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論　文

Biomass and Primary Production in Forests of Three Major Vegetation Zones of the Northwestern United States

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FUJIMORI, Takao, KAWANABE, Saburo, SAITO, Hideki, GRIER, Charles C. & SHIDEI, Tsunahide: **Biomass and primary production in forests of three major vegetation zones of the northwestern United States J. Jap. For. Soc. 58: 360～373, 1976** Above-ground biomass and net primary production of representative 90 to 130 year-old stands in the *Picea sitchensis*, *Tsuga heterophylla*, and *Abies amabilis* vegetation zones of the northwestern United States were determined by destructive analysis and leaf litter collection. Total above-ground biomass, leaf biomass, and above-ground net production were, respectively 875 t/ha, 7.9 t/ha, and 10.3 t/ha/yr for a 100～120 year-old *T. heterophylla-P. sitchensis* stand in the *P. sitchensis* zone; 669 t/ha, 11.1 t/ha, and 12.7 t/ha/yr for a 90～110 year-old *Pseudotsuga menziesii-T. heterophylla* stand in the *T. heterophylla* zone; and 882 t/ha, 17.5 t/ha, and 13.0 t/ha/yr for a 100～130 year-old *Abies procera-P. menziesii* stand in the *Abies amabilis* zone. Production structure, production efficiency, volumetric density, and other stand characteristics were presented and compared. Potential biomass accumulation for forests of *T. heterophylla* and *A. amabilis* zones was assessed by nondestructive stem biomass estimates of mature *P. menziesii-T. heterophylla* and *A. procera-P. menziesii* stands on sites comparable to those of corresponding younger stands. Stem biomass of these mature stands was 1591 t/ha and 1687 t/ha respectively.

藤森隆郎・川那辺三郎・斎藤秀樹・Charles C. GRIER・四手井綱英: 米国北西部の主要3植生帯の森林の現存量と生産量　日林誌 58: 360～373, 1976　米国北西部の主な三つの植生帯からそれぞれ代表的な林分を選び，それらの現存量，生産量，落葉量などの調査を行なった。太平洋に近い *Picea sitchensis* 帯の *Tsuga heterophylla-P. sitchensis* 林(100～120年生)の地上部現存量，葉量，地上部純生産量は 875 t/ha, 7.9 t/ha, 10.3 t/ha/yr であった。それより内陸の *T. heterophylla* 帯の *Pseudotsuga menziesii-T. heterophylla* 林 (90～110) のそれらは 669 t/ha, 11.1 t/ha, 12.7 t/ha/yr, カスケード山脈西側の亜高山帯に近い *Abies amabilis* 帯の *Abies procera-P. menziesii* 林 (100～130) のそれらは 882 t/ha, 17.5 t/ha, 13.0 t/ha/yr であった。調査で得た資料に基づき個々の林分の生産構造，葉の生産能率，現存量密度，その他を検討し，林分間の比較を行なった。上記調査林分とほぼ同環境にあり，極相に近づきつつある同型の林分を伐倒せず測定して得た幹の現存量は，*P. menziesii-T. heterophylla* 林で 1591 t/ha, *A. procera-P. menziesii* 林で 1687 t/ha であった。

I. Introduction

North American forests in western Oregon, northern California, Washington, and southern British Columbia are generally composed of dense stands of large and long-lived trees (FRANKLIN & DYRNESS, 1973). Species growing in these forests are tall (commonly over 60m at 100 years) with straight stems and with diameters of older trees often exceeding 200cm. Biomass accumulations in

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these forests appear to be outstandingly large.

Earlier reports have suggested potentially large biomass accumulations in forests of this region (HALLIN, 1934; WORTHINGTON, 1958). However, these early reports were concerned mainly with estimates of stem wood volume rather than total above-ground biomass and productivity. Only two studies of forest biomass and productivity have been reported for coniferous forests in this region (COLE *et al.*, 1967; FUJIMORI, 1971). Both of these studies were conducted in stands in the age range of peak productivity (35 and 26 years old) but well before the age range of maximum biomass accumulation.

The present study was intended to fill gaps in present knowledge of biomass accumulation and net primary productivity of northern temperate zone forests. In this study, methods of estimating biomass and productivity developed by the terrestrial primary productivity section of the Japanese International Biological Programme have been applied to stands in major northwest American forest types.

Study plots were located in three major coniferous forest zones of the U. S. Pacific Northwest. Three stands, one in each of the major forest zones and ranging from 90 to 130 years old were chosen for destructive biomass and productivity analysis. These stands were generally representative of productive sites in their respective forest zones. Nondestructive measurements were also made in mature seral, sub-climax stands growing on sites comparable to those of corresponding younger stands.

Results of this study provide reliable data on biomass and productivity in several forest types of the U. S. Pacific Northwest. Furthermore, these data now allow comparisons to be made between forests of this region and those in other parts of the world.

II. Characteristics of Study Area

This study was confined to western Oregon and Washington states in the USA. Detailed discussion of climate, geology, soils, physiography, and vegetation in this region is beyond the scope of this paper. The brief description following is drawn primarily from a more detailed treatment by FRANKLIN & DYRNESS (1973).

The physiography of western Oregon and Washington is dominated by the Coast and the Cascade Ranges. These mountain ranges are separated by several broad valleys; the Willamette Valley in Oregon and the Chehalis Valley and Puget Sound in Washington (Fig. 1). The Coast Range generally has low relief, relatively gentle slopes, and elevations ranging between 450m and 750m. In contrast, the Cascade Range has steep, deeply incised slopes with elevations normally reaching 1700 m to 2000m, but occasionally reaching over 3000m.

Fig. 1. Location of experimental stands

Numbers on map correspond with the following:

1: *Tsuga heterophylla-Picea sitchensis* stand, Cascade Head

2: *Pseudotsuga menziesii-Tsuga heterophylla* stand, Blue River

3: *Abies procera-Pseudotsuga menziesii* stand, Wildcat Mountain

4: Mature *Pseudotsuga menziesii-Tsuga heterophylla* stand, Middle Santiam

5: Mature *Abies procera-Pseudotsuga menziesii* stand, Goat Marsh, Res. Natural Area

The Coast Range is composed primarily of volcanic and sedimentary rocks. Soils derived from this material are normally fine textured deeply weathered except in areas of unstable soils. The Cascade Range south of latitude 47°15′ is composed primarily of a variety of volcanoclastic rocks interbedded with numerous lava flows and volcanic ash layers. Soils in the Cascade Range are relatively young; many being classed as regosols. However, because of the nature of the parent material, these soils typically have a high clay content. Geology of the Cascade Range north of latitude 47°15′ is exceedingly complex and incompletely mapped. Rocks in this area are a mixture of metamorphic, sedimentary, and igneous rock types.

The climate of western Oregon and Washington is generally mild for this latitude and annual temperature differences are relatively small. Annual precipitation in this region is usually greater than 1000mm and frequently exceeds 2500mm. Precipitation is concentrated in the winter months; normally, less than 10% of annual precipitation falls between 1 June and 1 September.

Vegetation zones of western Oregon and Washington have been described by FRANKLIN & DYRNESS (1973). The zones in which this study was conducted are the *Picea sitchensis* zone, the *Tsuga heterophylla* zone, and the *Abies amabilis* zone. These zones include the major portion of forests of this region.

The *Picea sitchensis* zone is a long-narrow strip along the coastline of Oregon and Washington. It is restricted to western slopes of the Coast Range and generally at elevations below 350 m. The climate in this zone is strongly influenced by the adjacent Pacific Ocean. One of the study plots for destructive analysis was located in the *Picea sitchensis* zone near Lincoln City, Oregon (Fig. 1). This plot was located in a 120-year-old *Tsuga heterophylla-Picea sitchensis* stand on the U. S. Forest Service, Cascade Head Experimental Forest (Photo. 1). Location, soils, vegetation, and climate of this research area are given in Tables 1～4. The study plot was representative of large areas of 120-year-old coastal forest in this region.

The *Tsuga heterophylla* zone is the most extensive forest zone in western Oregon and Washington. This zone is found at elevations between sea level and about 800 m elevation. In Oregon, this zone is found in the Coast and the Cascade Ranges but not in the Willamette Valley; in Washington, this zone is continuous from the coastal *Picea sitchensis* zone to about 800 m elevation in the Cascades. Climate of the *Tsuga heterophylla* zone is strongly maritime but with generally less precipitation and greater temperature extremes than in the *Picea sitchensis* zone. A second plot for the destructive analysis was located in this zone in a 110-year-old mixed stand of *Pseudotsuga menziesii-Tsuga heterophylla-Acer macrophyllum* in the Willamette National Forest near Blue River, Oregon (Fig. 1, Photo. 2). Location, soils, vegetation, and climate of the study plot area are given in Tables 1～4. This study plot was representative of large areas of seral *Pseudotsuga menziesii* forest of this age in this part of western Oregon. A study plot for non-destructive analysis of mature, sub-climax *Pseudotsuga menziesii-Tsuga heterophylla-Tsuja plicata* typical of productive sites in the *Tsuga heterophylla* zone was located in the upper Santiam River Drainage, Willamette National Forest, Oregon (Fig. 1). Climate and soils of this research area are essentially the same as in the 110-year-old stand near Blue River, Oregon.

The *Abies amabilis* zone lies between the temperate mesophytic *Tsuga heterophylla* zone of lowland western Oregon and Washington and the subalpine *Tsuga mertensiana* zone. This zone occurs in the Cascade Range, the Olympic Mountains of Washington and to a limited extent in the Coast Range at elevations from 1000 m to 1500 m. Like the other vegetation zones of this region, the climate of the *Abies amabilis* zone is strongly influenced by maritime storm systems, moving inland from the Pacific Ocean. Annual snowfall in this zone frequently exceeds 10 m and winter snow accumulations of 3～4 m are not uncommon. The third study plot for destructive analysis was located in a seral *Abies procera-Pseudotsuga menziesii-Abies amabilis* stand in the Wildcat Mountains Research Natural Area, Willamette National Forest, Oregon (Fig. 1, Photo. 3). Location, soils, vegetation, and climate of this study plot area are given in Tables 1～4. Non-destructive analysis of a mature sub-climax *Abies procera-Pseudotsuga menziesii* stand was conducted near Mt. St. Helens in the Gifford Pinchot National Forest in Washington (Fig. 1, Photo. 4). Climate and soils in this area are comparable with those in the younger *Abies procera-Pseudotsuga menziesii* stand in Oregon.

III. Methods

1. *Treatment for net production*

Net primary production (ΔP_N) estimates for trees in the destructive stands were based on the equation

$$\Delta P_N = Y_N + \Delta L_N + \Delta G_N$$

Table 1. General description of research areas

Forest type: (major tree species)	*Tsuga heterophylla-Picea sitchensis*	*Pseudotsuga menziesii-Tsuga heterophylla*	*Abies procera-Pseudotsuga menziesii-Abies amabilis*
Location:	Cascade Head Experimental Forest, Otis, OR	Blue River, OR	Wildcat Mountain Res. Natural Area, OR
Latitude:	45°	44°	44°
Longitude:	123°56′	122°30′	122°40′
Elevation (m):	200	450	1300
Soil characteristics:			
Type:	Reddish-Brown Lateritic	Reddish-Brown Lateritic	Brown Podzolic
Texture:	Silt Loam	Gravelly silty clay Loam	Sandy Loam
pH (A1 and B2 horizons respectively):	4.0～4.5	7.0～6.2	6.2～5.8
Soil Horizons (depths in cm)	A1; 0～14 A3～B1; 14～24 B2～B3; 24～70	A1; 0～20 A3; 20～38 B2; 38～104 B3; 104～125	A1; 0～20 A3～B1; 20～50 B2; 49～90 B3; 90～120
Rooting depth (cm)	70	125	120
Soil parent material	Marine sediments (siltstone)	Andesite and andesitic breccia	Andesite plus volcanic ash and pumice

Table 2. Description of stands on study plots

Study plot	Stand age (yr)	Slope, aspect and area of study plot	Height of dominant trees (m) Average / Range	Tree species present	Stand density[1] (stems/ha) Total and by species	Basal area[1] (m²/ha) at DBH Total and by species
Tsuga-Picea stand	100~120	0°	47.7	*T. heterophylla*	322	71.6
		64m×64m	43.0 to 55.9	*P. sitchensis*	51	26.6
		4096m²		Total	373	98.2
Pseudotsuga-Tsuga stand	90~110	18°	62.6	*P. menziesii*	234	57.4
		East facing	57.0 to 74.6	*T. heterophylla*	102	1.8
		80m×50m		*A. macrophyllum*	87	3.5
		3808m²		Other species	55	0.6
				Total	478	63.3
Abies-Pseudotsuga stand	100~130	21.5°	49.9	*A. procera*	136	54.7
		South facing	44.0 to 60.1	*P. menziesii*	116	39.2
		60m×60m		*A. amabilis*	92	4.1
		3374m²		*T. mertensiana*	6	0.1
				Total	350	98.1

[1] Trees≧4.5cm DBH only

Table 3. Tree, shrub, and herbaceous species present on study plots

Tsuga-Picea stand	*Pseudotsuga-Tsuga* stand	*Abies-Pseudotsuga* stand
Tree species:		
Tsuga heterophylla (RAF.) SARG.	*Pseudotsuga menziesii* (MIRB.) FRANCO	*Abies procera* REHD.
Picea sitchensis (BONG.) CARR.	*Tsuga heterophylla* (RAF.) SARG.	*Pseudotsuga menziesii* (MIRB.) FRANCO
	Acer macrophyllum PURSH	*Abies amabilis* (DOUGL.) FORBES
		Tsuga mertensiana (BONG.) CARR.
Shrub species:		
Menziesia ferruginea SMITH	*Acer circinatum* PURSH	*Acer circinatum* PURSH
Vaccinium parvifolium SMITH	*Vaccinium parvifolium* SMITH	
Oplopanax horridum (J. E. SMITH) MIQ.	*Gaultheria shallon* PURSH	
	Berberis nervosa PURSH	
	Taxus brevifolia NUTT.[1]	
	Cornus nuttallii AUD. ex T. & G.[1]	
	Rhamnus purshiana DC.[1]	
Herbaceous species:		
Oxalis oregana NUTT. ex T. & G.	*Linnaea borealis* L.	*Clintonia uniflora* (SCHULT.) KUNTH
Trillium ovatum PURSH	*Polystichum munitum* (KAULF.) PRESL.	*Asarum caudatum* LINDL.
Clintonia uniflora (SCHULT.) KUNTH	*Vancouveria hexandra* (HOOK.) MORR. & DEC.	*Smilacina stellata* (L.) DESF.
Polystichum munitum (KAULF.) PRESL.	*Tiarella trifoliata* L.	*Achlys triphylla* (SMITH) DC.
Viola sempervirens GREENE		*Goodyera oblongifolia* RAF.
Struthiopteris spicant (L.) WEIS.		*Vaccinium membranaceum* DOUGL. ex HOOK.
Athyrium felix-femina (L.) ROTH		*Pteridium aquilinum* (L.) KUHN. var. *pubescens* UNDERW.

[1] Tree species present as shrubs in this community.

where Y_N, ΔL_N, and ΔG_N respectively, are newly formed plant tissues in the interval T_1 to T_2 measured at T_2, losses out of newly produced matter due to mortality, and those by grazing in the same interval.

It is difficult to measure ΔL_N and ΔG_N, and they are generally considered far smaller than Y_N, so they were not considered in this study. Thus, ΔP_N was estimated using the equation

$$\Delta P_N \fallingdotseq Y_{NS}+Y_{NB}+Y_{NL}$$

where S, B, and L denote the tree components, stem, branch, and leaf, respectively. Although Y_{NS}, Y_{NB}, and Y_{NL} are not exactly the same as net production as mentioned above, it is allowed to call them net production of stem, branch, and leaf, respectively, in this study.

For this study, Y_{NR} (R denotes root) is not included in ΔP_N, so the net primary production of the stand is limited to above-ground production.

2. *Computations*

Tree biomass and productivity of the three younger stands were estimated by the allometric method (KIRA & SHIDEI, 1967) using logarithmic regressions of individual tree component biomass and net production on D^2H (diameter squared times height in cm²×m). Regression equations were calculated using data from destructive analysis of individual trees in each stand. Regressions used in this pa-

Table 4. Climatic data for study plots

A. Temperature and precipitation measured on study plots for 1973～1974 (two-year average)

		Study plot		
		Tsuga-Picea	*Pseudotsuga-Tsuga*	*Abies-Pseudotsuga*
Average temperature (℃):	Annual	9.9	9.2	7.4
	January	4.6	0.8	−1.4
	July	15.7	17.7	15.6
Precipitation (mm):	Annual	3423	2420	3620
	1 Dec. to 1 Mar.	1520	1440	2070
	1 June to 1 Sept.	227	110	215

B. Long-term cumulative average temperature and precipitation from U.S. Weather Bureau climatic station[1] nearest study plots.[2]

		Otis, Oregon	McKenzie Bridge, Oregon
Latitude		45°02′	44°12′
Elevation		49m	497m
Average temperature:	Annual	10.1	10.1
	January	4.5	1.4
	July	15.2	19.8
Precipitation:	Annual	3115	1789
	1 Dec. to 1 Mar.	1317	780
	1 June to 1 Sept.	237	106

1) U.S. Weather Bureau. 1974. Annual Summary: Climatological data-Oregon. U.S. Dept. Comm. Asheville, N.C.

2) Otis is near *Tsuga-Picea* study area, McKenzie Bridge is near *Pseudotsuga-Tsuga* study area.

per estimate component volume or weight for individual trees. Notation used in these regressions is as follows: D is DBH (cm), H is tree height (m), and V is stem volume (dm^3).

Equations relating tree component volume or biomass (Y, dm^3 or kg) to D^2H for the three destructively sampled stands were of the form:

$$\log_{10}Y = b\log_{10}(D^2H) - a \qquad (1)$$

or of the form:

$$\frac{1}{Y} = \frac{b}{D^2H} + a \qquad (2)$$

Coefficients a and b for these equations as used in the different stands are given in the following paragraphs.

For the *Tsuga-Picea* stand, tree height was estimated from the equation:

$$\frac{1}{H} = \frac{0.5000}{D} + 0.0132 \quad \text{(see Fig. 2)}$$

As relations between volume or weight of all components and D^2H show the same type of the relation between stem wood volume and D^2H shown in Fig. 3, all equations used in volume and weight computations for this stand were of form (1). Regression coefficients are given in the following table:

	Stem wood (volume)		Branch wood (weight)		Leaf (weight)		Net production of stem wood (volume)		Net production of branch wood (weight)		Net production of leaf (weight)	
	b	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*
Tsuga heterophylla	0.9495	1.2069	1.0554	3.4445	0.9405	3.5290	1.1021	4.1079	1.1435	5.8521	0.8861	3.6811
Picea sitchensis	0.9495	1.2069	1.0554	3.2569	0.9405	3.6343	1.1021	4.1079	1.1135	5.2407	0.8861	3.7851

For the *Pseudotsuga-Tsuga* stand, tree height was estimated from the equation:

$$\frac{1}{H} = \frac{0.5357}{D} + 0.0089 \quad \text{(see Fig. 2)}$$

Again, all regressions were of form (1), since relation between volume or weight of all components and D^2H showed the same type of relation between stem wood volume and D^2H as shown in Fig. 3. Coefficients for these regressions are given in the following table:

	Stem wood (volume)		Branch wood (weight)		Leaf (weight)		Net production of stem wood (volume)		Net production of branch wood (weight)		Net production of leaf (weight)	
	b	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*
Pseudotsuga menziesii	0.8885	0.9465	1.5171	5.8664	1.0172	3.7019	0.7621	2.1541	1.1830	5.4911	1.0172	4.3208

Biomass and net production of *Acer macrophyllum* and *Tsuga heterophylla* in this stand were estimated using the proportionality:

$$Y = Y' \cdot \frac{G}{G'}$$

where Y, Y', G, and G' are biomass of these spe-

Photo. 1. E
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Photo. 1. Experimental stand of *Tsuga heterophylla-Picea sitchensis*, Cascade Head

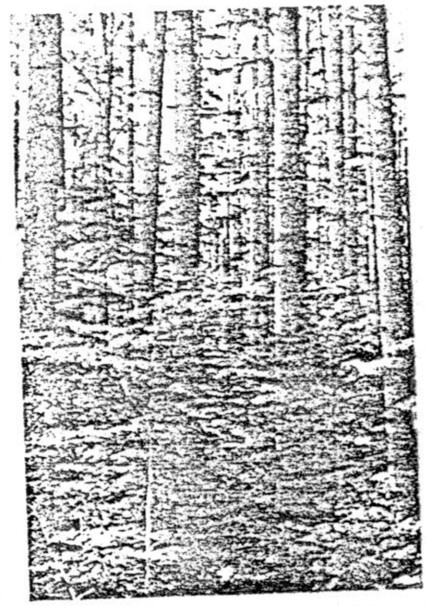

Photo. 2. Experimental stand of *Pseudotsuga menziesii-Tsuga heterophylla*, Blue River

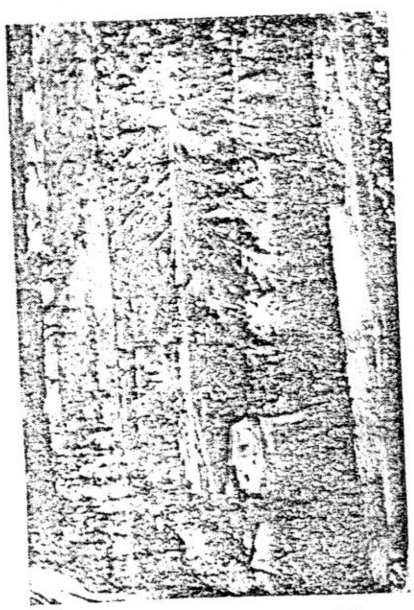

Photo. 3. Experimental stand of *Abies procera-Pseudotsuga menziesii*, Wildcat Mountain

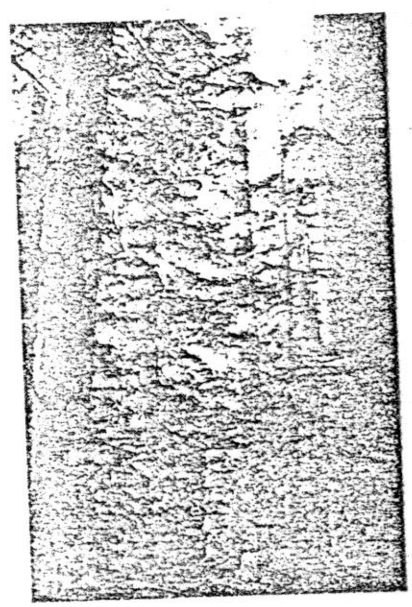

Photo. 4. Experimental stand of mature *Abies procera-Pseudotsuga menziesii*, Goat Marsh, Res. Natural Area

cies in sample plot, biomass of sample trees of these species, basal area (DBH) of these species in sample plot, and basal area (DBH) of sample trees of these species, respectively.

For the *Abies-Pseudotsuga* stand, tree heights were estimated from the equation:

$$\frac{1}{H}=\frac{0.9516}{D}+0.0087 \quad \text{(see Fig. 2)}$$

Components listed together with their regression coefficients in the following table were estimated using equation form (1). This is because relations between these components and D^2H show such regression line as shown in Fig. 3.

	Stem wood (weight)		Leaf (weight)		Net production of stem wood (weight)		Net production of branch wood (weight)	
	b	*a*	*b*	*a*	*b*	*a*	*b*	*a*
All species	0.9252	1.4953	0.6656	1.7056	0.8528	3.1109	0.8046	3.0324

As the relation between branch wood weight or net production of leaf and D^2H shows such regression curve as shown in Fig. 4, they were estimated using equation form (2) and coefficients are given in the following table:

	Branch wood (weight)		Net production of leaf (weight)	
	b	*a*	*b*	*a*
All species	714.29	0.0013	1.7105	0.0294

For the non-destructive mature stands, tree height was estimated from the equations in Figs. 5 and 6. Stem volumes of the non-destructive mature stands were calculated using

$$V=\pi/4(D^2H)F$$

where F is a stem taper coefficient determined by measuring fallen trees of each species in the plot. Values of F for the various species were *Pseudotsuga menziesii* 0.427, *Tsuga heterophylla* 0.491, *Thuja plicata* 0.427 in the *Pseudotsuga-Tsuga* stand and *Abies procera* 0.414, *Pseudotsuga menziesii* 0.393, *Tsuga heterophylla* 0.510, and *Abies amabilis* 0.510 for the *Abies-Pseudotsuga* stand.

3. *Sampling*

For destructive analysis, a sample plot was laid out in each stand. Sample plot dimensions are given in Table 2. Diameters (±0.1 cm) and species of all the trees and height (±1 m) of one-third of the trees on each plot were determined using a diameter tape for DBH and an Abney level for heights. Sample trees were chosen from each stand to represent the full range of tree size classes. The number of sample trees chosen was proportional to the number of trees in each size class and species on the plot. Sample trees were felled, tree dimensions were recorded and the dry weight of each tree component was determined by the stratified-clip method (MONSI & SAEKI, 1953).

Using the general stratified-clip method, the following procedure was applied to determine dry weight of components of individual sample trees: Intervals 3～4 meters long (strata) were marked along

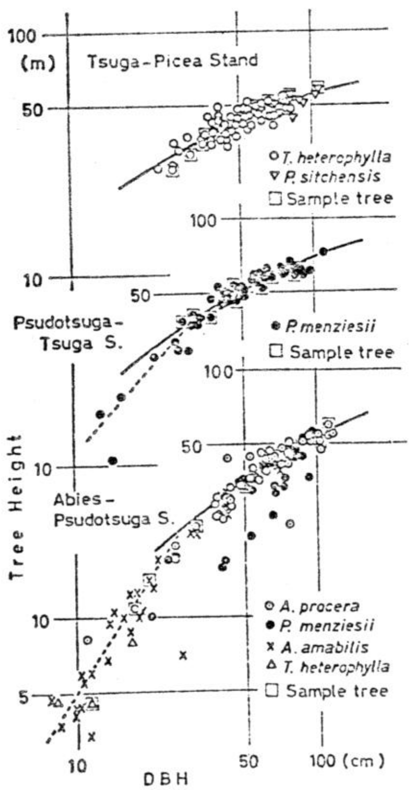

Fig. 2. Relation between diameter and tree height for the three experimental stands

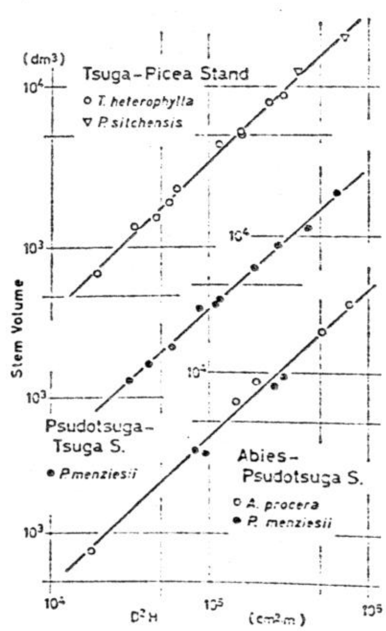

Fig. 3. Relation between D^2H and stem volume for the three experimental stands

The two smallest trees in the *Pseudotsuga-Tsuga* stand and the three smallest trees in the *Abies-Pseudotsuga* stand are not plotted on the graph.

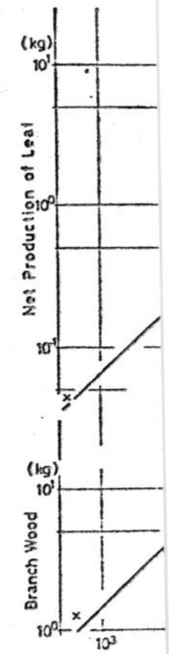

Fig. 4 Relati
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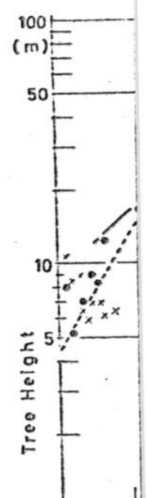

Fig. 5. Rela
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Pseudotsuga n

Tsuga heterop

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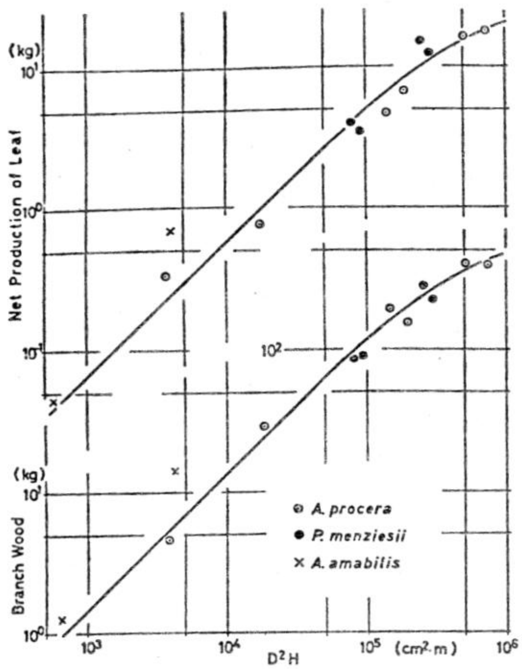

Fig. 4 Relation between D^2H and branch wood weight, and between D^2H and net production of leaf

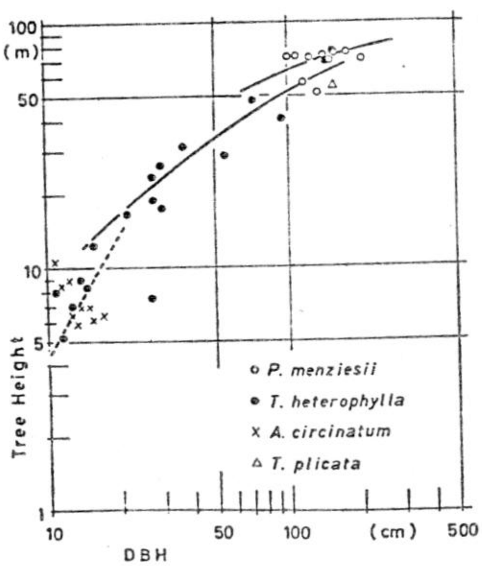

Fig. 5. Relation between diameter and tree height in mature *Pseudotsuga-Tsuga* stand at Middle Santiam

Pseudotsuga menziesii: $\frac{1}{H}=\frac{0.5913}{D}+0.0096$

Tsuga heterophylla: $\frac{1}{H}=\frac{1.0345}{D}+0.0086$ $(D\geqq 20\text{cm})$

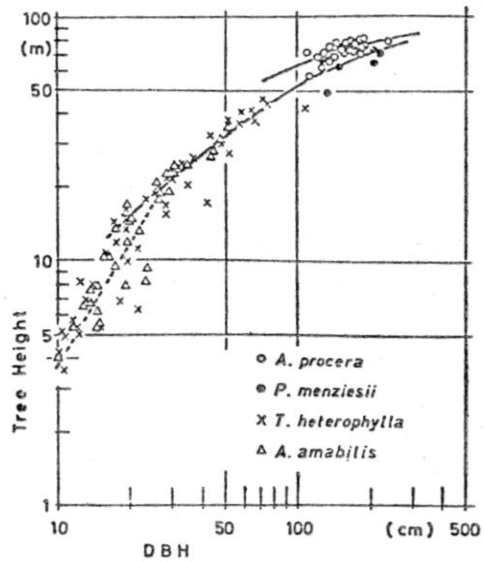

Fig. 6. Relation between diameter and tree height in mature *Abies-Pseudotsuga* stand at Goat Marsh Res. Natural Area

Abies procera: $\frac{1}{H}=\frac{0.6035}{D}+0.0095$

Pseudotsuga menziesii: $\frac{1}{H}=\frac{1.0087}{D}+0.0087$

Tsuga heterophylla and *Abies amabilis*: $\frac{1}{H}=\frac{1.1842}{D}+0.0066$ $(D\geqq 20\text{cm})$

the main stem of the felled tree. All branches originating in each 3∼4m stratum were removed and separated into foliage-bearing twigs and large branch components. Fresh weight of these components was determined on a spring scale. Representative subsamples of large branches and foliage-bearing twigs were taken from each 3∼4m stratum and fresh weight obtained. The subsample of foliage-bearing twigs was separated while fresh into new twig plus foliage and older twigs plus foliage fractions. Large branch and the foliage-twig samples were then dried. After drying, the foliage-twig samples were separated into foliage and twig components and percent water of the original subsample was computed together with ratios of new foliage to new twig plus foliage, older foliage to older twig plus foliage, and new twig plus foliage to total twig plus foliage. These ratios were used together with fresh weight of all twigs and foliage to compute dry weight of new and older twigs and foliage components in that stratum. Component weights for each tree were obtained by summing the respective weights in each stratum.

Cross-section discs were cut from the tree stem at each stratum mark. Diameter outside bark, diameter inside bark, and the thickness of current 5-year radial increment were measured on each section. Wood and bark density were also determined on samples from these sections. Stem, bark, and increment volume were computed using SMA-

LIAN's rule. The value of stem increment volume was averaged over the current five years.

Net production of branch was determined for the *Abies-Pseudotsuga* stand by two methods. In the first, three to five sample branches were chosen from each vertical stratum in direct proportion to the branch size frequency distribution, and with care to cover the whole characters of the branches in each stratum. Sample branches were cut into 5 to 50cm segments from bough to twigs, segment length being proportional to branch diameter. The annual rings of the segments were examined and the growth (net production) rate of branch volume was calculated using the common stem analysis method (SMALIAN). In the second method, net production of branch was computed by multiplying stem wood growth rate by branch biomass for each stratum. This method was used for the *Tsuga-Picea* and the *Pseudotsuga-Tsuga* stands and also, to provide comparative data, on the *Abies-Pseudotsuga* stand. Net production of stem bark was computed by multiplying stem wood growth rate times bark biomass. Net production of branch bark was similarly the product of branch wood growth rate and branch bark biomass.

All weights are reported as oven-dry weights at 90°C.

4. Field procedures

Tsuga-Picea stand: Fieldwork was done between August 28 and September 20, 1972. From the experimental plot (Tables 1, 2, Photo. 1), 12 sample trees (10 *Tsuga heterophylla* and 2 *Picea sitchensis*) were felled for analysis. Each sample tree was divided into 4m vertical strata except for the top (a variable length) and the base (1.3m). For estimation of understory biomass (DBH≦4.4cm), 5 sub-plots (4m×4m) were set at the four corners and the center of the plot. All vegetation in each sub-plot was harvested and directly weighed.

Pseudotsuga-Tsuga stand: Fieldwork was done between September 27 and October 17, 1972. From the experimental stand (Tables 1, 2, Photo. 2), 12 sample trees (10 *Pseudotsuga menziesii*, 1 *Tsuga heterophylla*, and 1 *Acer macrophyllum*) were felled for analysis. Each tree was divided into 4m strata except for the top and the base. Five sub-plots (5m ×2m) for estimating understory biomass (DBH≦4.4 cm) were set every 5m along the strata mid-line of the plot. That is to say, the vertical length of each sub-plot was 5m and the distance between each margin of those sub-plots was also 5m. All vegetation in each sub-plot was harvested and weighed.

Abies-Pseudotsuga stand: Fieldwork was carried out between August 3 and 25, 1972. In the experimental plot (Tables 1, 2, Photo. 3), 6 *Abies procera*, 4 *Pseudotsuga menziesii*, 1 *Abies amabilis*, and 1 *Tsuga mertensiana* were felled as sample trees. The sample trees were divided into 3m strata except for the top and the base. For estimating understory biomass (DBH≦4.4cm), the following method was used. The experimental plot was divided into 30 10m×10m sub-plots. In each sub-plot, percent cover by species of understory vegetation was recorded. Average cover values were then calculated. The sub-plot whose percent cover for each species was nearest the average values was chosen for total harvest. All of the subordinate vegetation on this sub-plot was cut and weighed.

Six litterscreens (1m×1m) were placed in each of the destructive analysis stands. Litterfall was collected monthly from these screens for two years. Senescent and living leaf litter were separated from other litter; all were weighed.

For non-destructive measurement of the mature *Pseudotsuga-Tsuga* stand, a 120m×80m plot was laid out in the stand. The plot was on level ground. The DBH of all trees with DBH≧9.5cm were measured. Tree heights which were not measured

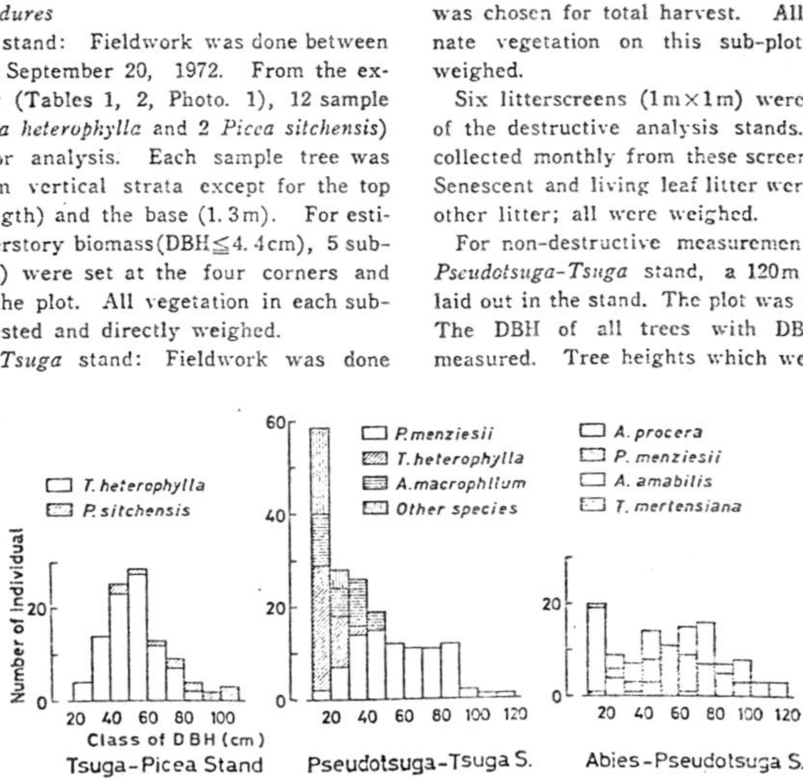

Fig. 7. Diameter frequency distributions for the three experimental stands

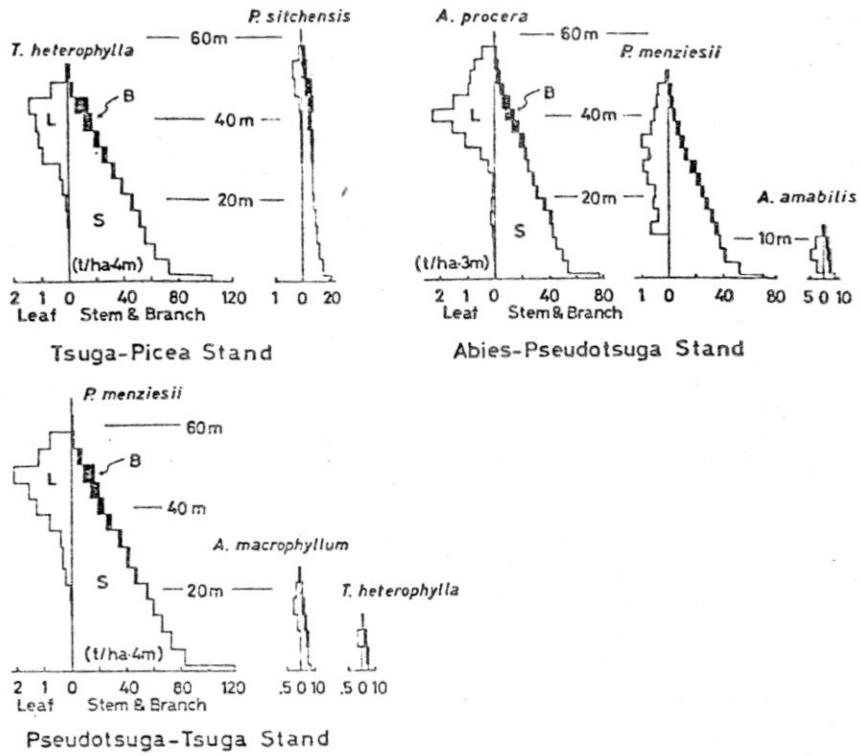

Fig. 8. Production structure of the three stands
L, S, and B denote leaf, stem, and branch dry weight respectively.

were estimated by the relationship between DBH and tree height really measured (Fig. 5). Fieldwork was done between November 6 and 8, 1972. The mature *Abies-Pseudotsuga* stand was analyzed the same way (Fig. 6). This plot was 100m×100 m and inclined 10° to the south. Fieldwork was done between October 20 and 25, 1972.

IV. Result and Discussion

Height-diameter relations and diameter frequency distribution for the three destructively sampled stands are shown in Figs. 2 and 7. It is difficult to distinguish between the dominant and sub-dominant tree layers in these stands. However, our observations indicate that canopies of dominant trees range between 43～56m, 57～75m, and 44～60m, respectively, in the *Tsuga-Picea, Pseudotsuga-Tsuga*, and *Abies-Pseudotsuga* stands. Few trees in the *Tsuga-Picea* stand are in the 5～25m height range (Fig. 2). In contrast, tree heights are distributed along the entire range of heights and diameters in both the *Pseudotsuga-Tsuga* and the *Abies-Pseudotsuga* stands (Fig. 2). An unusual characteristic of the *Pseudotsuga-Tsuga* stand is the high values of H/D (height in cm÷diameter in cm) for *Pseudotsuga menziesii*. Many trees in this stand, even dominants, have an H/D ratio exceeding 100 (Fig. 2). For example, the largest value of H/D in the dominant trees (57～75m in H) recorded 106.5 (60.6m in H, 56.9cm in D) in this stand.

The production structure of the three stands is diagrammed in Fig. 8. These data show vertical distribution of tree component biomass in the various species of each stand. The leaf biomass of the *Tsuga-Picea* stand is concentrated in the upper part of the canopy in comparison with the other two stands.

Above-ground biomass and net production of the *Tsuga-Picea* stand is shown in Table 5. Total stand biomass including subordinate vegetation is 875t/ha, of which about 75% is *Tsuga heterophylla*. Subordinate vegetation biomass (4.0t/ha) is a negligible component of this stand. Leaf biomass in this stand excluding subordinate vegetation is 7.9t/ha, less than 1% of total above-ground biomass. This value falls in the lowest class of leaf biomass for coniferous forests of Japan. In contrast, FUJIMORI (1971) reports leaf biomass of 21.1t/ha in a 26-year-old *Tsuga heterophylla* stand in the same experimental forest in which the present stand was sampled.

There are several possible explanations for the

Table 5. Biomass and net production of *Tsuga-Picea* stand at Cascade Head Experimental Forest, Oregon

Trees (≧4.5cm DBH)

		Dry weight (ton/ha)								Volume (m³/ha)		
		Stem			Branch					Stem		
		Wood	Bark	Total	Wood	Bark	Total	Leaf	Total	Wood	Bark	Total
Biomass	*Tsuga heterophylla*	560.7	56.0	616.7	24.4	4.5	28.9	6.03	651.6	1278.6	132.5	1411.1
	Picea sitchensis	190.8	7.2	198.0	18.3	1.5	19.8	1.88	219.7	544.8	22.6	567.4
	Total	751.5	63.2	814.7	42.7	6.0	48.7	7.91	871.3	1823.4	155.1	1978.5
Net production	*Tsuga heterophylla*	4.35	0.44	4.79	0.29	0.03	0.32	2.23	7.34	9.93	1.03	10.96
	Picea sitchensis	1.72	0.06	1.78	0.53	0.02	0.55	0.66	2.99	4.88	0.20	5.08
	Total	6.07	0.50	6.57	0.82	0.05	0.87	2.89	10.33	14.81	1.23	16.04

Subordinate vegetation		Dry weight (ton/ha)
		Total
Biomass	*Tsuga heterophylla*	2.55
	Broad leaf shrubs	1.14
	Herbaceous plants	0.05
	Ferns	0.29
	Total	4.03

low leaf biomass in this stand. The difference between this stand and the one reported by FUJIMORI may be due simply to differences in the growing stage of this stand and the younger stand studied by FUJIMORI. According to ANDO *et al.* (1972), leaf biomass of a mature *Tsuga sieboldii* stand in Japan is 7.8t/ha, nearly the same as in this stand. Another factor probably contributing to the low leaf biomass in this older stand is pruning of living foliage by winds associated with winter storms. Litterfall collections indicate that 1.5 and 1.0 t/ha/yr of living foliage of all age classes were broken from trees in this stand by winds during 1973 and 1974 respectively. In the same period, wind damage to younger stands in this experimental forest was minimal. However, longer term data is necessary to confirm these observations.

Annual total above-ground net production and net production of leaf (excluding subordinate vegetation) were 10.3 and 2.9t/ha/yr in this stand. Proportions of current foliage to total leaf dry weight in this stand were 37% for *Tsuga heterophylla* and 35% for *Picea sitchensis*. The value of net production of leaf in this stand is in good agreement with that of leaf litterfall; averaged over 2 years, leaf litterfall in this stand was 3.0t/ha/yr. Leaf efficiencies for production of above-ground portions (above-ground net production divided by total leaf biomass) of this stand were 1.2 and 1.6t/t/yr for *Tsuga heterophylla* and *Picea sitchensis*, respectively.

Above-ground biomass and net production of the *Pseudotsuga-Tsuga* stand is shown in Table 6. Total above-ground biomass of this stand is 669t/ha including subordinate vegetation. Biomass of *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Acer macrophyllum*, other tree species, and subordinate vegetation constitute about 95, 1, 2, 0.4, and 1% respectively of the total above-ground stand biomass. Excluding subordinate vegetation, leaf biomass of this stand is 11.1t/ha (13.9t/ha including subordinate vegetation) while total above-ground net production and net production of leaf are 12.7 and 2.84 t/ha/yr, respectively. Based on these data, leaf production efficiency of this stand is 1.1 and 1.2t/t/yr for *Pseudotsuga menziesii* and *Tsuga heterophylla*, respectively. Current foliage constitutes 24 and 42% respectively of total leaf biomass of *Pseudotsuga menziesii* and *Tsuga heterophylla*. Again for this stand, there was good agreement between the value of leaf litterfall (2.6t/ha/yr) and that of net production of leaf (2.8t/ha/yr).

Above-ground biomass and net production of the *Abies-Pseudotsuga* stand is shown in Table 7. Total biomass of this stand is 882t/ha with *Abies procera*, *Pseudotsuga menziesii*, *Abies amabilis*, *Tsuga mertensiana*, and subordinate vegetation constituting about 60, 37, 3, 0.02, and 0.2%, respectively, of this total amount. Excluding subordinate vegetation, leaf biomass of this stand is 17.5t/ha (17.6t/ha, including subordinate vegetation), while total above-ground net production and net production of leaf are respectively 13.0 and 3.22t/ha/yr. Based on these data, leaf production efficiencies in the *Abies-Pseudotsuga* stand are 0.76, 0.73, and 0.63t/t/yr for *Abies procera*, *Pseudotsuga menziesii*, and *Abies amabilis*, respectively. In this stand, current foliage constitutes 19, 18, and 13% of total foliage for *Abies procera*, *Pseudotsuga menziesii*, and *Abies amabilis*, respectively. The value of leaf litterfall in this stand was 3.0t/ha/yr, which is also in good agreement with that of net production of leaf (3.2 t/ha/yr).

When comparing net production of branch among stands, the different methods used should be noted.

Table 6. Biomass and net production of *Pseudotsuga-Tsuga* stand at Blue River, Oregon

Trees (≧4.5cm DBH)

		Dry weight (ton/ha)								Volume (m³/ha)		
		Stem			Branch					Stem		
		Wood	Bark	Total	Wood	Bark	Total	Leaf	Total	Wood	Bark	Total
Biomass	*Pseudotsuga menziesii*	510.2	69.2	579.4	40.5	5.8	46.3	10.50	636.2	1172.8	183.0	1355.8
	Tsuga heterophylla	4.11	0.49	4.60	1.07	0.18	1.25	0.31	6.16	9.43	1.28	10.71
	Acer macrophyllum	13.50	1.25	14.75	1.07	0.10	1.17	0.20	16.12	31.10	3.31	34.41
	Other species	2.11	0.21	2.32	0.28	0.04	0.32	0.07	2.71	4.87	0.56	5.43
	Total	529.9	71.2	601.1	42.9	6.1	49.0	11.1	661.2	1218.2	188.2	1406.4
Net production	*Pseudotsuga menziesii*	6.70	0.90	7.60	1.40	0.22	1.62	2.47	11.69	15.39	2.38	17.77
	Tsuga heterophylla	0.20	0.02	0.22	0.01	T[1]	0.01	0.13	0.36	0.45	0.06	0.51
	Acer macrophyllum	0.28	0.03	0.31	0.02	T	0.02	0.20	0.53	0.63	0.07	0.70
	Other species	0.06	0.01	0.07	T	T	T	0.04	0.11	0.14	0.02	0.16
	Total	7.24	0.96	8.20	1.43	0.22	1.65	2.84	12.69	16.61	2.53	19.14

Subordinate vegetation

		Dry weight (ton/ha)		
		Stem and branch	Leaf	Total
Biomass	*Acer circinatum*	1.10	0.07	1.17
	Taxus brevifolia	2.98	0.66	3.64
	Vaccinium parvifolium	0.15	0.01	0.16
	Berberis nervosa	0.17	0.48	0.65
	Gautheria shallon	0.25	0.18	0.43
	Tsuga heterophylla	0.08	0.03	0.11
	Seedlings[2]	0.02	0.01	0.03
	Herb layer		0.13	0.13
	Polystichum munitum		1.23	1.23
	Total	4.75	2.80	7.55

1) T≦10kg/ha/yr
2) Primarily 1 to 6-year-old *Tsuga heterophylla* seedlings

Table 7. Biomass and net production of *Abies-Pseudotsuga* stand at Wildcat Mountain

Trees (≧4.5cm DBH)

		Dry weight (ton/ha)								Volume (m³/ha)		
		Stem			Branch[1]					Stem		
		Wood	Bark	Total	Wood	Bark	Total	Leaf	Total	Wood	Bark	Total
Biomass	*Abies procera*	411.6	67.9	479.5	28.3	10.7	39.0	10.19	528.7	1083.2	151.0	1234.2
	Pseudotsuga menziesii	252.9	41.1	294.0	19.2	7.4	26.6	6.65	327.3	602.1	97.9	700.0
	Abies amabilis	18.50	2.88	21.38	1.57	0.61	2.18	0.63	24.19	48.68	6.10	54.78
	Tsuga mertensiana	0.15	0.02	0.17	0.01	T	0.01	0.01	0.18	0.37	0.04	0.41
	Total	683.2	111.9	795.1	49.1	18.7	67.8	17.48	880.4	1734.4	255.0	1989.4
Net production	*Abies procera*	3.98	0.61	4.59	2.57 0.98	0.87 0.18	3.44 1.16	1.97	10.00 7.72	10.47	1.36	11.83
	Pseudotsuga menziesii	2.52	0.38	2.90	1.45 0.66	0.56 0.12	2.01 0.78	1.17	6.08 4.85	6.00	0.90	6.90
	Abies amabilis	0.21	0.03	0.24	0.13 0.07	0.05 0.01	0.18 0.08	0.08	0.50 0.40	0.55	0.06	0.61
	Tsuga mertensiana	T[2]	T	T	T T	T T	T T	T	T T	T	T	T
	Total	6.71	1.02	7.73	4.15 1.71	1.48 0.31	5.63 2.02	3.22	16.58 12.97	17.02	2.32	19.34

Subordinate vegetation

		Dry weight (ton/ha)		
		Stem and branch	Leaf	Total
Biomass	*Acer circinatum*	1.39	0.11	1.50
	Herb layer		0.02	0.02
	Total	1.39	0.13	1.52

1) Net production of branch: Upper value for each species was obtained from direct branch analysis, values on lower lines were obtained from product of branch biomass and stem growth rate in the corresponding stratum.
2) T≦10kg/ha/yr

Net production of branch in the *Tsuga-Picea* and the *Pseudotsuga-Tsuga* stands was computed as the product of branch biomass and stem growth rate in the corresponding stratum (method 2). This same method was used in the *Abies-Pseudotsuga* stand to provide comparative values, but branch analysis (method 1) was also used to provide an independent estimate. In Table 7, two values are given for net

Table 8. Descriptions of mature stands

Place: Forest type	Species	Stand age (yr)	Tree number/ha[1]	Height of the highest tree (m)	Total basal area of stem (m^2/ha)[1] at DBH	Stem volume (m^3/ha)[1]
Middle Santiam:	*Pseudotsuga menziesii*		71	78.3	105.69	3234.0
Elevation-480m	*Tsuga heterophylla*		167	48.3	18.41	319.9
	Thuja plicata	>500	1	56.6	1.95	45.63
Pseudotsuga menziesii and *Tsuga*	*Acer circinatum*		33	10.9	0.50	0.50
heterophylla stand	*Cornus nuttallii*		1	17.5	0.50	T
	Acer macrophyllum		1	8.0	0.01	T
	Total		274		127.06	3600.0
Goat Marsh Res.	*Abies procera*		48	82.2	86.00	2675.6
Natural Area:	*Pseudotsuga menziesii*	About	19	75.0	38.90	1097.7
Elevation-1000m	*Tsuga heterophylla*	310	120	65.9	16.74	381.0
Abies procera and *Pseudotsuga menziesii* stand	*Abies amabilis*		137	37.3	5.79	57.48
	Total		324		147.43	4211.8

[1] Trees ≧ 9.5cm DBH only

production of branch, the upper values estimated by method 1, the lower values estimated by method 2. Apparently the values obtained by method 2 are smaller than those obtained by method 1. It could be said that the value obtained by method 1 is more precise than that by method 2. Providing that this is permitted, it can be safely said that the growth rate of stem inside its crown is far smaller than that of the branches of the tree. Therefore, when the net production of branch is estimated by the product of branch biomass and the stem growth rate in the corresponding stratum, there is a possibility of underestimating the value.

On a comparative basis, above-ground biomass and net production in the three experimental stands were similar. Total biomass of the *Pseudotsuga-Tsuga* stand was about 75% of the totals for the *Tsuga-Picea* or the *Abies-Pseudotsuga* stands. On the other hand, net production was about 20% less in the *Tsuga-Picea* stand than in the *Pseudotsuga-Tsuga* or the *Abies-Pseudotsuga* stands. Expressed as percentages, proportions of above-ground net production per unit total above-ground biomass were 1.2, 1.9, and 1.5% for the *Tsuga-Picea*, *Pseudotsuga-Tsuga*, and *Abies-Pseudotsuga* stands, respectively.

Leaf biomass of the *Abies-Pseudotsuga* stand is 2.2 and 1.6 times greater respectively than that of the *Tsuga-Picea* and the *Pseudotsuga-Tsuga* stands. However, net production of leaf in these stands is about the same (Tables 5~7). This indicates a longer period of foliage retention in the *Abies-Pseudotsuga* stand than in the other two. Observations made during destructive analysis showed the oldest leaves on both *Abies procera* and *Abies amabilis* to be 18~20 years old. Typical needle retention in *Pseudotsuga menziesii* and *Tsuga heterophylla* are 5 and 4 years respectively. However, foliage of *Pseudotsuga menziesii* in the *Abies-Pseudotsuga* stand was retained about a year longer than that in the lower elevation *Pseudotsuga-Tsuga* stand. This implies some environmental influence on foliage retention at least for *Pseudotsuga menziesii*.

However, leaf production efficiencies in the three stands are inversely related to leaf biomass with average values for the *Tsuga-Picea*, *Pseudotsuga-Tsuga*, and *Abies-Pseudotsuga* stands being about 1.3, 1.1, and 0.74 t/t/yr, respectively. So at least in these experimental stands, leaf production efficiency decreases with increasing elevation.

In a forest, the above-ground biomass divided by the height of dominant trees gives the apparent density of dry organic matter per unit volume occupied by a forest. The volumetric dry organic matter density of the *Tsuga-Picea*, *Pseudotsuga-Tsuga*, and *Abies-Pseudotsuga* stands were 1.82, 1.06, and 1.76 kg/m^3 when computed using average heights of the dominant trees in respective stands of 48, 63, and 50 m (Table 2). In closed forests in Japan, dry matter densities usually range between 1 and 1.5 kg/m^3 with no relation to normal stand height, although there are exceptions in shorter stands as reported by KIRA & SHIDEI (1967) and YODA (1971).

Results of the non-destructive surveys of the mature *Pseudotsuga-Tsuga* stand at the proposed Middle Santiam Research Natural Area, Oregon and of the roughly 310-year-old *Abies-Pseudotsuga* stand at the Goat Marsh Research Natural Area in Washington are shown in Figs. 5 and 6, and Table 8. These two stands may be regarded as a potential result of continued growth by the corresponding younger experimental stands of this study. Total basal areas of stem (m^2/ha) of the mature *Pseudotsuga-Tsuga* and *Abies-Pseudotsuga* stands are 127 and 147. These values are much higher than reported for stands outside this region.

Total stem volumes including bark for trees ≧ 9.5 cm DBH were 3600 and 4212 m^3/ha in the mature *Pseudotsuga-Tsuga* and *Abies-Pseudotsuga* stands, respectively. These values are computed without volume deductions for stem defects such as heart-rot since there were few defective trees in either plot.

Stem biomass for these two mature stands was computed using wood and bark specific gravities and wood to bark ratios obtained during destructive sampling of the corresponding younger stands. Stem biomass of these two stands were nearly identical. Stem biomass was 1591 t/ha in the *Pseudotsuga-Tsuga* stand and 1687 t/ha in the *Abies-Pseudotsuga* stand. Based on these stem biomass estimates, the volumetric density of these stands are 2.12 kg/m^3 for the 75 m high *Pseudotsuga-Tsuga* stand and 2.31 kg/m^3 for the 73 m high *Abies-Pseudotsuga* stand.

Biomass estimates for the two mature stands are conservative in that they do not include biomass of branches, foliage or subordinate vegetation. Even so, these underestimates of biomass and volumetric densities for these mature coniferous forests are higher than those reported for forests anywhere outside this region. Future research should confirm the large biomass accumulations in forests of the northwestern United States and southwestern Canada.

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