in this study were similar to rates for other old-growth stands of comparable age in the Cascade Range,² although the length of record from other stands is much shorter than the record at T. T. Munger RNA. Rates for *Pseudotsuga* and *Tsuga* at a series of plots in Mount Rainier National Park, Washington, were 0.50 and 0.37, respectively, over an 8-year period.² The 1.05% per annum rate for *Abies arnabilis* in the RNA is much higher than the 0.49% per annum value at Mount Rainier; one factor may

be that *Abies arnabilis* is near its lower elevational limit in the RNA.

Stand dominance is shifting slowly from *Pseudotsuga menziesii* to *Tsuga heterophylla*. Although both species have similar mortality rates (0.61 and 0.59% per annum, respectively), no recruitment of the shade-intolerant *Pseudotsuga* is occurring. We expect that *Pseudotsuga* will persist in the stand for a long time, however. Extinction of *Pseudotsuga* is predicted in about 755 years, if extinction is defined as a decline to 1% of its density in 1948 (i.e., 0.53 individuals per hectare). The calculated age at extinction for the *Pseudotsuga* (450 years current age plus 755 or 1205 years) is close to the 1200-year maximum life-span suggested for *Pseudotsuga* (Franklin and Dyrness 1973). These calculations are based on a critical assumption that *Pseudotsuga* will continue to die at the current rate. This assumption could, of course, prove erroneous in either direction, for example, if mortality rates actually do decline with increased size or age, as is suggested by existing data, or if episodes of pathogen- or wind-induced mortality occur.

Mortality rates in smaller size classes (up to 50 cm dbh) were greater than for larger tree sizes (Table 3), a pattern that was not observed in averaged values for old-growth stands of similar age and composition at H. J. Andrews Experimental Forest, Oregon (see footnote 2). The data from the T. T. Munger RNA indicated thinning of the sapling population of *Abies*, *Tsuga*, and *Taxus*, possibly related in part to increasing numbers of larger *Tsuga*; *Tsuga* carries a larger leaf area than *Pseudotsuga* per unit of diameter, and its increased importance in the overstory would reduce light near the ground. Large *Tsuga* have a strong negative influence on tree reproduction (Stewart 1984).

Mortality agents at T. T. Munger RNA are of comparable importance to those observed in similar old-growth stands in the Cascade Range (see footnote 2). At Mount Rainier National Park, 45.5% of the mortality was caused by wind or was wind related and 39.4% was from suppression or unknown causes. Wind-related mortality was lower (33.2% of the total) at H. J. Andrews Experimental Forest.

Conclusions

Tree populations were dynamic over a 36-year period in the old-growth *Pseudotsuga menziesii* - *Tsuga heterophylla* forest at T. T. Munger RNA: nearly 22% (113/ha) of the original stems died at an annual rate of 0.75%; small (6 to 23 cm dbh) *Tsuga*, *Abies arnabilis*, and *Taxus brevifolia* were recruited at the rate of 117/ha; and growth produced upward shifts in diameter distributions of species.

Diameter distributions and relative species composition were nearly identical at the beginning and end of the 36-year period. This apparent stability gives no indication of the actual dynamism of the tree populations and emphasizes the need for permanent sample plots with tagged trees. Insights into population processes would be quite limited without the perspective provided by identifiable individuals.

Major compositional changes are occurring slowly. Loss of the major seral dominant, *Pseudotsuga menziesii*, will take centuries at the current rate of mortality.

Clearly, based on this and other studies, old-growth forests are dynamic ecosystems. We need to expand our knowledge of patterns and rates of population change if we are to understand population functioning, predict direction and rate of successional change, and develop appropriate

²Franklin, J. F., Klopsch, M., Luchessa, K., and Harmon, M. 1986. Tree mortality in some mature and old-growth forests in the Cascade Range of Oregon and Washington. Manuscript on file at Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331.

management strategies for old-growth forests and associated wildlife.

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- BROCKWAY, D.G., TOPIK, C., HEMSTROM, M.A., and EMMINGHAM, W.H. 1983. Plant association and management guide for the Pacific Silver Fir Zone, Gifford Pinchot National Forest. USDA For. Serv. Pac. Northwest Reg. (Portland, OR) Publ. No. R6-Ecol-130a-1983.
- DEBELL, D.S., and FRANKLIN, J.F. 1987. Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. *West. J. Appl. For.* **2**: 111-114.
- FORD, E.D., MALCOLM, D.C., and ATTERSON, J. 1979. The ecology of even-aged forest plantations. Institute of Terrestrial Ecology, Cambridge, U.K.
- FRANKLIN, J.F., and DYRNESS, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.
- FRANKLIN, J.F., and WARING, R.H. 1979. Distinctive features of northwestern coniferous forests: development, structure and function. *In* Forests: fresh perspectives from ecosystem analysis. Edited by R.H. Waring. Oregon State University Press, Corvallis, OR. pp. 59-86.
- FRANKLIN, J.F., HALL, F.C., DYRNESS, C.T., and MASER, C. 1972. Federal research natural areas in Oregon and Washington: a guidebook for scientists and educators. USDA For. Serv., Pacific Northwest Forest and Range Experiment Station, Portland, OR.
- FRANKLIN, J.F., CROMACK, K., JR., DENISON, W., MCKEE, A., MASER, C., SEDELL, J., SWANSON, F., and JUDAY, G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-118.
- HARPER, J.L. 1977. Population biology of plants. Academic Press, New York.
- HARRIS, L. 1985. The fragmented forest. University of Chicago Press, Chicago, IL.
- KIMMINS, J.P. 1987. Forest ecology. Macmillan Publishing Co., New York.
- LAWRENCE, D.B. 1939. Some features of the Columbia River Gorge with special reference to asymmetry in forest trees. *Ecol. Monogr.* **9**: 217-257.
- SHAFFER, M.L., and SAMSON, F.B. 1985. Population size and extinction: a note on determining critical population sizes. *Am. Nat.* **125**: 144-152.
- SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* **12**: 18-28.
- STEWART, G.H. 1984. Forest structure and regeneration in the *Tsuga heterophylla* - *Abies amabilis* transition zone, central western Cascades, Oregon. thesis, Oregon State University, Corvallis, OR.