Old-Growth Pseudotsuga menziesii Communities of a Western Oregon Watershed: Biomass Distribution and Production Budgets

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OLD-GROWTH *PSEUDOTSUGA MENZIESII* COMMUNITIES OF A WESTERN OREGON WATERSHED: BIOMASS DISTRIBUTION AND PRODUCTION BUDGETS[1]

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Abstract. Living biomass, organic matter distribution, and organic matter production budgets were determined for plant communities of a small watershed dominated by 450-yr-old *Pseudotsuga menziesii* (Mirb.) Franco forests. Dominant trees in the communities were large, up to 175 cm diam and 80 m tall.

Aboveground tree biomass of the various communities ranged from 491.8–975.8 tonnes/hectare, total aboveground living biomass ranged from 500.4–982.5 t/ha, total leaf biomass ranged from 10.4–16.3 t/ha and total organic matter accumulations ranged from 1,008.3–1,513.7 t/ha.

Total tree biomass in the various communities was more related to past mortality than habitat differences. Biomass of standing dead trees and fallen logs was generally inversely related to aboveground tree biomass. Amounts of woody detritus were large, ranging from 59.0–650.6 t/ha or 4.3%–43.0% of total community organic accumulation. Aboveground tree biomass increment was negative in all communities, ranging from −2.9 to −6.2 t/ha. Positive increment by shrubs and trees <15 cm dbh, produced overall aboveground biomass increment of −2.5 to −5.0 t/ha. Mortality averaged 1% of standing biomass.

Aboveground net primary production in the various communities ranged from 6.3 to 10.1 $t \cdot ha^{-1} \cdot yr^{-1}$ and was roughly proportional to standing biomass. Net primary production consisted entirely of detritus. Total community autotrophic respiration ranged from 102.9–203.7 $t \cdot ha^{-1} \cdot yr^{-1}$ of which ≈70% was by foliage. Gross primary production ranged from 111.2–216.8 $t \cdot ha^{-1} \cdot yr^{-1}$ of which only 6.0%–7.9% was net primary production. Net ecosystem production ranged from 0.12–5.6 $t \cdot ha^{-1} \cdot yr^{-1}$, entirely as an accumulation of woody detritus on the soil surface.

Available evidence indicates larger peak biomass in seral *P. menziesii* than in climax *Tsuga heterophylla* forests. These communities may be in the process of declining from seral peak to steady-state climax biomass.

Key words: Biomass; biomass regressions; coniferous forests; detritus; ecosystem study; forest structure; old-growth forests; Oregon; organic matter distribution; production budgets; Pseudotsuga menziesii.

INTRODUCTION

The primary objective of this study was to measure and compare biomass and production budgets of plant communities in the diverse habitats of a small watershed in the western Cascade mountains of Oregon. Vegetation of the watershed was dominated by a 450-yr-old Douglas-fir (*Pseudotsuga menziesii* [Mirb] Franco) forest; habitat differences were reflected in differences in understory species composition. Of specific interest were primary production, its distribution among the various species and vegetative strata, and the proportions of primary production accumulating as woody biomass or detritus.

Old-growth *Pseudotsuga* forests of the Pacific Northwest are among the largest and oldest forests in the world. Individual *Pseudotsuga* can live >1,000 yr (Franklin and Dyrness 1973) and old-growth stands of this species can have aboveground biomass in excess of 1,600 tonnes/hectare (Fujimori et al. 1976). In spite of its size and long life, *P. menziesii* is a pioneering tree species; over much of its range it is succeeded by the relatively short-lived climax species, *Tsuga heterophylla* (Franklin and Dyrness 1973). In the western Oregon Cascades the typical pattern of forest succession after disturbance is establishment of, and 100–200 yr of nearly total site domination by, *Pseudotsuga*, followed by gradual establishment of and increasing dominance by *Tsuga*. Thus, a second objective of this study was to examine production relations in some late-successional *Pseudotsuga* stands.

Most earlier studies of primary production by *Pseudotsuga* have been done in young, relatively pure stands (Heilman 1961, Cole et al. 1967, Riekerk 1967, Turner and Long 1975, Fujimori et al. 1976). In general, these studies indicated that, although primary production by stands of *Pseudotsuga* is relatively high, patterns of biomass accumulation in younger stands are similar to those described for other forest types (Odum 1969, Switzer and Nelson 1972, Marks 1974). However, beyond the first 100 yr of stand development, little is known of production or accumulation of biomass and detritus in *Pseudotsuga* forests.

The first 100 yr after tree establishment represent only a small part of the potential life-span of these forests. Thus, there has been a considerable gap in information about the relation between production and

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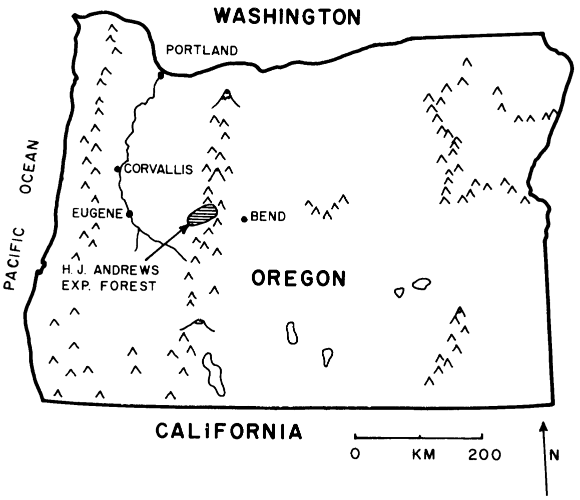

FIG. 1. Map showing location of H. J. Andrews Experimental Forest.

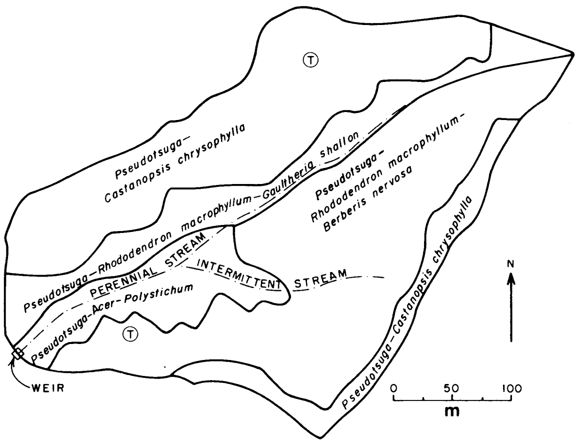

FIG. 2. Map of Watershed 10, H. J. Andrews Experimental Forest showing locations of major plant communities. Communities are named for dominant understory species. Circled "T" shows location of soil and air temperature recorder.

succession for *Pseudotsuga* forests in particular and temperate zone forests in general.

A number of researchers have proposed that biomass approaches a more-or-less stable "steady state" level as a forest approaches a climax vegetation state (Kira and Shidei 1967, Odum 1969, Whittaker et al. 1974). This pattern of biomass accumulation with time is normally shown as a smooth sigmoid function of age having steady state biomass as an asymptote. The idea behind these hypothetical curves is reasonable; biomass can accumulate only as long as there is a positive difference between net photosynthesis and woody tissue respiration. Accumulation of respiring woody tissue with age narrows this difference until at climax, biomass accumulation should be balanced by mortality. However, these ideas relating production and succession have been developed from studies of smaller forests in other parts of the world. For this reason, a final objective of this study was to see if primary production and biomass accumulation in these large, late successional forests of pioneering trees conformed to patterns proposed for forests in other parts of the world.

RESEARCH AREA

The study was conducted on Watershed 10 of the U.S. Forest Service, H. J. Andrews Experimental Forest in the western-central Cascade Mountains of Oregon (Fig. 1). The Andrews Experimental Forest is located at latitude 44°N, longitude 122°30′W, near the town of Blue River, Oregon.

Watershed 10 is a 10.24-ha research watershed on the western boundary of the Andrews Experimental Forest and is typical of the steep, deeply incised, small drainages in this part of the Cascades. Elevations range from 430 m at the stream gauging station to ≈670 m at the southeastern ridgeline. Average slope along the main stream is ≈24°; side slopes are much steeper, ranging between 25° and 50°.

The climate is relatively mild and constant compared to that of other temperate zone forests. Average annual precipitation is 2,300 mm with >75% of this precipitation falling as rain between October and March (Fredriksen 1972). Precipitation during the growing season is normally <300 mm. The growing season here is considered as the 5-mo interval between the beginning of *P. menziesii* bud-swell and the first full frost. Snow accumulations of ≤30 cm occasionally occur in winter months but these seldom last more than 2 wk. Based on 1970–1972 data averaged for 2 locations (Fig. 2) on the watershed, average daytime and nighttime air temperatures (measured 100 cm above the soil) for the watershed are respectively: January, +1°C and −1°C; July, 21°C and 16°C; and growing season, 16°C and 11°C. Observed temperature extremes have ranged from a high of 41°C in August 1972 to a low of −20°C in December 1972. Mean annual temperature is 8.5°C.

Soil and air temperatures of specific areas of the watershed are related to their topographic position. For example, average daytime air temperature and average soil temperature at a 29-cm depth were ≈1°C higher in July on upper south-facing slopes than on north-facing slopes or in areas along the stream draining the watershed. Average daytime air temperatures in January were relatively uniform across the watershed but 20-cm soil temperatures were ≈1°C higher on south-facing than on north-facing slopes. Mean annual incoming shortwave global radiation is 165W/m^2 and the growing season average is 247W/m^2.

Soils are generally deep and well drained. Rock outcrops occur in some locations along the streams and on steep sideslopes, mainly along south-facing slopes.

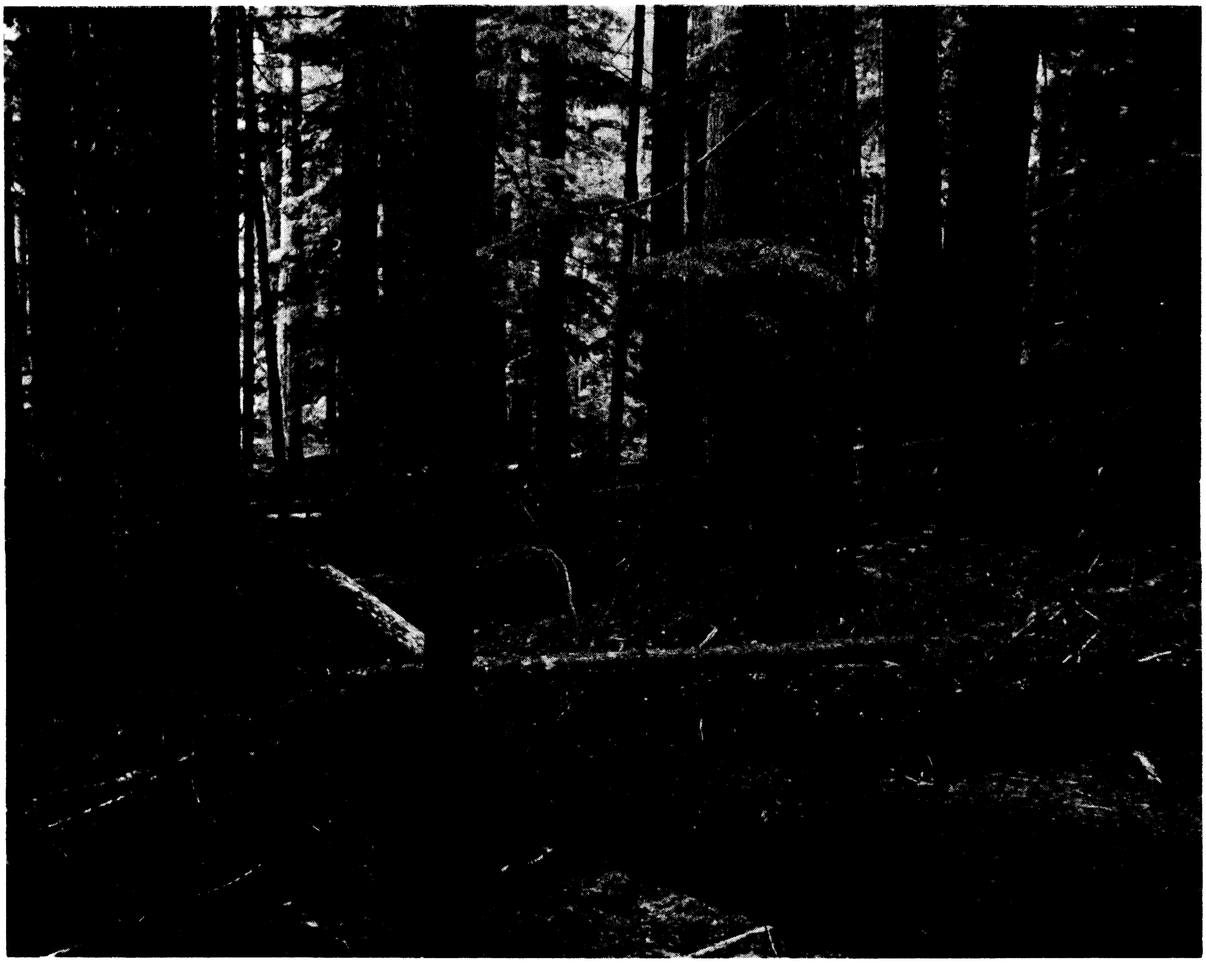

FIG. 3. Large numbers of fallen logs are present in most communities on Watershed 10.

Vegetation rooting is almost entirely in the upper 100 cm except in soils <100 cm deep near rock outcrops.

Soils are classified as typic distrochrepts (Soil Survey Staff, 1960) and characteristically have about 20 cm of a weakly developed *A*1–horizon overlying 50–80 cm of a weakly developed *B*1-*B*2-*B*3 sequence. Soil textures range from gravelly, silty clay loam to very gravelly, clay loam. The <2-mm particle fraction of these soils contains from 30% to 50% clay by weight and gravel content ranges from 15% to 50% of soil volume. All soils have granular structure at the surface becoming blocky to sub-angular blocky in the *B* horizon. Soil pH measured in a 1:1 soil-water mixture ranges from 5.9 to 6.3 in the *A*1-horizon and from 5.9 to 6.2 in the *B*1-*B*3 sequence. Bulk densities average 0.9 g/cm^3 throughout the *B*-horizon, *A*1-horizon values range from 0.7 to 1.0 g/cm^3. Soil data were provided by R. Brown (*personal communication*).

The average forest floor (*O*1 + *O*2–horizons excluding fallen logs) is ≈4 cm thick, although thickness is strongly influenced by vegetation and topography. These forest floors are classified as duff-mulls according to the classification system of Hoover and Lunt (1952). In addition, all communities have large numbers of fallen logs on the soil surface (Fig. 3).

The entire watershed is dominated by a 450-yr-old, site class II–III (Dilworth 1974) Douglas-fir (*Pseudotsuga menziesii*) forest. A range of different environments occurs within the old-growth forest of the watershed ranging from relatively hot and dry to cool and moist (Fig. 2). Local community structure and species distribution reflect these environmental differences.

Four major plant community types were identified on Watershed 10. In terms of temperature and summer moisture stress, these communities rank from the relatively xeric *Pseudotsuga–Castanopsis* (Fig. 4), through the warm-mesic *Pseudotsuga–Rhododendron–Gaultheria*, and mesic *Pseudotsuga–Rhododendron–Berberis* (Fig. 5), to the cool-moist *Pseudotsuga–Acer–Polystichum* plant communities. These communities were mapped and described on the basis of understory vegetation and formed the basic units used for description and comparison of biomass and production in this paper.

Major plant species present in the 4 major commu-

FIG. 4. Stand representative of the relatively xeric north slope *Pseudotsuga–Castanopsis* community on Watershed 10. Note the sclerophyllous tall shrub layer composed mainly of *Castanopsis chrysophylla* and *Rhododendron macrophyllum* and low shrub layer of *Gaultheria shallon*.

nity types and their percent cover are presented in Table 1. These data indicate some of the differences among communities, with respect to both understory vegetation and tree species associated with *Pseudotsuga* in the canopy. The relative dominance of different tree species is shown by the diameter distribution of these species (Table 2).

The following descriptions of the 4 major plant communities are intended to describe briefly differences among communities. Vegetation cover and basal area data are from Hawk (no date). For a description of survey methods see Dyrness et al. (1974).

The Pseudotsuga—Castanopsis *community*

The *Pseudotsuga–Castanopsis* community has developed in the hot-dry environments of ridgetops and upper south-facing slopes (Fig. 2). Overstory vegetation consists primarily of a canopy of *P. menziesii* with a dense shrubby understory primarily of *Castanopsis chrysophylla* (Table 1). The xeric nature of this habitat is reflected in the predominance of sclerophyllous evergreen hardwood genera, such as *Castanopsis*, *Rhododendron*, and *Gaultheria* in the various understory strata (Table 1, Fig. 4). Basal area of trees >15 cm dbh in this community averages 75 mm^2/ha.

Summer water stress in this community is higher than observed in other plant communities of the watershed. Late-summer predawn moisture stress values (Waring 1969) average ≈18 bars [= 1,800 kilopascals] (Zobel et al. 1976). As previously noted, summer temperatures are higher in this community than in others on the watershed.

The *Pseudotsuga–Castanopsis* community occupies 37.1% of the area of Watershed 10 and contains few inclusions of other community types.

Pseudotsuga—Rhododendron—Gaultheria *community*

This warm-mesic community type is found primarily along the lower third of the south-facing slope of

TABLE 1. Principle species and their percent cover in major plant community types of Watershed 10, H. J. Andrews Experimental Forest, Oregon. Plant species and cover data are assembled from an unpublished report by Hawk (see Literature Cited)

	Percent cover			
Species	*Pseudotsuga—Castanopsis* (Xeric)	*Pseudotsuga—Rhododendron—Gaultheria* (Warm mesic)	*Pseudotsuga—Rhododenron—Berberis* (Mesic)	*Pseudotsuga—Acer—Polystichum* (Cool–moist)
Overstory tree stratum				
Acer macrophyllum	0	1	0	0
Pinus lambertiana	0	2	0	0
Pseudotsuga menziesii	36	45	45	49
Thuja plicata	0	3	13	21
Tsuga heterophylla	7	20	45	0
Understory tree stratum				
Acer macrophyllum	0	0	0	2
Castanopsis chrysophylla	27	3	0	0
Cornus nuttallii	4	13	3	1
Pinus lambertiana	1	0	0	0
Pseudotsuga menziesii	5	0	0	0
Taxus brevifolia	0	4	4	5
Thuja plicata	0	1	2	7
Tsuga heterophylla	4	8	8	7
Tall shrub stratum				
Acer circinatum	14	26	12	36
Rhododendron macrophyllum	39	44	6	4
Vaccinium parvifolium	0	1	2	1
Low shrub stratum				
Berberis nervosa	4	9	7	9
Gaultheria shallon	26	19	2	3
Herb stratum				
Chimaphila umbellata	0	2	1	0
Coptis laciniata	0	0	5	13
Linnaea borealis	3	2	18	3
Polystichum munitum	0	1	2	20
Rubus nivalis	0	0	1	0
Rubus ursinus	0	0	0	0
Trillium ovatum	0	0	0	1
Vancouveria hexandra	0	0	0	1
Viola sempervirens	0	0	2	3
Whipplea modesta	0	0	0	0
Xerophyllum tenax	7	3	0	0
Total cover value	177	207	178	186

the watershed (Fig. 2) and as patchy inclusions in the *Pseudotsuga–Rododendron–Berberis* community. Total plant cover here is greater than in any other plant community on Watershed 10 (Table 1). As in the *Pseudotsuga–Castanopsis* community, sclerophyllous evergreen species such as *Rhododendron* and *Gaultheria* are a major component of the shrubby strata and the herb layer is a relatively minor component. Tree basal area (trees >15 cm dbh) is 76 m²/ha.

Summer temperatures in this community average ≈0.5°C cooler than in the adjacent *Pseudotsuga–Castanopsis* type and predawn moisture stress values average around 15 bars [= 1,500 kPa] during late summer.

The *Pseudotsuga–Rhododendron–Gaultheria* community occupies 13.6% of the watershed area.

Pseudotsuga—Rhododendron—Berberis *community*

This community occupies mesic habitats of north- and northwest-facing slopes (Fig. 2). Overstory tree cover is denser here than in other communities on the watershed (Table 1) and for this reason, understory tree and shrub layers are sparse compared to the *Pseudotsuga–Castanopsis* or *Pseudotsuga–Rhododendron–Gaultheria* communities (Fig. 5). The understory tree and shrub layer consists primarily of shade tolerant species such as *T. heterophylla*, *Taxus brevifolia*, and *Acer circinatum*. A well-developed herb layer is present. Tree basal area is ≈75 m²/ha.

Summer air temperatures in this community are generally about 1°C cooler than in the *Pseudotsuga–*

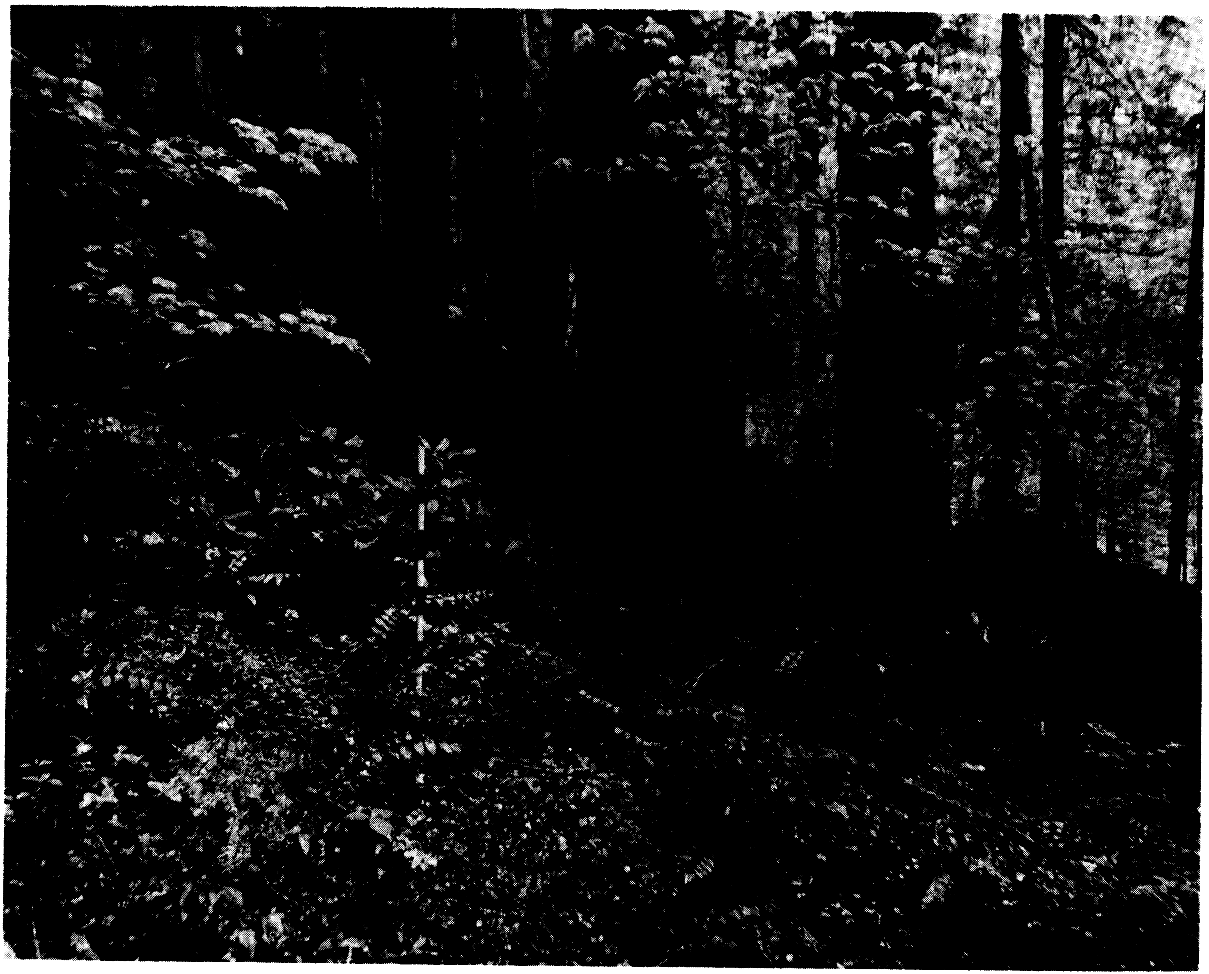

FIG. 5. Stand representative of the more mesic *Pseudotsuga–Rhododendron–Berberis* community of Watershed 10. Note the relatively sparse understory in this community dominated primarily by *Rhododendron macrophyllum* and *Berberis nervosa* but with some *Acer circinatum* and *Polystichum munitum* present. The large tree in the middle of the photo is ≈150 cm dbh. Small stems scattered through stand are climax *Tsuga heterophylla*.

TABLE 2. Size class distribution of trees on Watershed 10, H. J. Andrews Experimental Forest, Oregon. Abbreviations are as follows: PSME = *Pseudotsuga menziesii*; TSHE = *Tsuga heterophylla*; CACH = *Castanopsis chrysophylla; THPL* = *Thuja plicata*; PILA = *Pinus lambertiana*; LIDE = *Libocedrus decurrens*; ACMA = *Acer macrophyllum*; TABR = *Taxus brevifolia*; CONU = *Cornus nuttallii*; ALRU = *Alnus rubra*; ARME = *Arbutus menziesii*; ACCI = *Acer circinatum*

Size class (cm)	Tree species											
	PSME	TSHE	CACH	THPL	PILA	LIDE	ACMA	TABR	CONU	ALRU	ARME	ACCI
15–30	408	559	524	65	34	1	113	53	26	2	1	1
30–45	95	210	8	42	11	2	15	12		1		
45–60	29	64		16	11	2	1					
60–75	37	15		8	4	2						
75–90	53	4		5	3							
90–105	82	4			2	2						
105–120	119			2	2							
120–135	88				2							
135–150	58											
150–165	19											
165–180	8											
Total	996	856	532	138	69	9	129	65	26	3	1	1
Grand total = 2,825 trees												

Castanopsis type and late summer predawn moisture stress averages about 12 bars [= 1,200 kPa].

The *Pseudotsuga–Rhododendron–Berberis* community occupies 39.1% of the watershed area and contains inclusions of *Pseudotsuga–Rhododendron–Gaultheria* and *Pseudotsuga–Acer–Polystichum* communities amounting to ≈10% of its area.

Pseudotsuga—Acer—Polystichum *community*

This community has developed in relatively shallow soils along the lower portion of the stream system of Watershed 10 (Fig. 2). Overstory tree canopy density here is less than in adjacent communities (Table 1). The understory shrub stratum of this community is well developed and together with the understory tree and herb strata is composed of relatively shade tolerant, relatively non-sclerophyllous species such as *A. circinatum* (Table 1). Tree basal area averages 70 m^2/ha, lower than in other communities on Watershed 10.

The *Pseudotsuga–Acer–Polystichum* community occupies the coolest and wettest part of Watershed 10. Air temperatures here are ≈0.5°C cooler and soil temperatures are ≈1°C cooler than those of the *Rhododendron–Berberis* type. Because of topographic position, subsoil water from deeper soils higher on the side slopes moves into the vegetation rooting zone throughout the year. For this reason, summer predawn moisture stress is seldom >10 bars [= 1,000 kPa].

The *Pseudotsuga–Acer–Polystichum* community is relatively homogeneous and occupies 10.1% of the watershed.

METHODS

Forest survey

As preparation for this study a 25- × 25-m grid was surveyed on Watershed 10 during 1971; grid corners were marked with aluminum stakes. This grid system was used as a position reference for vegetation and soil surveys of the watershed. Maps prepared from these surveys provided a descriptive basis for dividing the watershed into areas of relatively homogeneous vegetation (Fig. 2).

In October and November 1971, all tree stems on the watershed with dbh (breast height diameter outside bark) >15 cm were numbered, tagged, and measured to the nearest 0.1 cm for trees 15–50 cm dbh and to the nearest 1.0 cm for trees >50 cm dbh. Species, major community type, and location relative to the grid system (±1 m) were recorded for each tree. At the same time the location, large end diameter, and height or length of all standing dead trees and fallen logs were recorded. Tree measurement data were used to prepare a computer file of location, diameter, and species of all trees in each community type on the watershed.

Increment cores were taken from 440 trees representing the range of diameter classes in each species. Diameter class intervals were 10 cm for trees 15–95 cm dbh and 20 cm for trees >95 cm dbh.

During the summer of 1973, all trees on the watershed were checked to determine mortality since 1971.

Field sampling

With the exception of aboveground tree and shrub biomass sampling, all field sampling was designed to estimate biomass, productivity, and litterfall of each community of the watershed. Destructive sampling for tree and shrub biomass determination was done by species instead of community type and was conducted in comparable communities adjacent to the watershed.

Aboveground tree biomass.—Aboveground tree biomass was estimated from regressions of new and total foliage, live branch, dead branch, stembark, and stemwood dry weight on stem diameter. Because of the number of tree species, the large range of diameters of some species, and their varied morphological characteristics, separate sets of regression equations were developed for the 5 major species on the watershed.

In all, 61 trees of the major species of the watershed were destructively sampled to determine component dry weights. Trees selected for sampling were considered to be of average vigor. Altogether, 18 *Acer macrophyllum*, 19 *C. chrysophylla*, 16 *P. menziesii*, 5 *Pinus lambertiana*, and 2 *Thuja plicata* were sampled. All but the sampled *P. menziesii* were representative of the size range of these species on Watershed 10. Considerable data of component dry weight of smaller-sized (2 cm–23 cm dbh) *P. menziesii* were available from published sources (Heilman 1961; Dice 1970). For this reason, sampling of *Pseudotsuga* for this study was restricted to those diameter classes present on Watershed 10 for which there were no reported data. A portion of the sampling of *Pseudotsuga* was done as part of a separate study. These data are summarized by Fujimori et al. (1976). Data of the full size range of *T. heterophylla* were available from Kurmlik (1974) and T. Fujimori (*personal communication*).

Some average physical characteristics of trees used in computing tree biomass regressions are given in Table 3. These data include, under separate headings, data of trees sampled for this study and those obtained from other sources. In all cases, the largest individual of each species sampled was near the diameter of the largest representative of that species on the watershed. Sampling of *T. plicata* was done so that results of the *T. heterophylla* regressions used for this species could be adjusted for its different wood density, wood:bark ratios, and the photosynthetic twigs.

Logarithmic regressions of new foliage, total foliage, dead branch, live branch, stem wood, and stem bark dry weight on diameter (breast height) were calculated from individual tree data. Regressions were then corrected for logarithmic bias using the procedure de-

TABLE 3. Some physical characteristics of sample trees used in computing dry weight regressions for species on Watershed 10. Data from literature sources (‡) are presented separately from those obtained by sampling areas adjacent Watershed 10 (†)

	Pseudotsuga menziesii (†)	*Pinus lambertiana* (†)	*Thuja plicata* (†)	*Castanopsis chrysophylla* (†)	*Acer macrophyllum* (†)	*Pseudotsuga menziesii* (‡[a])	*Tsuga heterophylla* (‡[b])
Linear dimensions							
No. of trees	19	5	2	19	18	10	18
$\bar{x}$ dbh (cm)	73.1	28.8	32.3	16.9	20.4	13.4	18.3
Diam range sampled (cm)	25.9–163	20.6–43.3	23.2 & 41.4	5.8–36.0	7.6–35.3	2.3–22.6	2.1–49.0
$\bar{x}$ height (m)	53.0	16.7	19.7	10.7	20.6	...	15.4
Height range sampled (m)	34.6–76.5	13.0–26.6	15.5 & 23.9	4.1–17.4	9.6–32.4	...	5.4–27.7
$\bar{x}$ terminal shoot elongation (cm)	6.2	15.3	14.5	13.0	12.2	...	...
$\bar{x}$ radial wood increment at breast-height (mm)	0.8	2.5	2.5	1.5	1.6	...	...
$\bar{x}$ bark thickness at breast-height (cm)	2.12	1.40	0.44	0.65	0.59	...	...
Mean dry weights (kg)							
Stem wood	4,616.5	172.6	277.8	66.1	157.4	54.7	148.4
Stem bark	595.0	37.3	22.7	21.2	32.1	8.4	16.5
Living branches	350.1	39.2	72.6	23.6	29.6	6.2	45.0
Dead branches	39.9	4.5	10.9	4.3	2.2	3.7	6.1
Total foliage	78.4	19.2	15.4	6.4	3.3	4.1	9.6
Current year's foliage	15.5	3.9	3.8	1.1	3.3	0.9	2.7

[a] Dice (1970).

[b] Fujimori, unpublished data summarized by Fujimori (1971); Krumlik (1974).

scribed by Baskerville (1972). Arithmetic confidence limits for tree biomass estimates were computed using procedures outlined by Baskerville (1972).

Component biomass of trees sampled during this study was determined by felling the tree and using the following procedure. Stem length was measured and points at 1.3 m above the soil surface, the midpoint of the unbranched main stem, a point 5 cm below the first live primary branch, and the midpoint of the crown were marked on the main stem. The main stem was cut into sections at these points, the distance between these points was measured, and a stem cross-section was cut from the bottom of each stem section. Stem diameter inside and outside bark, wood radial increment thickness for the past 5 yr, and sapwood thickness were measured on each stem cross-section along the shortest and longest radii of that section. The entire cross-section, or for the larger trees, a wedge-shaped piece of stem cross-section from pith to outside bark was taken for wood and bark density and wood:bark ratio determinations. The crown was divided into thirds along the main stem. All live and dead branches originating in each section were removed and except for *A. macrophyllum* all twigs having attached foliage were clipped from branches. Leaves and petioles were removed individually from *A. macrophyllum* twigs. Epicormic and dead branches below the main canopy were included as part of the lowest ⅓ of the canopy. Fresh weights of living and dead branches and foliage plus twigs (or foliage) in each section of the canopy were determined on spring scales or beam balances to the nearest 100 g. Representative subsamples of these components were weighed in the field to the nearest 1.0 g then returned to the laboratory for determining H_2O content at 105°C. Subsamples from small trees were normally heat-killed within 24 h and those from the largest trees within 4 days of felling. Samples were subject to whatever respiration loss occurred in this period (Forrest 1968).

In the laboratory, wood and bark densities of stem cross-sections were determined by a water immersion weighing method (Forest Products Laboratory 1952) using green volumes and ovendry weight. Stem wood and stem bark volumes were computed using Smalian's formula (Husch 1963) and field measurements of stem dimensions. Stump wood and bark volume was computed as that of a cylinder using wood and bark radius at dbh, then multiplying the cylindrical volume by 1.3 to account for butt-swell. Bark and wood volumes of a stem section times bark and wood density of the stem cross-section at the base of that stem section gave dry weight of stem wood and stem bark for larger trees. Dry weights of smaller stems were calculated from field weights and stem cross-section fresh weight:dry weight ratios. Bark and wood weights of smaller trees were computed from the bark cross-section dry weight:stem cross-section dry weight ratios and the dry weight of stem sections above each stem cross-section.

Live and dead branch dry weights were computed from field weights and the fresh weight:dry weight ratios determined for each third of the canopy of each sample tree.

Foliage dry weight of all trees was determined individually for each third of each tree canopy, then summed to obtain total amount. Foliage dry weight of *A. macrophyllum* was computed from the leaf fresh weight:dry weight ratios and field leaf weights. For conifers (except *T. plicata*) and *C. chrysophylla*, leaf plus twig samples were separated into current and older foliage plus twigs, weighed, dried, separated into current foliage, current twigs, older foliage, and older twigs, then reweighed. The following ratios were computed for each subsample and used sequentially to estimate dry weights of current and older foliage and current and older twigs for each tree: (1) dry weight of total foliage plus twigs/fresh weight, (2) dry weight of current foliage plus twigs/dry weight of total foliage plus twigs, (3) dry weight of current foliage/dry weight of current foliage plus twigs, and (4) dry weight of older foliage/dry weight of older foliage plus twigs. *Thuja plicata* foliage and twigs were not separated since leaf-bearing twigs of this species are photosynthetic. Otherwise, foliage dry weights for this species were determined in the same way as for other conifers.

An independent check on regression estimates of stem biomass was provided by a U.S. Forest Service scaling of logs removed when Watershed 10 was clearcut in June–July 1975. All logs removed were scaled on trucks at the U.S. Forest Service, Blue River log scaling station using scaling standards defined by the Columbia River Log Scaling and Grading Bureau, Portland, Oregon (Dilworth 1974). Larger logs in cull piles were also scaled using the same methods. Measurements included log length to the nearest 2.54 cm and log small and large end diameter, inside and outside bark, to the nearest 2.54 cm. Also, tree species and an estimate of log volume affected by decay was recorded.

These direct measurements of wood and bark volumes by log scale included about 80% of tree biomass on the watershed because most stem biomass on the watershed was in large stems. Log volumes were converted to biomass using average wood and bark densities of the various species. Log volumes were not obtained for individual communities.

Aboveground small tree, shrub, and herb biomass.—Biomass and biomass increment of trees <15 cm dbh and shrub and herb strata were determined by Russell (1974). Values reported in this paper are averages computed from this more detailed study; methods used by Russell are briefly described here.

Biomass and biomass increment were determined on variable-sized plots centered on trees >15 cm dbh. Plots were established in each of the 4 major community types; 11 plots were located in the *Pseudotsuga–Castanopsis* and 4, 6, and 12 plots, respectively, were located in the *Pseudotsuga–Rhododendron–Gaultheria, Pseudotsuga–Acer–Polystichum*, and *Pseudotsuga–Rhododendron–Berberis* communities. Sides of plots were formed by extending lines at right angles from points bisecting base lines drawn between a chosen tree and its nearest neighbors. These lines form a closed "polygon of occupancy" (Overton et al. 1973); polygons centered on all trees would cover the entire watershed with no overlap. Plot size ranged from 9.8 to 162.2 m^2 and averaged 60.7 m^2. Plots were centered around trees drawn randomly from the >15-cm-dbh tree population of each community. Details of plot layout and statistical design are given by Russell (1974) and Overton et al. (1973).

Large and small shrub and herb strata were defined on the basis of species rather than size; species included in each stratum are listed in Table 1.

Basal diameters and lengths or heights of stems of all large shrubs (Table 1) and trees <15 cm dbh on each plot were measured and recorded. Measurements of small shrubs and herbs (Table 1) were made in subplots placed on transects between plot center and polygon corners, and plot center and the midpoint of each polygon side. Subplots were 20 cm × 50 cm. There were 4 evenly spaced subplots per transect and 4–8 transects per polygon. In each subplot, ground-level diameters and stem lengths of all stems of small shrubs were measured. Percent cover of herbs was estimated in each subplot using the unequal-size cover class method given by Daubenmire (1968).

Biomass and productivity of the small tree, shrub, and herb strata of Watershed 10 were estimated using the nondestructive measurements described above, together with regressions of stem and/or leaf biomass and productivity on either stem or plant diameter at the soil surface (dgh), (dgh)^2 × stem length, or estimated percent cover.

The regression equations were prepared from data of destructive sampling of shrub and herb layer species in comparable areas adjacent to the watershed. Details of procedures used in developing regressions are provided by Russell (1974).

Root biomass.—Coarse root biomass (>5 mm diam) for all species on Watershed 10 was estimated using regression equations of coarse root and root crown biomass on stem diameter. For trees 15–50 cm dbh, regressions were calculated from data in this size range reported by Dice (1970) and unpublished data summarized by Riekerk (1967). For trees >50 cm dbh, regressions based on trees 94–135 cm dbh were used (Santantonio et al. 1977). Coarse root biomass of trees <15 cm dbh and large shrubs was calculated from the small tree regression described above, and stem diameters measured on the irregular polygons by Russell (1974).

Fine root (<5 mm diam) biomass was determined by Santantonio et al. (1977). Fine root biomass was estimated by separating fine roots from soil cores taken in the 4 major plant communities. Soil cores for fine root estimates were obtained from 22 of the 33 irregular polygons described earlier. Sampling polygons were distributed so that about the same proportion of each community was sampled; 8 polygons were located in the *Pseudotsuga–Castanopsis* and 2, 4, and 8, respectively, were located in the *Pseudotsuga–Rhododendron–Gaultheria, Pseudotsuga–Acer–Polystichum,* and *Pseudotsuga–Rhododendron–Berberis* communities. An average of 18 5-cm-diam cores per plot were removed along transects from plot center to the midpoint of each side. These cores were obtained using a hammered core-sampler which removed a 100-cm deep core. Soil cores were taken in late August and September 1972, during the period of summer drought.

Details of methods used in estimating fine root biomass are provided by Santantonio et al. (1977). Roots of small shrubs and herbs were included in fine root biomass estimates.

Forest floor, logs, and soil organic matter.—In this study, the forest floor and large woody detritus such as standing and fallen dead trees were treated as separate components of the ecosystem. This was primarily to facilitate estimating their dry weights. Forest floor was defined as the $O1 + O2$ horizons including woody material <15 cm large end diam. The standing and fallen dead trees category included all woody detritus ≥15 cm diam.

Forest floor material was sampled at 65 locations on the watershed. Sampling points were located at regular intervals prior to sampling so approximately the same proportion of each community type was sampled. Samples were removed using a circular cutting frame held perpendicular to the slope. Slope of the forest floor surface was recorded for each sampling point. All organic matter within the sampling frame was removed either to the surface of the mineral soil or to the point where living roots were encountered. Rooting appeared confined to mineral soil horizons except in highly decomposed logs. Those logs in which plants were rooted were treated as soil and sampled during soil sampling.

All forest floor samples were dried to moisture equilibrium at 65°C for later chemical analysis. Dry weights at 65°C were corrected to dry weight at 105°C using data from subsamples subsequently redried at the higher temperature.

Ash-free dry weight of forest floor material was determined by weight loss on ignition. Samples were ground to pass through a 40-mesh screen and mixed thoroughly. A 6-g (at 105°C) sample of ground material was ignited at 450°C and reweighed. Computed ash content was then used to calculate ash-free dry weight of each sample. This step was necessary because field samples contained large amounts of soil and gravel. Finally, forest floor dry weights were adjusted to horizontal measure using slope measurements made during field sampling.

Dry weight of standing dead and fallen logs was estimated by computing volumes from large end diameter and length. A normal taper of 1–50 was assumed and used to compute small end diameter. Volumes were computed using Smalian's formula (Husch 1963); dry weight was then calculated using an average density of 0.38. This density was obtained by averaging the mid-stem cross-sectional density of 10 fallen and 5 standing dead trees. Cross-sectional densities were determined using a water immersion weighing method (Forest Products Laboratory 1952).

Soil sampling locations were randomly chosen from among those locations where forest floor was sampled; four pits were dug in the *Pseudotsuga–Castanopsis* and 2, 2, and 4 pits, respectively, were dug in the *Pseudotsuga–Rhododendron–Gaultheria*, *Pseudotsuga–Acer–Polystichum*, and *Pseudotsuga–Rhododendron–Berberis* communities. Samples were removed from the 0–20-cm and 20–100-cm depths of the soil profile. These depths corresponded to averaged thickness of the $A1$ and $B1 + B2 + B3$-horizons, respectively. Samples were dried at 65°C and ground to pass a 40-mesh screen. Organic matter was determined on duplicate samples using the Walkley-Black procedure (Jackson 1958). Soil organic matter was computed using the analytical results, bulk densities, and gravel and stone contents determined at the respective sampling locations to express soil organic matter on a volumetric basis.

Litterfall and leaching.—Litterfall was collected on 65 traps located at regular intervals on the watershed so that about the same proportion of each of the major plant communities was sampled. Eleven of these traps were placed directly above the permanent stream of the watershed. The stream traps provided litterfall data both for this study and a concurrent study of carbon processing by the stream biota (Sedell et al. 1974). Traps placed above the stream were square, with 1.0-m² surface area and were mounted ≈20 cm above the stream surface. The remaining 54 traps were square, with 0.26-m² surface area; the trap surface was ≈10 cm above the soil surface. All litter traps were lined with approximately 150 mesh (i.e., 0.1-mm holes) nylon fabric. Trap liners were changed at each collection.

Litterfall collections were made monthly except when snow occasionally prevented locating the screens. Litter was dried at 65°C, removed from the nylon liners, and separated into the following components: conifer needles; hardwood leaves; twigs, branches, and other woody material; reproductive parts; living branchlets removed by mechanical damage (live litter); and miscellaneous material (frass, epiphytes, insect parts, etc.). Dry weight of total litter was determined monthly for each screen. Dry weight of litterfall components in each community type was obtained by combining specific components from all traps in each community and determining total weight. During sorting, an estimate of proportions of frass relative to the total weight of the miscellaneous category was made to provide an estimate of herbivore consumption. Dry weights at 65°C were corrected to dry weight at 105°C using data from subsamples of each component subsequently redried at the higher temperature.

Throughfall was collected in 65 collectors located adjacent to each litter trap. Collectors were 20-cm-diam polypropylene funnels fitted with a plastic screen (approximately 150 mesh) ≈10 cm below the funnel mouth. Funnels were inserted in opaque polyethylene 19-l bottles. Throughfall collections were made monthly or as necessary to avoid overflow. Litter accumulating in the funnels was removed at each collection and often at 2-wk intervals to minimize leaching of organic matter from litter accumulated in the funnels. Reported values of organic matter in throughfall are probably underestimates due to respiration losses between collections.

Stemflow was collected from 15, 10-m × 10-m plots in which each stem >5 cm dbh was fitted with a polyurethane stemflow collar at breast height (Likens and Eaton 1970). Five stemflow plots were located in the *Pseudotsuga–Castanopsis* and 2, 3 and 5 plots were located in the *Pseudotsuga–Rhododendron–Gaultheria*, *Pseudotsuga–Acer–Polystichum*, and *Pseudotsuga–Rhododendron–Berberis* communities, respectively. On each plot, water was piped from the collars to a group of opaque 125-litre polyethylene trash cans fitted with tight lids. Collections were made as necessary to avoid overflow with a maximum interval of 1 mo. Again, respiration losses of organic matter were not determined.

Concentrations of dissolved organic matter in water percolating from the rooting zone were determined in soil solution samples extracted from the soil profile at the 1-m depth using cup lysimeters. The lysimeters were installed in 2 plots with 6 lysimeters per plot. One plot was located in the *Pseudotsuga–Castanopsis* community and one in the *Pseudotsuga–Rhododron–Berberis* community. Soil solution data were provided by F. L. Glen (*personal communication*). Organic matter leaching was estimated from the above data and 1972–1973 streamflow volume, (R. Fredriksen, *personal communication*) assuming that streamflow was equal to water volumes percolating past the 1-m soil depth.

Dissolved organic matter concentrations in throughfall, stemflow, and soil leachates were determined using methods described by Golterman (1971).

Computation procedures

Biomass and biomass increment.—Logarithmic regressions of foliage, live branch, dead branch, stem wood, and stem bark dry weight on diameter (breast height) were computed for *P. menziesii*, *P. lambertiana*, *T. heterophylla*, *A. macrophyllum*, and *C. chrysophylla*. Tree biomass was computed using these regressions and diameter and species data obtained during the forest survey. Regressions for major species were applied to minor species as follows: regressions for *Pseudotsuga* were used for *Libocedrus decurrens; Tsuga* for shade tolerant conifers (*T. plicata* and *T. brevifolia); Acer* for deciduous hardwoods (*Cornus nuttallii* and *Alnus rubra*); and *Castanopsis* for evergreen hardwoods (*Arbutus menziesii*). Except for *Thuja*, species for which regressions were substituted constituted a small proportion of plant communities on the watershed. *Thuja plicata* made a significant contribution to plant cover in several community types. Results of destructive sampling of this species were used to check results of regressions applied to this species.

Annual biomass accumulation or growth of stems and branches of surviving trees was calculated by difference for each community type. Radial stem increment averaged over the current 5-yr period was computed for each diameter class of each species from wood increment core data using ΔBark + ΔWood = ΔWood × (radius outside bark at dbh) ÷ (stem wood radius at dbh). Tree biomass in each community type was then recomputed using stem diameters to which the appropriate average annual radial increment had been added. Annual biomass accumulation was then estimated by subtracting the initial biomass estimate from the estimate having increment added.

Biomass increment (ΔB) was computed by subtracting mortality from biomass accumulation. Biomass of annual mortality was calculated by summing live branch, stem wood, stem bark, and coarse root biomass of observed mortality as computed from biomass regressions for that species.

Annual foliage production by trees and understory was estimated both from measurement of leaf litterfall and from regressions of leaf production on stem diameter for each species.

Dry matter production by the herb layer was the difference between June and January estimates of herb layer biomass. Clipping measurements of herb layer biomass were made in June 1974, the seasonal peak of herb layer biomass in these forest types, and again in January 1975, the seasonal low point in herb layer biomass. For both determinations, herbs were clipped from 14 randomly located 0.1-m^2 plots in each community type.

Coarse root production was estimated for each community type by multiplying total coarse root biomass by the ratio of total aboveground stem and branch dry matter production to total aboveground stem and branch biomass.

Fine root production and death were estimated to be 20% of fine root biomass per year. These estimates were based on the assumptions that: (1) the same proportionality existed between foliage production and foliage biomass as between fine root production and fine root biomass, and (2) on an annual basis, fine root biomass did not change.

Contribution to litterfall by the herb layer was estimated by assuming that annual herb layer production became litterfall during October.

Leaf area of the various tree strata were computed using leaf dry weight to surface area conversions reported for these species by Gholz et al. (1976).

Respiration.—Yearly respiration in plant communities of Watershed 10 was estimated by summing daytime and nighttime respiration of tree components computed on a daily basis for 1 yr. Mean daytime and nighttime soil (20-cm depth) and air (100 m above soil) temperatures for 1974 were computed by integrating continuous temperature measurements made in the *Pseudotsuga–Castanopsis* and *Pseudotsuga–Acer–Polystichum* communities. Temperature data were recorded on Partlow, two-pen thermographs as described by Zobel et al. (1976). Day and night length were computed using a standard sine function approximation which calculated day length at this latitude as a function of Julian date. Hourly respiration of plant tissues at mean daytime and nighttime temperature was computed from published values of respiration using a Q_{10} value of 2.0 (Tranquilini and Schütz 1970). Daytime and nighttime hourly rates were then multiplied by day and night length and summed for each day of the year. Air temperature was used for aboveground and soil temperature for belowground stand components. Temperatures measured in the *Pseudotsuga–Castanopsis* community were used for the *Pseudotsuga–Rhododendron–Gaultheria* community, temperatures measured in the *Pseudotsuga–Acer–Polystichum* community were used in the *Pseudotsuga–Rhododendron–Berberis* community.

Amounts of respiring tissue and respiration data were obtained as follows: stem respiration was computed from conic bark surface area (Whittaker and Woodwell 1967) and bark respiration data for *Picea abies* measured during October (Tranquilini and Schütz 1970). Respiration of branches without foliage (>0.5 cm) was computed from regression estimates of branch dry weight, after deducting 5% of dry weight for branches with attached foliage, and data of branch respiration as related to dry weight for *P. abies* (Tranquilini and Schütz 1970), for a weighted average branch diameter of 5 cm. Dry weight of twigs and attached foliage was computed from regression estimates of leaf weight plus 5% of branch dry weight to account for foliage-bearing twigs. This was used with night respiration of Douglas-fir twigs plus foliage measured at 20°C (Brix 1971) to compute foliage and small twig respiration. Daytime twig and foliage respiration was assumed to be exponentially proportional to night respiration as a function of temperature. Seasonal fluctuations in leaf biomass were computed by adopting the convention that new foliage appeared, fully expanded, on 15 May and all leaf litterfall took place on 31 October. Coarse root respiration (>5 mm) was computed from dry weight estimates using the same tissue respiration rate as for branches. Fine root respiration was estimated from dry weight and respiration rates for *Liriodendron tulipifera* computed using procedures described by Sollins et al. (1973).

In this estimation procedure, no attempt was made to account for increased respiration during active growth (Tranquilini and Schütz 1970) or reduced respiration during periods of water stress.

RESULTS

Regression equations

Regression equations used in estimating tree biomass for the communities of Watershed 10 are given in Table 4. Slopes of regressions were tested for differences among species using procedures outlined by Husch (1963). Differences, significant at the 99% level, were found between slopes of regressions for stem wood, stem bark, living branches, total foliage, and new foliage for all species. Slopes of regressions for dead branches were not significantly different between *P. menziesii* and *T. heterophylla*. However, there were differences significant at the 99% level between slopes of equations for *C. chrysophylla* and *A. macrophyllum*, and between *A. macrophyllum* or *C. chrysophylla* and either *P. menziesii, T. heterophylla* or *P. lambertiana*.

Differences in component biomass among species are shown in a more comparable form in Table 5. There were large differences among species for stemwood and stembark biomass. These differences were due to a combination of differing bark:wood ratios, differing wood densities, and greater height:diameter ratios for *Pseudotsuga* than other conifers, and for conifers in general than for hardwoods. Living branch biomass of *Tsuga* was greater than that of the other species. Leaf biomass of conifers differs by as much as 12.9 kg among species for a 35-cm-dbh tree while all conifers and *Castanopsis* had greater leaf biomass than *A. macrophyllum*. Leaf area of *Tsuga* is large relative to the other species, but that of *Pinus* is between *Tsuga* and *Pseudotsuga*. Leaf area of *Castanopsis* was less than that of *Pseudotsuga*, but leaf area of *A. macrophyllum* was lower than that of all evergreen species.

Tree biomass

There were large differences in tree biomass among the different community types of the watershed (Table 6). Tree biomass was lowest in the *Pseudotsuga–Rhododendron–Gaultheria* community and highest in the *Pseudotsuga–Castanopsis* community along the south ridgeline of the watershed (Fig. 2). Aboveground tree biomass of the south ridge *Pseudotsuga–Castanopsis* community was 1.5× greater than that of the north slope *Pseudotsuga–Castanopsis* community. This was in spite of similarities of plant cover observed during vegetation mapping of the watershed. Be-

TABLE 4. Regressions of tree component dry weight on stem diameter for major tree species of Watershed 10, H. J. Andrews Experimental Forest, Oregon. Equations are of the form $Y = \exp(A + B \ln_e X)$ where X is stem diameter at dbh (cm) and Y is component dry weight (kg). Values of the Y intercept (A) are corrected for logarithmic bias. Columns headed N, r^2 and $S^2_{y \cdot x}$ show number of individuals included in regression, correlation coefficient, and mean square residual (Husch 1963), respectively

Component	A	B	N	r^2	$S^2_{y \cdot x}$
Pseudotsuga menziesii					
Stem wood	−2.656	2.530	29	0.99	0.088
Stem bark	−4.108	2.390	29	0.99	0.083
Living branches	−4.786	2.389	29	0.97	0.188
Dead branches	−2.455	1.400	17	0.86	0.530
Total foliage	−4.151	1.982	29	0.96	0.176
Current year's foliage	−5.888	2.039	29	0.93	0.323
Tsuga heterophylla					
Stem wood	−2.172	2.257	18	0.99	0.014
Stem bark	−4.373	2.258	18	0.99	0.019
Living branches	−5.149	2.778	18	0.98	0.177
Dead branches	−2.409	1.312	18	0.62	0.641
Total foliage	−4.130	2.128	18	0.96	0.189
Current year's foliage	−5.379	2.124	10	0.81	0.517
Pinus lambertiana					
Stem wood	−3.984	2.667	5	0.96	0.038
Stem bark	−5.295	2.619	5	0.91	0.080
Living branches	−7.637	3.365	5	0.81	0.300
Dead branches	−5.413	2.172	5	0.49	0.559
Total foliage	−4.023	2.032	5	0.52	0.438
Current year's foliage	−5.846	2.085	5	0.43	0.656
Castanopsis chrysophylla					
Stem wood	−3.708	2.658	19	0.98	0.044
Stem bark	−5.923	2.989	19	0.97	0.068
Living branches	−4.579	2.576	19	0.89	0.224
Dead branches	−7.124	2.883	19	0.81	0.538
Total foliage	−3.123	1.693	19	0.81	0.185
Current year's foliage	−4.365	1.535	19	0.56	0.514
Acer macrophyllum					
Stem wood	−3.493	2.723	18	0.99	0.014
Stem bark	−4.574	2.574	18	0.98	0.058
Living branches	−4.236	2.430	18	0.88	0.225
Dead branches	−2.116	1.092	18	0.15	1.862
Foliage	−3.765	1.617	18	0.87	0.101
Coarse roots (all species)					
Trees < 50 cm dbh[a]	−4.352	2.579	33	0.90	0.208
Trees > 50 cm dbh[b]	−4.643	2.652	3	0.94	0.200

[a] After Dice (1970), Riekerk (1967).

[b] Santantonio et al (1977).

TABLE 5. Average component dry weight (in kilograms) for a 35-cm-diam representative of major tree species on Watershed 10, H. J. Andrews Experimental Forest, Oregon

Component	*Pseudotsuga menziesii*	*Tsuga heterophylla*	*Pinus lambertiana*	*Castanopsis chrysophylla*	*Acer macrophyllum*
Stem wood	566.2	348.1	244.2	311.7	487.0
Stem bark	80.6	38.7	55.5	110.4	97.3
Living branches	40.8	113.0	75.9	97.5	81.7
Dead branches	12.4	9.5	10.1	22.8	5.8
Total foliage	18.1	31.0	24.6	18.1	7.3
Current foliage	3.9	8.8	4.8	3.0	...
Total	720.9	540.3	410.3	589.7	679.1
Leaf area[a] (m²)	315.7[b]	632.4[b]	428.0[b]	253.4[c]	164.2[c]

[a] Computed from reported average leaf area per unit dry weight for the above species (Gholz et al. 1976) times foliage biomass.

[b] Leaf area for all sides of conifer needles.

[c] Leaf area for 1 side of hardwood leaves.

TABLE 6. Tree biomass distribution (in kilograms per hectare) in plant communities of Watershed 10, H. J. Andrews Experimental Forest, Oregon. Values <10 kg/ha or 0.1% are indicated by T. Standard error of regression estimate (SEE) expressed as percent of the estimate

Community type Species	Stem wood	Stem bark	Living branches	Total foliage	Current foliage	Dead branches	Aboveground total	Roots >5 mm	Total	Species % of total
Pseudotsuga—Castanopsis, north slope (xeric)										
Pseudotsuga menziesii	499,900	60,890	30,910	8,770	2,010	3,320	603,790	115,080	718,870	90.1
Tsuga heterophylla	11,460	1,270	4,620	980	160	340	18,670	4,600	23,270	2.9
Pinus lambertiana	12,450	2,420	1,920	630	140	310	17,730	6,720	24,450	3.1
Libocedrus decurrens	3,380	650	510	160	40	70	4,770	1,830	6,600	0.8
Thuja plicata	1,470	140	540	150	30	60	2,360	590	2,950	0.4
Taxus brevifolia	470	50	140	40	10	20	720	160	880	0.1
Castanopsis chrysophylla	9,180	2,790	2,980	860	150	600	16,410	3,780	20,190	2.5
Arbutus menziesii	20	10	10	T	T	T	40	10	50	T
Acer macrophyllum	330	70	60	10	10	10	480	90	570	0.1
Cornus nuttallii	160	30	30	T	T	10	230	40	270	T
Total	538,820	68,320	41,720	11,600	2,550	4,740	665,200	132,900	798,100	
% SEE	29.7	28.9	45.6	47.1	96.4	84.1	31.8	57.0	36.0	
Pseudotsuga—Castanopsis, south ridge (xeric)										
Pseudotsuga menziesii	742,520	89,270	45,320	12,360	2,860	3,670	893,140	171,700	1,064,840	91.0
Tsuga heterophylla	33,190	3,690	12,390	1,320	500	920	51,510	12,730	64,240	5.5
Thuja plicata	6,960	660	3,380	300	100	160	11,460	3,300	14,760	1.2
Pinus lambertiana	2,700	520	420	130	30	50	3,820	1,460	5,280	0.4
Libocedrus decurrens	510	110	90	40	10	20	770	260	1,030	0.1
Castanopsis chrysophylla	8,570	2,630	2,780	350	140	480	14,810	3,520	18,330	1.6
Cornus nuttallii	160	40	30	T	T	10	240	50	290	T
Acer macrophyllum	70	10	10	T	T	10	100	20	120	T
Total	794,680	96,930	64,420	14,500	3,640	5,320	975,850	193,040	1,168,890	
% SEE	29.3	28.8	45.3	70.8	137.0	83.9	31.4	57.0	35.6	
Pseudotsuga—Rhododendron—Gaultheria (warm mesic)										
Pseudotsuga menziesii	368,120	44,290	22,480	6,190	1,430	2,300	443,380	85,120	528,500	89.7
Tsuga heterophylla	17,910	1,990	7,010	1,540	260	530	28,980	7,080	36,060	6.1
Thuja plicata	5,380	480	1,490	380	70	150	7,880	1,590	9,470	1.6
Pinus lambertiana	3,050	590	470	150	30	80	4,340	1,650	5,990	1.0
Taxus brevifolia	1,500	200	530	160	30	80	2,470	600	3,070	0.5
Castanopsis chrysophylla	930	280	300	90	20	60	1,660	380	2,040	0.3
Acer macrophyllum	1,960	400	340	40	40	30	2,770	500	3,270	0.6
Cornus nuttallii	220	50	40	10	10	10	330	60	390	0.1
Total	399,070	48,280	32,660	8,560	1,890	3,240	491,810	96,980	588,790	
% SEE	29.2	28.5	45.2	47.2	85.7	85.4	31.3	57.0	35.5	
Pseudotsuga—Rhododendron—Berberis (mesic)										
Pseudotsuga menziesii	604,460	72,320	36,710	9,930	2,290	3,580	727,000	140,040	867,040	89.6
Tsuga heterophylla	34,260	3,810	12,040	3,020	540	1,200	54,330	12,690	67,020	6.9
Thuja plicata	7,610	720	3,590	720	120	220	12,860	3,530	16,390	1.7
Pinus lambertiana	3,000	570	450	140	30	60	4,220	1,630	5,850	0.6
Taxus brevifolia	960	110	270	90	20	50	1,480	310	1,790	0.2
Libocedrus decurrens	180	40	30	10	T	T	260	90	350	T
Castanopsis chrysophylla	1,640	510	530	140	20	110	2,930	670	3,600	0.4
Acer macrophyllum	2,790	590	520	60	60	60	4,020	740	4,760	0.5
Cornus nuttallii	320	70	70	10	10	10	480	90	570	T
Alnus rubra	30	10	T	T	T	T	40	10	50	T
Total	655,250	78,750	54,210	14,120	3,090	5,290	807,620	159,800	967,420	
% SEE	29.1	28.4	45.1	47.2	87.4	85.8	31.2	57.0	35.4	
Pseudotsuga—Acer—Polystichum (cool moist)										
Pseudotsuga menziesii	375,610	45,280	22,990	6,380	1,470	2,430	452,690	86,800	539,490	80.9
Tsuga heterophylla	31,040	3,450	10,690	2,750	490	1,100	49,030	11,370	60,400	9.0
Thuja plicata	21,330	2,020	12,070	1,930	290	490	37,840	11,060	48,900	7.3
Taxus brevifolia	2,650	300	800	240	40	110	4,100	900	5,000	0.7
Acer macrophyllum	6,890	1,420	1,230	130	130	130	9,800	1,800	11,600	1.7
Alnus rubra	680	140	120	10	10	10	960	170	1,130	0.2
Cornus nuttallii	80	20	20	T	T	T	120	20	140	T
Total	438,280	52,630	47,920	11,440	2,430	4,270	554,540	112,120	666,660	
% SEE	27.8	27.4	44.9	46.7	96.4	88.5	30.5	57.0	35.0	

TABLE 7. Organic matter distribution (in kilograms) in plant communities of Watershed 10, H. J. Andrews Experimental Forest, Oregon

Organic matter component	*Pseudotsuga—Castanopsis,* north slope (xeric)	*Pseudotsuga—Castanopsis,* south ridge (xeric)	*Pseudotsuga—Rhododendron—Gaultheria* (warm mesic)	*Pseudotsuga*—Rhododendron—*Berberis* (mesic)	*Pseudotsuga—Acer—Polystichum* (cool moist)	Watershed average
Trees						
Foliage	11,600	14,500	8,560	14,120	11,440	12,400
Living branches	41,720	64,410	32,660	54,220	47,910	47,830
Dead branches	4,740	5,320	3,240	5,310	4,270	4,760
Stem wood	538,820	794,680	399,070	655,230	438,280	575,750
Stem bark	68,320	96,930	48,280	78,740	52,630	70,380
Large shrub (>1 m tall)						
Leaves	810	850	1,250	460	640	720
Stems	4,590	4,810	6,110	3,930	8,540	4,950
Small shrub (<1 m tall)						
Leaves	890	930	520	640	700	720
Stems	60	60	670	550	300	360
Herb layer	20	20	80	20	80	30
Total aboveground	671,570	982,510	500,440	813,220	564,760	717,900
Roots						
Coarse (>5 mm)	132,900	193,040	96,980	159,800	112,120	141,270
Fine (<5 mm)	10,900	11,000	7,900	13,000	10,500	11,270
Total plant	815,370	1,186,550	605,320	986,020	687,380	870,440
Detritus						
Forest floor[a]	57,170	49,270	27,540	56,820	45,690	51,160
Standing dead	34,500	3,800	15,600	13,100	70,000	24,600
Fallen logs	124,800	55,200	239,800	148,600	580,600	190,000
Total detritus	216,470	108,270	282,940	218,520	696,290	265,760
Soil 0–100 cm[b]	101,000	90,000	120,000	120,000	130,000	112,960
Ecosystem total	1,132,840	1,384,820	1,008,260	1,324,540	1,513,670	1,249,160

[a] Ash-free dry weight.

[b] Organic matter determined using Walkley-Black procedure (Jackson 1958).

cause of this difference in tree biomass, the 2 *Pseudotsuga–Castanopsis* communities were treated separately during the remainder of the study.

Pseudotsuga menziesii biomass ranged from 80.9% to 91.0% of total tree biomass in different communities of the watershed (Table 6). *Pseudotsuga* constituted the smallest percent of tree biomass in the cool-moist *Pseudotsuga–Acer–Polystichum* community while its percent of total biomass increased toward more xeric habitats (Table 6).

In the warm mesic *Pseudotsuga–Rhododendron–Gaultheria*, the mesic *Pseudotsuga–Rhododendron–Berberis*, and cool-moist *Pseudotsuga–Acer–Polystichum* communities, *T. heterophylla* was 6%–9% of total tree biomass compared to <2% in the north slope *Pseudotsuga–Castanopsis* community. *Thuja plicata* was 7.3% of total tree biomass in the mesic *Pseudotsuga–Acer–Polystichum* community but <2% in the other communities.

Comparing the 2 *Pseudotsuga–Castanopsis* communities, *T. heterophylla* constituted 2.9% of total tree biomass on the north slope but 5.5% on the south ridge community while *Castanopsis* contributed 2.5% and 1.6%, respectively, to total tree biomass in these communities.

Regression and log-scaling estimates of stem biomass agreed within 6%. Average stem biomass computed from regressions was 646 t/ha. Of this amount, ≈90% or 581 t/ha was considered to be merchantable logs. The merchantable portion of a tree is normally about 90% of its stem volume (Turnbull et al. 1963), thus, an additional 10% was deducted to account for stump and unmerchantable top. These calculations yielded a regression estimate of 523 t/ha merchantable stem biomass which was within 6% of the 496 t/ha stem biomass estimate obtained from scaling logs.

Based on log-scaling data and using an average density for decayed stem wood of 0.38 g/cm^3, a deduction from stem biomass of 18.3 t/ha should be made for weight loss due to stem decay in living trees. This value was the average for the entire watershed; distribution of this loss among the different communities could not be ascertained with available data. No biomass deduction for stem decay was made in Tables 6 or 7.

The major contribution to stem biomass in all plant communities was made by a relatively few trees. Figure 6 shows how stem biomass, leaf area, stem basal area, and stem diameter frequency were distributed across the range of stem diameters in each community. In all but the *Pseudotsuga–Acer–Polystichum* community type, >80% of stem biomass was located in trees >80 cm dbh. In the *Pseudotsuga–Acer–Polystichum* community 75% of stem biomass was in trees >80 cm dbh. However, trees >80 cm dbh constituted only 18.8%, 15.8%, 11.0%, 15.1%, and 18.8% of the total number of stems >15 cm dbh in the north slope *Pseudotsuga–Castanopsis*, *Pseudotsuga–Rhododendron–Gaultheria*, *Pseudotsuga–Acer–Polystichum*, *Pseudotsuga–Rhododendron–Berberis* and south ridge *Pseudotsuga–Castanopsis* communities, repectively.

The relation between leaf area distribution and stem diameter distribution contrasted with stem biomass distribution over diameter in several communities. (Fig. 6). In the cool-moist *Pseudotsuga–Acer–Polystichum* community, 45% of total tree leaf area was on trees <80 cm dbh. In the warm-mesic *Pseudotsuga–Rhododendron–Gaultheria* and mesic *Pseudotsuga–Rhododendron–Berberis* communities, 32.4% and 34.0% of leaf area was on trees <80 cm dbh while for the more xeric north slope and south ridge *Pseudotsuga–Castanopsis* communities, the respective percentages were 26.5% and 29.2%.

The vertical difference between curves for basal area and leaf area in smaller diameter classes (Fig. 6) was greatest in the cool-moist *Pseudotsuga–Acer* and smallest in the relatively xeric *Pseudotsuga–Castanopsis* communities. This pattern coincided with the patterns of percent cover of *Tsuga*, *T. plicata*, and *T. brevifolia* in the understory tree layer (Table 1), that is, increasing cover of these climax species along the gradient from hot and dry to cool and moist. *Tsuga* has about 2× the leaf area of comparable size *Pseudotsuga* (Table 5). Limited sampling of *Thuja* and *Taxus* during this study and by Russell (1974) indicated these species were comparable to *Tsuga* in leaf biomass for a given diameter.

Organic matter distribution

Large differences in tree biomass among communities were also reflected in patterns of organic matter distribution through these communities (Table 7).

Differences in understory leaf biomass were not consistently related to overstory canopy characteristics (Table 7). Understory leaf biomass was nearly equal in the 2 *Pseudotsuga–Castanopsis* and the *Pseudotsuga–Rhododendron–Gaultheria* communities in spite of large leaf biomass differences in the tree strata.

All communities on the watershed had large amounts of detritus on the soil surface, much of it slowly decomposing woody material (Table 7). Standing dead and fallen log biomass ranged from 59.0 to 650 t/ha in the various communities and averaged 214.6 t/ha for the entire watershed. In all but the south ridge *Pseudotsuga–Castanopsis* community, weight of standing and fallen logs was greater than that of forest floor material (Table 7). Forest floor biomass in the various communities, exclusive of fallen logs, ranged from 27.5–57.2 t/ha ash-free dry wt. The lowest forest floor biomass was in the *Pseudotsuga–Rhododendron–Gaultheria* community. Forest floor weights in the other communities were relatively similar ranging from 45.7–57.2 t/ha.

Total detritus on the soil surface ranged from 7.8%–46% of the total organic matter accumulation in the various communities while the average for the watershed was 21.2%.

Tree biomass increment

In Fig. 7 stem wood annual radial increment averaged over the most recent 5 yr is plotted against stem diameter for the various tree species. There was no significant difference in radial increment for any species or diameter class among communities; variation within a given species diameter class in a community was about the same as among communities. Coefficients of variation averaged about 45% within diameter classes of the various species.

Radial increment of *P. menziesii* and *P. lambertiana* increased to 60 cm dbh then generally decreased with increasing stem diameter (Fig. 7). *Libocedrus decurrens* increment decreased between 20 and 50 cm dbh then increased again with increasing stem diameter; for other tree species, there was no consistent relation between diameter breast height and stem wood radial increment. In all cases, radial increment was relatively small in comparison to that of rapidly growing younger stands of *P. menziesii* and other western conifers (Gessel et al. 1965).

Table 8 shows annual biomass accumulation on trees alive at the time of the 1973 mortality check and its distribution among species in the different communities. Subtracting annual mortality from these values gives annual biomass increment.

Aboveground tree biomass accumulation was not directly proportional to aboveground tree biomass for all communities. Aboveground biomass accumulation expressed as a percent of aboveground tree biomass ranged from 0.36%–0.76%; the highest percentage was in the *Pseudotsuga–Acer–Polystichum* community; the others ranged from 0.36%–0.38%.

Annual biomass accumulation by a tree species was not directly related to its proportion of biomass in the community. Annual biomass accumulation by *Pseudotsuga* ranged from 44.3% of total in the *Pseudotsuga–Acer–Polystichum* community to 61.6% in the north slope *Pseudotsuga–Castanopsis* commu-

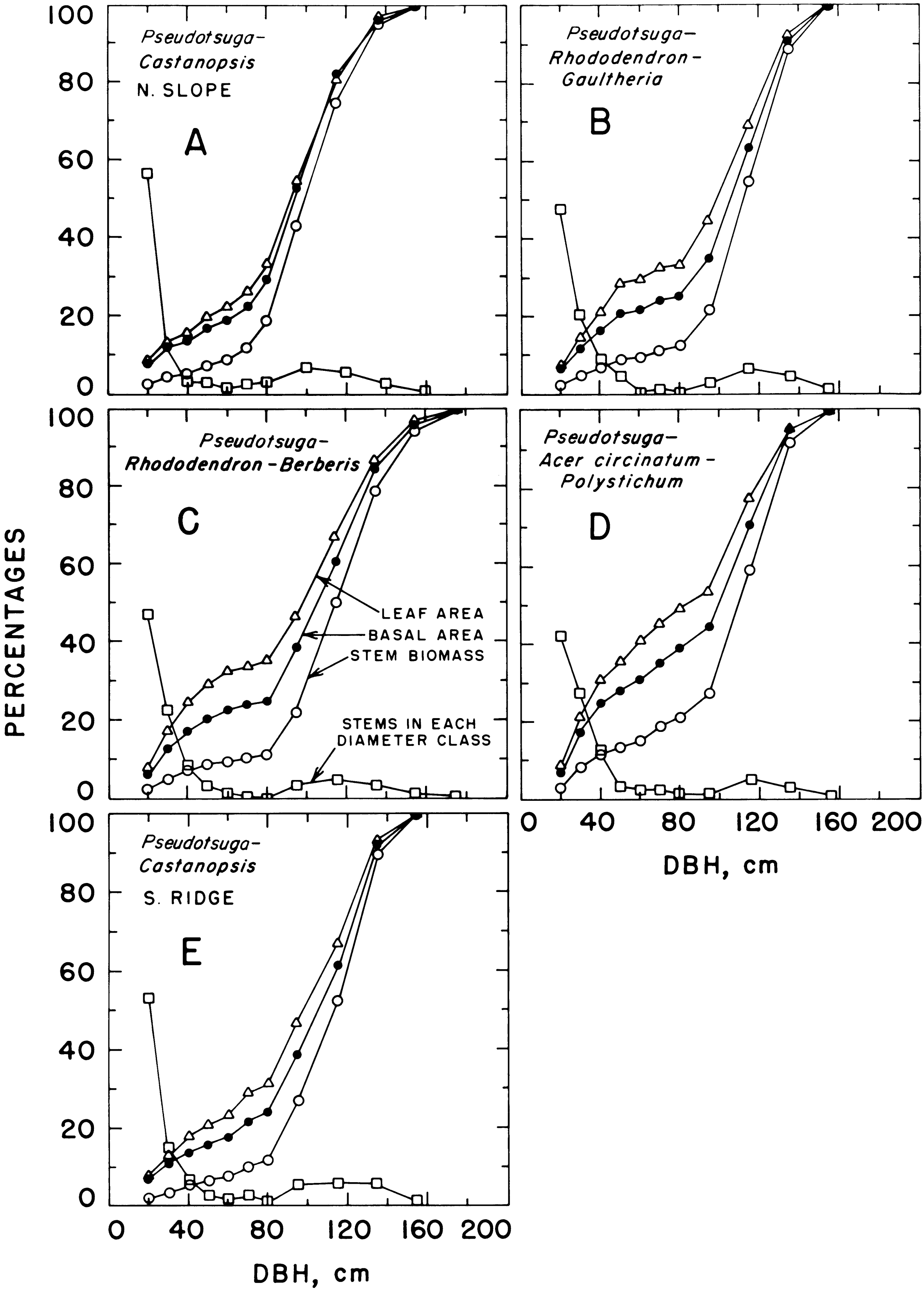

FIG. 6. Percentage of stems and cumulative percentage of leaf area, stem biomass (wood plus bark) and stem basal area as related to stem diameter for community types on Watershed 10, H. J. Andrews Experimental Forest, Oregon.

TABLE 8. Annual tree biomass accumulation (in kilograms per hectare) and its distribution by species in plant communities of Watershed 10, H. J. Andrews Experimental Forest, Oregon. Biomass accumulation is defined as dry weight increase of trees alive at end of growth measurement interval; mortality in that interval is not deducted. Values <10 kg/ha or 0.1% are indicated by T. Species percent of total will not necessarily sum to 100% due to rounding error

Community type Species	Stem wood	Stem bark	Living branches	Dead branches	Above-ground total	Roots >5 mm	Total	Species % of total
Pseudotsuga—Castanopsis, north slope (xeric)								
Pseudotsuga menziesii	1,360	160	80	10	1,610	320	1,930	61.5
Tsuga heterophylla	170	20	70	T	260	70	330	10.5
Pinus lambertiana	170	30	30	T	230	90	320	10.2
Libocedrus decurrens	20	T	T	T	20	10	30	1.0
Thuja plicata	30	T	10	T	40	10	50	1.6
Taxus brevifolia	T	T	T	T	T	T	T	T
Castanopsis chrysophylla	210	70	70	20	370	90	460	14.6
Arbutus menziesii	T	T	T	T	T	T	T	T
Acer macrophyllum	10	T	T	T	10	T	10	0.3
Cornus nuttallii	T	T	T	T	10	T	10	0.3
Total	1,970	280	260	30	2,550	590	3,140	
Pseudotsuga—Castanopsis, south ridge (xeric)								
Pseudotsuga menziesii	1,790	210	110	10	2,120	440	2,560	59.1
Tsuga heterophylla	560	60	230	10	860	230	1,090	25.2
Thuja plicata	90	10	50	T	150	50	200	4.6
Pinus lambertiana	30	T	T	T	30	20	50	1.2
Libocedrus decurrens	T	T	T	T	10	T	10	0.2
Castanopsis chrysophylla	190	70	60	10	330	80	410	9.5
Cornus nuttallii	T	T	T	T	10	T	10	0.2
Acer macrophyllum	T	T	T	T	T	T	T	T
Total	2,660	350	450	30	3,510	820	4,330	
Pseudotsuga—Rhododendron—Gaultheria (warm mesic)								
Pseudotsuga menziesii	920	110	60	10	1,100	230	1,330	60.2
Tsuga heterophylla	250	30	110	10	400	100	500	22.6
Thuja plicata	80	10	40	T	130	40	170	7.7
Pinus lambertiana	40	10	10	T	60	20	80	3.6
Taxus brevifolia	10	T	T	T	10	T	10	0.4
Castanopsis chrysophylla	20	10	10	T	40	10	50	2.3
Acer macrophyllum	30	10	10	T	50	10	60	2.7
Cornus nuttallii	10	T	T	T	10	T	10	0.4
Total	1,360	240	240	20	1,800	410	2,210	
Pseudotsuga—Rhododendron—Berberis (mesic)								
Pseudotsuga menziesii	1,430	170	90	10	1,700	360	2,060	54.9
Tsuga heterophylla	610	70	240	20	940	250	1,190	31.7
Thuja plicata	110	10	60	T	180	50	230	6.1
Pinus lambertiana	30	10	T	T	40	20	60	1.6
Taxus brevifolia	10	T	T	T	10	T	10	0.3
Libocedrus decurrens	T	T	T	T	T	T	T	T
Castanopsis chrysophylla	40	10	10	T	60	20	80	2.1
Acer macrophyllum	60	10	10	T	80	20	100	2.7
Cornus nuttallii	10	T	T	T	10	T	20	0.5
Alnus rubra	T	T	T	T	T	T	T	T
Total	2,300	280	410	30	3,020	720	3,750	
Pseudotsuga—Acer—Polystichum (cool moist)								
Pseudotsuga menziesii	990	120	60	10	1,180	240	1,420	44.8
Tsuga heterophylla	570	60	220	10	860	230	1,090	34.4
Thuja plicata	200	20	110	T	330	100	430	13.6
Taxus brevifolia	10	T	T	T	10	10	20	0.6
Acer macrophyllum	120	20	20	T	160	30	190	6.0
Alnus rubra	10	T	T	T	20	T	20	0.6
Cornus nuttallii	T	T	T	T	T	T	T	T
Total	1,900	220	410	20	2,560	610	3,170	

nity; *Pseudotsuga* comprised 80.9% and 90.1% of total tree biomass in these communities. On the other hand, *Tsuga* comprised only 9.0% and 2.9%, respectively, of tree biomass in the *Pseudotsuga–Acer–Polystichum* and north slope *Pseudotsuga–Castanopsis* communities yet contributed 34.3% and 10.6% of total annual biomass accumulation in the respective communities.

In general, *Tsuga* and *T. plicata* contributed a relatively larger portion of annual biomass accumulation

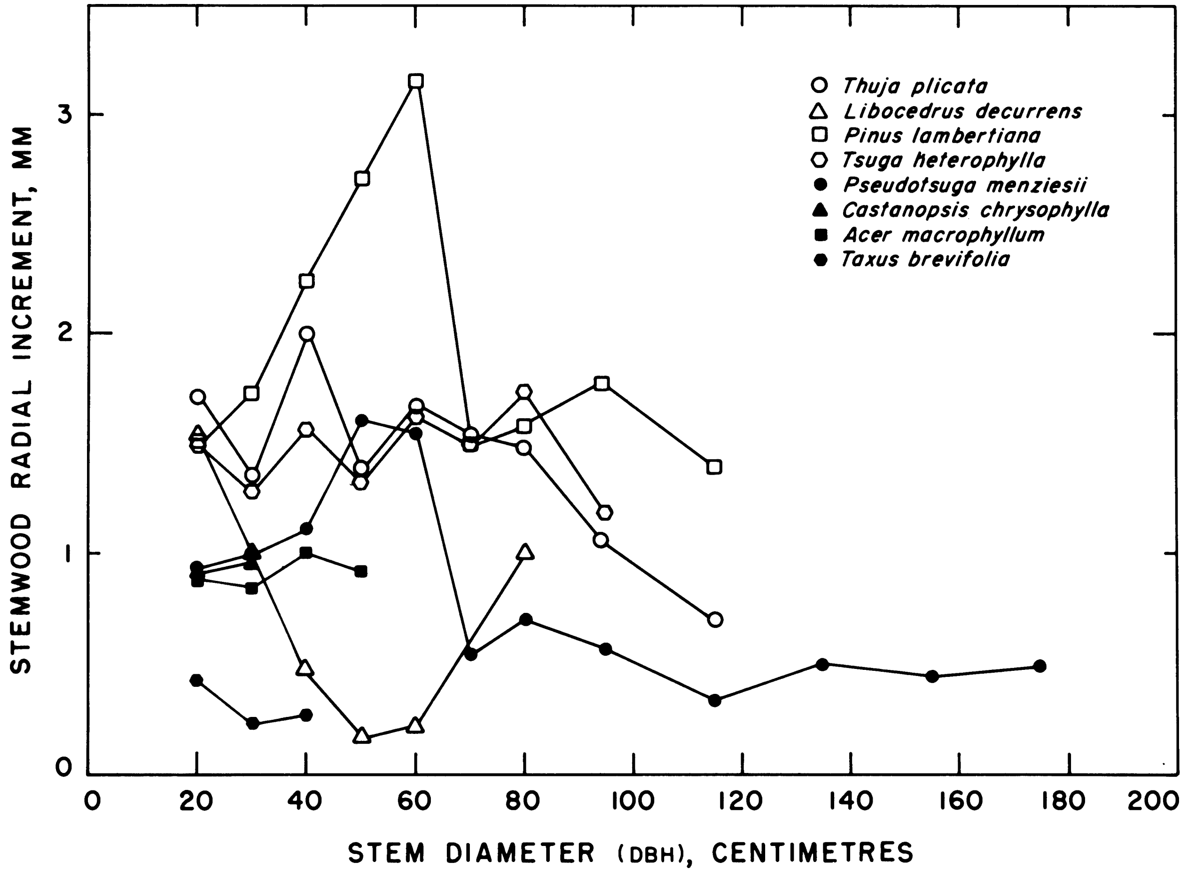

FIG. 7. Radial stem increment as related to stem diameter for tree species of Watershed 10, H. J. Andrews Experimental Forest, Oregon.

than biomass in the mesic *Pseudotsuga–Rhododendron–Berberis* and the cool-moist *Pseudotsuga–Acer–Polystichum* communities. In contrast, *Castanopsis* and *Tsuga* contributed a larger proportion of biomass accumulation than biomass in the *Pseudotsuga–Castanopsis* communities. *Acer macrophyllum*, the principal deciduous hardwood tree species, contributed 2.4%, 2.6%, and 6.2% of annual biomass accumulation in the *Pseudotsuga–Rhododendron–Gaultheria, Pseudotsuga–Rhododendron–Berberis*, and *Pseudotsuga–Acer–Polystichum* communities, respectively, but only 0.3% and 0.2% in the north slope and south ridge *Pseudotsuga–Castanopsis* communities. *Acer macrophyllum* was <1% of total biomass except in the *Pseudotsuga–Acer–Polystichum* community; here it was 1.7% of total tree biomass. *Pinus lambertiana* was 10.1% of annual biomass accumulation in the north slope but only 1.2% in the south ridge *Pseudotsuga–Castanopsis* community. Biomass and biomass accumulation of *P. lambertiana* decreased along the gradient from relatively xeric to cool-moist. Minor species including the conifers *T. brevifolia* and *L. decurrens*, deciduous hardwoods such as *C. nuttallii* and *A. rubra*, and the evergreen hardwood *A. menziesii* were conspicuously present in, but contributed little biomass or annual biomass accumulation to, their repective communities.

Net primary production

Net primary production in plant communities was computed using NPP = ΔB + L + G, where ΔB is biomass increment (annual biomass accumulation minus branch, stem and coarse root mortality), L is litterfall (including aboveground and belowground mortality and fine root turnover) and G is grazing, primarily by insects.

Litterfall in the various plant communities is given in Table 9. The 2-yr average for total litterfall was roughly proportional to tree biomass in the respective communities; the lowest total litterfall was in the *Rhododendron–Gaultheria* and the highest was in the south ridge *Castanopsis* communities. These communities had the lowest and highest respective tree biomass on the watershed.

Regression estimates of leaf production by tree and shrub species were tested by calculating leaf production from leaf litterfall data. Cromack (1973) and Stachurski and Zinka (1975) report an average weight loss of 20% prior to abcission for deciduous and coniferous leaves. Using this estimate of weight loss, an

TABLE 9. Litterfall (in kilograms per hectare) in plant communities of Watershed 10, H. J. Andrews Experimental Forest, Oregon. Twigs and woody, reproductive parts, green litter and frass, epiphytes and other material were not separated during second year of collection

Collection interval and community type	Conifer needles	Hardwood leaves	Twigs and woody	Reproductive parts	Green litter[a]	Epiphytes and other[b]	Total
1 May 1973–1 May 1974							
Pseudotsuga—Castanopsis, north slope	1,350	680	600	410	10	440	3,490
Pseudotsuga—Castanopsis, south ridge	2,190	650	430	440	50	390	4,150
Pseudotsuga—Rhododendron—Gaultheria	1,970	440	580	560	5	300	3,855
Pseudotsuga—Rhododendron—Berberis	2,050	360	820	400	10	290	3,930
Pseudotsuga—Acer—Polystichum	2,020	380	650	670	5	560	4,285
Watershed average	1,840	490	670	450	10	410	3,870
1 May 1974–1 May 1975							
Pseudotsuga—Castanopsis, north slope	1,170	550					5,040
Pseudotsuga—Castanopsis, south ridge	1,940	620					4,750
Pseudotsuga—Rhodendron—Gaultheria	1,910	460					3,690
Pseudotsuga—Rhododendron—Berberis	1,750	400					4,855
Pseudotsuga—Acer—Polystichum	1,910	450					4,140
Watershed average	1,630	470					4,660
2-yr average							
Pseudotsuga—Castanopsis, north slope	1,260	615					4,265
Pseudotsuga—Castanopsis, south ridge	2,065	635					4,950
Pseudotsuga—Rhododendron—Gaultheria	1,940	450					3,770
Pseudotsuga—Rhododendron—Berberis	1,900	380					4,390
Pseudotsuga—Acer—Polystichum	1,965	415					4,210
Watershed average	1,740	480					4,260

[a] Green litter: foliage and small twigs broken from trees by wind and snow while still living; includes foliage of all age classes.

[b] "Other" category includes bark particles and unidentifiable material, $\approx$10% epiphytes.

independent check on regression estimates of current foliage or annual leaf production was computed for plant communities of the watershed. Leaf litterfall estimates of annual leaf production were (rounded to the nearest 10 kg) 2,550, 1,830, 2,300, 3,020, and 3,640 kg/ha for the north slope *Pseudotsuga–Castanopsis*, *Pseudotsuga–Rhododendron–Gaultheria*, *Pseudotsuga–Acer–Polystichum*, *Pseudotsuga–Rhododendron–Berberis* and south ridge *Pseudotsuga–Castanopsis* communities, respectively. If the difference between litterfall and regression estimates, including understory leaf production computed from Russell (1974), is expressed as a percent of regression estimates, the results indicate the amount and direction of disagreement between the 2 estimates. With respect to the litterfall leaf production estimates, disagreement was −17.3%, −23.0%, +8.4%, −5.5%, and −7.7%.

Stem mortality was greater than annual biomass accumulation in all communities on the watershed. As a consequence, annual biomass increment averaged −0.49% per year for the watershed. Loss of organic matter by leaching from the rooting zone was $\approx$60 kg$\cdot$ha$^{-1}\cdot$yr^{-1} or $<$0.3% of annual net primary production (NPP), indicating efficient use of net production by decomposers.

Estimates of aboveground and belowground NPP and the various components of NPP are given in Table 10.

Respiration and production balances

Autotrophic respiration in communities of Watershed 10 was estimated as described earlier. Difficulties in estimating autotrophic respiration are well known and most reported estimates contain errors from a variety of sources (Woodwell and Botkin 1970). In addition to the normal difficulties involved in respiration estimates, values reported here are based in part on respiration rates measured for species other than *P. menziesii*. On the other hand, procedures were similar to those used by other investigators (Woodwell and Botkin 1970; Sollins et al. 1973) and so should be reasonably comparable with results of other studies.

Estimates of heterotroph respiration were also subject to some error. Mean residence time (forest floor weight divided by litterfall) for organic matter in forest floors ranged from 10 to 13.4 yr. There was no evidence that fire or other disturbance to forest floors had occurred here within the past 25–30 yr. Thus, forest floors in the various plant communities were likely at or near steady-state, so litterfall was assumed equal to forest floor heterotroph respiration.

Respiration by heterotrophic organisms in fallen logs and standing dead trees was harder to assess due to slow decomposition rates for this material. Observations made on the watershed by aging of trees rooted on fallen logs indicate that an average turnover rate for fallen logs may be on the order of 150 yr (R. Fogel, *personal communication*) so annual log and standing

TABLE 10. Net primary production, components of NPP, autotrophic respiration, gross primary production, and net ecosystem production (in kilograms per hectare) for plant communities of Watershed 10, H. J. Andrews Experimental Forest, Oregon

Parameter	*Pseudotsuga—Castanopsis*, north slope (xeric)	*Pseudotsuga—Castanopsis*, south ridge (xeric)	*Pseudotsuga—Rhododendron—Gaultheria* (warm mesic)	*Pseudotsuga—Rhododendron—Berberis* (mesic)	*Pseudotsuga—Acer—Polystichum* (cool moist)	Watershed average
Biomass increment (ΔB)						
Trees (stem plus branch)	−4,060	−6,180	−3,060	−4,970	−2,920	−4,340
Large shrub (>1 m tall) stems	1,110	1,200	240	140	390	550
Small shrub (<1 m tall) stems	10	20	30	20	10	20
Herb layer turnover	10	10	40	10	40	20
Total aboveground	−2,930	−4,950	−2,750	−4,800	−2,480	−3,750
Coarse root (>5 mm)	−740	−1,100	−560	−880	−510	−770
Total biomass increment	−3,670	−6,050	−3,310	−5,680	−2,990	−4,520
Other organic matter transfers						
Grazing	40	60	60	60	60	50
Litterfall	4,260	4,950	3,770	4,390	4,210	4,290
Fine root death	2,180	2,200	1,580	2,600	2,100	2,260
Throughfall	340	340	340	340	340	340
Stemflow	20	30	20	10	10	20
Mortality						
Stem and branch	6,570	9,640	4,840	7,960	5,450	7,020
Coarse roots	1,330	1,930	970	1,600	1,120	1,410
Net Primary Production (NPP)						
Aboveground	8,300	10,070	6,280	7,960	7,590	7,970
Belowground	2,770	3,030	1,990	3,320	2,710	2,900
Total	11,070	13,100	8,270	11,280	10,300	10,870
Autotrophic respiration (as $C_6H_{10}O_5$)						
Aboveground	108,700	158,100	79,900	128,800	104,000	116,100
Belowground	31,300	45,600	23,000	38,800	27,600	33,900
Total	140,000	203,700	102,900	167,600	131,600	150,000
Gross Primary Production (GPP)						
Aboveground	117,000	168,170	86,180	136,760	111,590	124,070
Belowground	34,070	48,630	24,990	42,120	30,310	36,800
Total	151,070	216,800	111,170	178,800	141,900	160,870
Heterotrophic respiration						
Aboveground						
Forest floor	4,260	4,950	3,770	4,390	4,210	4,260
Standing and fallen logs	1,100	400	1,700	1,100	4,300	1,400
Belowground	1,760	2,060	1,280	2,100	1,610	1,840
Total	7,180	7,470	6,810	7,650	10,180	7,560
Leaching loss	60	60	60	60	60	60
Net Ecosystem Production (NEP)						
Aboveground	2,940	4,720	810	2,470	−920	2,310
Belowground	950	910	650	1,160	1,040	1,000
Total	3,890	5,630	1,460	3,630	120	3,310
Total NNP/GPP %	7.9	6.0	7.4	6.3	7.2	6.8
Total ΔB/GPP %	−2.4	−2.8	−3.0	−3.1	−2.1	−2.8
Total ΔB/NPP %	−33.1	−46.2	−40.0	−50.3	−29.0	−41.6

dead decomposition rates were computed by dividing their biomass by 150.

Belowground heterotrophic respiration was assumed equal to half of the coarse and fine root mortality. Preliminary studies (K. Cromak, *personal communication*) suggest a turnover time of ≈2 yr for fine roots. Estimates of heterotrophic respiration and net ecosystem production are given in Table 10.

DISCUSSION

Regressions—Species differences

There are statistically significant differences in stem biomass, leaf biomass, and leaf area for trees of the same diameter among coniferous and hardwood species of Watershed 10 (Table 5). Differences in leaf biomass and leaf area among three major conifer species appear to be related to their relative shade tolerance. *Pseudotsuga menziesii*, an intolerant species (Franklin and Dyrness 1973), has the smallest leaf biomass and area for a given diameter while the very shade tolerant *T. heterophylla* has the largest leaf biomass and area. *Pinus lambertiana* is intermediate in both shade tolerance and leaf biomass and area to *Pseudotsuga* and *Tsuga*.

Compared to coniferous species of eastern North America, *T. heterophylla* and *P. lambertiana* have larger leaf biomass and area while those of *P. menziesii* are roughly comparable. For example, regression estimates of leaf area for 15-cm-dbh *Pinus rigida* and *Pinus echinata* are 56.8 m^2 and 48.6 m^2 (Whittaker and Woodwell 1968) but *P. rubens* is 41.1 m^2 (Whittaker et al. 1974). These values contrast distinctly with the 100-m^2 leaf area of a 15-cm-dbh *T. heterophylla* or the 76 m^2 of *P. lambertiana*. Leaf area of a 15-cm-dbh *P. menziesii* is 59.1 m^2, 1.2× and 1.4× greater than that of *P. echinata* or *P. rubens* but about comparable to that of *P. rigida*.

In a similar comparison, stem biomass of 15-cm-dbh, *P. menziesii* and *T. heterophylla* were 2× and 1.5× greater than that of *P. rigida*. In contrast, stem biomass of *P. lambertiana* was 0.8× that of *P. rigida*.

Component weight to diameter relations for *A. macrophyllum* were similar to those reported for an eastern North American maple, *Acer saccharum*, (Whittaker et al. 1974). Leaf area, total branch dry weight, and total stem dry weight were 37.6 m^2, 13.3 kg, and 75.4 kg, respectively, for *A. saccharum* and 41.6 m^2, 10.4 kg, and 59.5 kg, respectively, for *A. macrophyllum*. *Acer macrophyllum* occurs primarily as an understory tree on Watershed 10 growing in lightgaps of the old-growth *Pseudotsuga* forests. Considering the different ecological roles and the different climates in which these species are found, their structure, especially for leaf area, is quite similar.

Comparative data for sclerophyllous evergreen hardwoods such as *C. chrysophylla* are relatively scarce. One comparison is provided by Attiwill (1966) who reports leaf and branch weight regressions for *Eucalyptus obliqua*, a sclerophyllous evergreen hardwood species of southeast Australia. According to his regressions, a 35-cm-dbh *E. obliqua* has estimated leaf and branch weights of 11.6 kg and 35.7 kg, respectively, compared to 18.1 kg and 97.5 kg, respectively, for *Castanopsis*. Leaf weight differences are within the range of differences observed for conifers and may result from different leaf retention times or from different climatic regimes. On the other hand, the greater branch weight of *Castanopsis* is likely due to its shrubby growth habit in the understory of these *Pseudotsuga* forests compared to the tree habit of the *Eucalyptus*.

Comparisons of component dry weight among species growing in the same and in different environments suggest there is a relation between physical environment and relative proportions of functional components of trees. For example, in dry-summer climates, leaf area as a transpiring surface probably must be balanced against leaf area as a photosynthetic surface. Less leaf area would be expected for species adapted to drier sites (*P. menziesii* and *P. lambertiana*) than to mesic sites (*T. heterophylla*). In another example, the sapwood basal area to foliage biomass ratio of conifers may be related to the water status of the environment in which a species evolved (Grier and Waring 1974). Also, as pointed out earlier, leaf area of conifers may be related to shade tolerance. Further research is needed before relations between physical environment and tree morphological characteristics can be more than suggested. However, these observations do indicate that substitution of regressions, when none are available for a given species, should be done cautiously, at least with conifers.

Community differences

Tree biomass and detritus.—In terms of temperature and moisture stress, sites on Watershed 10 rank from the relatively xeric *Pseudotsuga–Castanopsis* communities through the warm-mesic *Pseudotsuga–Rhododendron–Gaultheria* and mesic *Pseudotsuga–Rhododendron–Berberis* to the cool-moist *Pseudotsuga–Acer–Polystichum* community. Patterns of biomass distribution for *Castanopsis, Tsuga*, and *Thuja* are consistent with this ranking. *Castanopsis* is a significant stand biomass component only in relatively xeric locations while *Thuja* is a significant biomass component only in the cool-moist site. *Tsuga* biomass increases along the gradient from xeric to cool-moist. The higher proportion of *Tsuga* and lower proportion of *Castanopsis* biomass in the south ridge *Pseudotsuga–Castanopsis* community suggests this community has a more mesic environment than that of the north slope *Pseudotsuga–Castanopsis* community.

Foliage biomass in the *Pseudotsuga–Rhododendron–Berberis* and south ridge *Pseudotsuga–Castanopsis* communities is higher than the previously reported 9–12 t/ha for Douglas-fir ecosystems (Heilman 1961, Cole et al. 1967, Riekerk 1967, Turner and Long 1975, Fujimori et al. 1976). Much of this apparent difference may be due to comparing biomass on steep slopes of this watershed with results of studies done on level ground. All values reported in this paper are expressed in terms of horizontal area. However, an ecosystem sloping 35° has 22% more land surface per horizontal unit than does an equivalent area of level ground. Other things being equal, this same ecosystem will also have 22% more rooting volume and so has room for 22% more trees than equivalent level ground. If appropriate slope adjustments are made for biomass data, leaf biomass on Watershed 10 is comparable to or less than values reported for younger, fully stocked Douglas-fir stands on level ground.

Aboveground tree biomass for all communities of the watershed is higher than previously listed for forests in most other parts of the world (Art and Marks 1971, Sollins et al. 1973). However, higher aboveground biomass values have been reported for ecosystems in other parts of the U.S. Pacific Northwest. For example, Fujimori et al. (1976) report aboveground stem biomass values for old-growth (>500 yr) stands of *P. menziesii–T. heterophylla* and *Abies procera–P. menziesii* of 1,591 and 1,687 t/ha, respectively; substantially higher than aboveground tree biomass for Watershed 10. Moreover, in the same paper, Fujimori et al. (1976) report aboveground biomass values of 871.3, 661.2 and 880.4 t/ha for 100- to 130-year-old stands of *T. heterophylla–Picea sitchensis, P. menziesii–T. heterophylla*, and *A. procera–P. menziesii–Abies amabilis*, respectively, in western Oregon. The values for these younger stands are comparable with those of the 450-year-old stands of this watershed.

Higher aboveground biomass values have also been reported for coastal *Sequoia sempervirens* (D. Don) Endl. stands of northwestern California. Westman and Whittaker (1975) estimate 3,200 t/ha of aboveground biomass for *Sequoia* growing on alluvial flats and 1,150 t/ha for *Sequoia* of Coast Range slopes. The latter figure is somewhat larger than the 982 t/ha aboveground biomass of the south ridge *Pseudotsuga-Castanopsis* community.

Percent standard error of estimates for tree biomass (Table 6) are large, although probably no larger than those associated with any forest of this sort. Most of this variability is associated with the irregular form of large old-growth trees due to broken tops and missing branches. Standard errors of estimate were smaller for other species (Table 6) but these equations did not include the wide range of tree sizes included in regressions for *Pseudotsuga*.

Log-scaling estimates of stem biomass were within 6% of the regression estimates after adjustments were made to account for differences between total and merchantable biomass. Since Watershed 10 was clearcut in June–July of 1975, these comparisons are, after a fashion, a large-scale comparison between total harvest and regression biomass estimates in a heterogeneous ecosystem. Agreement between estimates was well within the standard error of the regression estimate for stem wood plus bark (Table 6).

There was also relatively good agreement between regression and litterfall estimates of leaf production. Agreement here was within 10% for about 60% of the watershed and within about 20% for the remainder. Error terms for leaf production regressions were larger than those of other regressions (Table 6).

There were nearly twofold differences in total living biomass among communities (of Watershed 10). Highest biomass was in the south ridge *Pseudotsuga–Castanopsis* community, the lowest was in the *Pseudotsuga–Rhododendron–Gaultheria* and *Pseudotsuga–Acer–Polystichum* communities. The 2 communities having lowest biomass are located in a relatively narrow zone along the main stream, primarily on its north side where soils are shallower than in other locations on the watershed. Windthrow has probably played a large role in reducing stand biomass in these communities. Clearly, mortality of some sort has been greater in the *Pseudotsuga–Rhododendron–Gaultheria* and *Pseudotsuga–Acer–Polystichum* communities than in the others; biomass of standing dead and especially fallen logs in these communities is 2–10× higher than in adjacent community types (Table 7).

Detritus biomass.—Except in the *Pseudotsuga–Rhododendron–Gaultheria* and *Pseudotsuga–Acer–Polystichum* communities, standing and fallen log biomass is inversely proportional to aboveground tree biomass (Table 7). Observations made on the watershed indicate that much of the fallen log biomass of the *Pseudotsuga–Acer–Polystichum* community originally grew in the adjacent *Pseudotsuga–Rhododendron–Gaultheria* community but fell downslope into this community.

The inverse relation between aboveground living biomass and fallen logs (Table 7) indicates that these forests are in the age range where a combination of external factors such as wind and internal factors such as stem decay and insect damage are making periodic inroads into standing biomass of pioneering trees species (primarily *Pseudotsuga*). Decay weakens tree stems making them susceptible to wind breakage. The broken tops of many large trees suggest this may be a major factor in reducing biomass and opening the canopy for successional species such as *Tsuga*.

The major factor causing differences in standing biomass of these communities is apparently the history of mortality. Mortality in forests of this sort appears to occur periodically due to fire, windstorm, or insect attacks. For example, during the Columbus Day Storm, 12 October 1962, high winds caused large decreases in timber volume in many forests throughout the Pacific Northwest, in both seral and near climax forests. Stem decay, which is generally more common in older trees, appears to increase the probability of wind damage. The watershed average of 18.3 t/ha stem biomass loss due to decay of living stems was concentrated in the larger, older *Pseudotsuga*. Large, periodic, biomass fluctuations of this sort raise questions as to whether the concept of "steady-state" or climax biomass accumulation (e.g., Whittaker et al. 1974) is valid in forests where such changes in biomass may be the rule rather than the exception.

Comparative data on biomass of large woody detritus in other communities is limited but reported values are typically much lower than those reported here. For example, Cole et al. (1967) report woody detritus biomass of 6.3 t/ha in a 37-year-old *P. menziesii* stand in western Washington, and Harris et al. (1973) report

15.7 t/ha for pine, 18.1 t/ha for oak-hickory, 18.4 t/ha for chestnut-oak, and 7.5 t/ha for yellow poplar stands in eastern Tennessee.

Weight of forest floor material in the various communities is greater than reported for younger *P. menziesii* stands in the Pacific Northwest (Gessel and Balci 1965, Cole et al. 1967, Grier and McColl 1971), especially if the average ash content of 21.6% is added to the present data to make them comparable with earlier reports. Forest floors of the watershed are in the dry weight range of 45–57 t/ha except for the 27.5 t/ha in the *Pseudotsuga–Rhododendron–Gaultheria* community. The generally higher values for these old-growth forests are probably a result of the high proportion of slowly decomposing woody litter produced by these communities (Table 9) compared to litter produced by younger ecosystems.

During data processing a negative correlation (r^2 = .52) between slope angle and forest floor dry weight was observed. This correlation may explain the lower forest floor biomass in the *Pseudotsuga–Rhododendron–Gaultheria* community. Slopes in this community were about 10°–15° steeper than the average for sampling points in other communities. Downslope movement of litterfall from steeper to gentler slopes may be responsible for the low forest floor biomass in this community.

Detritus constitutes a large part of total organic matter in these communities. Forest floor, standing dead, and fallen logs are from 7.8% to 41% of total organic matter in the various communities; detritus is 21.3% of total organic matter for the entire watershed. These proportions are greater than those reported for most younger forest ecosystems. For example, detritus was 6.7% of total organic matter in a 37-year-old *P. menziesii* stand in western Washington (Cole et al. 1967) and 4.4% in a *Quercus stellata–Quercus marilandica* forest in Oklahoma (Johnson and Risser 1974). On the other hand, Reiners (1972) reports that detritus comprised 37%, 76%, and 84%, respectively, of the total organic matter accumulation in oak, fen, and swamp forests of southern Minnesota. These large proportions of detritus compared to forests of Watershed 10 probably result from low decomposition rates in the colder Minnesota winters and from the O_2-poor decomposition environment in fen and swamp detritus layers.

Biomass accumulation and increment.—Differences in production potential resulting from different site qualities on the watershed apparently were not large enough to produce differences in radial stem increment. Even in smaller diameter classes, there was no detectable difference in radial increment among communities. Annual biomass accumulation and biomass increment were primarily related to standing crop biomass; this in turn was apparently related to the history of mortality.

Annual biomass accumulation in the different communities was roughly proportional to standing crop biomass. In all but the *Pseudotsuga–Acer–Polystichum* community, biomass accumulation was 0.36%–0.38% of standing crop biomass. In the *Pseudotsuga–Acer–Polystichum* community, this ratio was 0.46%; the greater accumulation indicating a possible reduction in competition due to recent high mortality.

Biomass increment was negative for tree strata and positive for shrub strata in all communities of the watershed (Table 10). Biomass increment in the various communities ranged from −2,920 kg/ha to −3,180 kg/ha. As previously noted, these losses of standing biomass were largely due to mortality in the larger diameter classes. Mortality in all diameter classes may have been above average during the study period; 1973 was a dry year in that the normal, warm summer dry period was prolonged well into November. The death of several large trees was recorded during this dry period.

The death of a large tree represents a large biomass loss. For example, the dry weight of stem plus branches of a 100-cm-dbh *P. menziesii* is about 9,500 kg. Our estimate of aboveground mortality for the entire watershed was 7,020 $\mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$ (Table 10). This mortality figure would be met by the death of roughly 1.5, 100-cm-dbh trees per hectare over the 2 yr of this study.

In proportion to biomass, annual biomass accumulation by *Tsuga, Thuja, Castanopsis, Pinus*, and minor species was greater than that by seral *Pseudotsuga*. In the cool-moist *Pseudotsuga–Acer–Polystichum* community, aboveground biomass accumulation by *Pseudotsuga* was only 44.8% of the community total (Table 8). In contrast, *T. heterophylla* and *T. plicata* accounted for 34.4% and 13.6%, respectively, of annual biomass accumulation with only 9.0% and 7.3%, respectively, of the aboveground biomass (Table 6). In the relatively xeric north slope *Pseudotsuga–Castanopsis* community, *Pseudotsuga* contributed only 61.5% of biomass accumulation but 90.1% of the total aboveground biomass. In this community, *Castanopsis, Tsuga*, and *P. lambertiana* contributed 14.6%, 10.5%, and 10.2%, respectively, of annual biomass accumulation but only 2.5%, 2.9%, and 3.1% of the total biomass.

Similar patterns of biomass accumulation were observed in other communities (Tables 6 and 8). In general, annual biomass accumulation by *Pseudotsuga* was less than its contribution to community biomass. On the other hand, the percentage of annual biomass accumulation contributed by potential climax species such as *Tsuga* and *Thuja* or species in small diameter classes was generally 3–5× their percent of total biomass. In cool-moist and mesic communities the greatest proportion of annual biomass accumulation relative to biomass was contributed by *Tsuga*, the climax species for all these communities (Franklin and Dyrness 1973). In the drier *Pseudotsuga–Castanopsis* communities, *Tsuga* was not as well established so *Tsuga* and *Castanopsis* contributed about equally to annual biomass accumulation.

Successional patterns.—On Watershed 10 succession appears further advanced in some communities than in others. This can be seen in the proportions of biomass of climax *Tsuga* and *Thuja* in the different communities (Table 6), in the distribution of biomass accumulation between the pioneering *Pseudotsuga* and *Tsuga* and *Thuja* in the different communities (Table 8), and in the differences between basal area and leaf area distribution as they relate to stem diameter distribution in the different communities (Fig. 6).

Changes in the relation between leaf area and basal area are a good indication of how far succession is advanced in these communities. *Tsuga heterophylla* has a larger leaf area for a given diameter than *P. menziesii* (Tables 4 and 5). Its presence in the smaller diameter classes can be seen in Fig. 6 in the vertical distance between cumulative curves for basal area and leaf area. The greater the vertical distance between curves, the greater the proportion of *Tsuga* present in the community.

Curves in Fig. 6 show both the relative proportions of *Tsuga* in the communities and the diameter classes in which it is a significant component. In the *Pseudotsuga–Acer–Polystichum* community, *Tsuga* is a significant stand component in diameters <100 cm. In the mesic *Pseudotsuga–Rhododendron–Berberis* and *Pseudotsuga–Rhododendron–Gaultheria* communities, *Tsuga* is present in smaller proportions and primarily in diameter classes <80 cm. In the 2 relatively xeric *Pseudotsuga–Castanopsis* communities, *Tsuga* is a small component of vegetation. Here the basal area and leaf area curves nearly match. In comparing the 2 *Pseudotsuga–Castanopsis* communities, however, the curves for the south ridge community (Fig. 6) suggest the presence of more *Tsuga* than in the north slope community. This is confirmed by leaf biomass data (Table 6).

Any number of factors can influence the rate at which a pioneer tree species is replaced by a climax species. On Watershed 10, 2 factors appear to dominate. The first is peak summer water stress in the community; the second is mortality. Succession seems to proceed more rapidly in mesic than in xeric communities. For example, the mesic *Pseudotsuga–Rhododendron–Berberis* community is further advanced toward climax than the xeric north slope *Pseudotsuga–Castanopsis* community in spite of lower overstory leaf biomass and greater shrub biomass in the latter community.

The other major factor affecting succession rate is clearly the history of mortality. Openings in the canopy created by mortality have surely played a major role in the establishment and growth of climax species. Because they are interrelated, the relative importance of mortality and site water status to rates of succession cannot be certainly stated. However, considering the large fallen log biomass, it seems likely that mortality, whatever the cause, has played the larger role in advancing succession in these forests.

Net Production.—Aboveground net primary production (NPP) in the various communities of Watershed 10 ranged from 6.3 to 10.1 t/ha and averaged ≈8 t/ha across the entire watershed (Table 10). Net production in the various communities was roughly proportional to their standing biomass.

Values of aboveground NPP are comparable to reported values for younger *P. menziesii* ecosystems in the Pacific Northwest. For example, Cole et al. (1967) report NPP of 10 t/ha by a 37-year-old *Pseudotsuga* ecosystem in western Washington and Fujimori et al. (1976) report NPP of 13 t/ha by a 110-year-old *Pseudotsuga* ecosystem in the western Oregon Cascades. There is a major difference between NPP by these younger ecosystems and that of the old-growth forests of Watershed 10. In the younger forests, biomass increment was 75%–80% of NPP. On Watershed 10, NPP consisted entirely of detritus production (Table 10). In fact, depending on the community, between 3 and 6 t/ha of annual NPP were at the expense of standing biomass.

The amount and character of detritus production by forests changes with age. In young forests litter is small, primarily leaves, twigs and small branches and stems. Average litterfall in temperate zone forests is about 3.5 $t \cdot ha^{-1} \cdot yr^{-1}$ (Bray and Gorham 1964) and averages ≈30% nonleaf litter. Litterfall collected in litter traps alone during this study averaged about 4.3 $t \cdot ha^{-1} \cdot yr^{-1}$ across the watershed; of this amount, ≈45% was woody material (Table 9). Total litterfall values reported here are 15%–36% below the average reported by Abee and Lavender (1972) for similar forests of this area; however, the relative proportions of woody to leaf litter are comparable.

Tree mortality can be another major source of litter input. During this study organic matter inputs to the forest floor from mortality averaged about 7 $t \cdot ha^{-1} \cdot yr^{-1}$ across the watershed. This mortality, together with litter collected in traps, is the main part of NPP on the watershed. These data confirm the observation by Odum (1969) that, with increasing maturity, ecosystem net production changes from biomass to detritus. At the same time, the detritus produced changes from primarily small, easily decomposed material to larger, more refractory woody material.

Estimates of belowground net primary production range from ≈2–3.3 $t \cdot ha^{-1} \cdot yr^{-1}$ for the various communities and average 2.9 $t \cdot ha^{-1} \cdot yr^{-1}$ across the watershed (Table 10). These values also include a biomass loss due to large root mortality associated with aboveground mortality. The largest component of belowground NPP is fine root death (Table 10). These values are most likely underestimates. Harris et al. (1973) have reported that root turnover was the largest flux of organic matter in a mixed southern hardwood forest; amounting to ≈7,500 $kg \cdot ha^{-1} \cdot yr^{-1}$. Similar data were not available for *P. menziesii* ecosystems so we used what was felt to be a conservative estimate based on an assumed relation between fine root and foliage turnover. Future studies will probably show fine root turnover to be greater than present estimates.

Autotrophic respiration.—Estimates of total autotrophic respiration ranged from 102.9 $t \cdot ha^{-1} \cdot yr^{-1}$ to 203.7 $t \cdot ha^{-1} \cdot yr^{-1}$ in the various communities and averaged 150.0 $t \cdot ha^{-1} \cdot yr^{-1}$ overall for the watershed. These values are very large compared to estimates reported for other forest types. For example, Woodwell and Botkin (1970) estimated autotrophic respiration for the mixed oak-pine Brookhaven forest to be 15.2 $t \cdot ha^{-1} \cdot yr^{-1}$ and Sollins et al. (1973) report a similar value of 15.9 $t \cdot ha^{-1} \cdot yr^{-1}$ for a *Liriodendron* forest in eastern Tennessee.

Although large compared to estimates by Woodwell and Botkin (1970) and Sollins et al. (1973), autotrophic respiration values appear reasonable when differences between these forests and the oak-pine or *Liriodendron* forests are considered. First, average total biomass for the watershed is large compared to the 101.9 t/ha for the oak-pine Brookhaven forest or the 177.1 t/ha for the *Liriodendron* forest. This 4- to 7-fold difference in respiring biomass may account for a large part of the difference. Another factor is the difference between evergreen and deciduous forests. Foliage respiration accounted for 68% of total autotrophic respiration in the evergreen forest of Watershed 10 while respiration by stems, branches, fine roots, and coarse roots accounted respectively for 2.2%, 7.2%, 2.6% and 10% of total respiration. Yoda et al. (1965) found similar proportions of foliage respiration in two *Abies sachalinensis* stands on Hokkaido, Japan. In these *Abies* stands, foliage respiration for 1 mo was 63.0% and 68.3% of total autotrophic respiration. In the deciduous *Liriodendron* forest (Sollins et al. 1973) foliage respiration was only 34% of total autotrophic respiration. Thus, the presence of respiring foliage during winter appears to increase annual respiration requirements considerably, especially in the relatively warm winters of the U.S. Pacific Northwest.

Use of literature values of root, bole, and stem respiration probably reduces the reliability of respiration estimates given here. However, since foliage respiration accounted for nearly 70% of total respiration and measured foliage respiration rates for *P. menziesii* (Brix 1971) were used in calculating foliage respiration, even a ±50% error in respiration rates of all other components would result in $\approx \pm 15\%$ error in total respiration.

Gross production.—In keeping with the large values for autotrophic respiration, estimates of gross primary production (GPP) were also large compared to results from other studies. Woodwell and Botkin (1970) estimated GPP of the Brookhaven forest to be 27.2 $t \cdot ha^{-1} \cdot yr^{-1}$ and Sollins et al. (1973) report a similar estimate of 27.6 $t \cdot ha^{-1} \cdot yr^{-1}$ for the *Liriodendron* forest. Average GPP for all communities of the watershed is 160.9 $t \cdot ha^{-1} \cdot yr^{-1}$, roughly 6× the reported estimates for eastern forests.

Net primary production is a small part of gross production in these communities. The ratio of NPP to GPP ranged from 6.0% to 7.9% for the various communities of the watershed (Table 10). Reported ratios in other, younger forests are 42.4% for a *Liriodendron* forest (Sollins et al. 1973) and 45% for the Brookhaven oak-pine forest (Woodwell and Botkin 1970).

A decreasing proportion of net to gross production as forests age is the expected result of normal forest growth (Kira and Shidei 1967, Odum 1969). Gross primary production should remain roughly constant as succession proceeds because of relatively constant foliage biomass. At the same time, however, increasing woody biomass places increasing demands on carbohydrate production for maintenance respiration.

The large GPP values for old-growth forests in this area imply high net production by younger stands. Leaf biomass in *P. menziesii* forests appears to stabilize at age 20–40 yr (Turner and Long 1975) and gross production after this should be about equal to that of older stands. With less woody biomass maintenance requirement, peak net production may approach the 50 t/ha difference between GPP and the foliage plus fine root respiration of forests of Watershed 10. Net production approaching the above figure has been observed in this region by Fujimori (1971) who reports above- plus belowground NPP of 36.2 t/ha in a 26-year-old *T. heterophylla* stand near the Oregon coast.

Net ecosystem production.—Net ecosystem production (NEP) in the *Pseudotsuga–Acer–Polystichum* community of the watershed is near the theoretical zero of steady-state biomass climax forest while average NEP for the watershed is 3.3 $t \cdot ha^{-1} \cdot yr^{-1}$ (Table 10). Values for Watershed 10 are generally below the 5.4 $t \cdot ha^{-1} \cdot yr^{-1}$ reported for the oak-pine forest at Brookhaven (Whittaker and Woodwell 1969), but higher than the 2.9 $t \cdot ha^{-1} \cdot yr^{-1}$ estimate for hardwood forests at Hubbard Brook, New Hampshire (Whittaker et al. 1974).

It is possible that forests of Watershed 10 and similar forests of the Pacific Northwest may have a period during succession in which NEP is negative. This would occur if climax biomass were less than peak biomass of seral forests. There is some evidence that this is the case during *Pseudotsuga* to *Tsuga* succession. Table 5 shows that *Tsuga* has a smaller stem biomass than does a comparable size *Pseudotsuga*. Thus, for the same basal area, biomass of a *Tsuga* stand would be less than that of a *P. menziesii* stand.

A limited determination of stand basal area was made in old-growth (>400 yr old) *Pseudotsuga* and near climax *Tsuga–Pseudotsuga* stands in the western Oregon Cascades. A cruising prism was used for the determination (Dilworth 1974). Maximum basal area measured was 140 m^2/ha in an old-growth *Pseudotsuga* stand, while the observed range was 70 m^2/ha–140 m^2/ha. The few predominantly *Tsuga* stands we could locate ranged from 70 m^2/ha to 84 m^2/ha, lower than all but a few of the *Pseudotsuga* stands. These limited data suggest a lower biomass for climax *Tsuga* stands than for seral *Pseudotsuga* stands near peak biomass. Moreover, these observations imply that achievement of steady-state biomass in these forests may be somewhat more complicated than is suggested for other forest types (Whittaker et al. 1974).

One final point deserves discussion. If mortality rates observed during this study were not typical of long-term averages for these communities, production relations in these communities would be somewhat different. For example, if long-term mortality on Watershed 10 were 0.1% of standing biomass instead of the observed 1%, the watershed average biomass increment would increase from $-4.5\ t\cdot ha^{-1}\cdot yr^{-1}$ to $1.8\ t\cdot ha^{-1}\cdot yr^{-1}$. In spite of this change, NPP, GPP, and NEP would remain the same.

As mentioned earlier, it is possible that long-term mortality is lower than that observed during this study. Values of NPP and NEP are more like those of seral forests than an ecosystem approaching climax as would be indicated by the negative biomass increment (Table 10). Potential biomass accumulations in this region are large; Fujimori et al. (1976) report a stem biomass accumulation alone of 1,590 t/ha for one old-growth *Pseudotsuga* forest in the western Oregon Cascades. Thus, it is possible that our period of observation coincided with a mortality event. If so, contrary to data in Table 10, biomass in the communities may continue to increase for several hundred years. On the other hand, if biomass of these forests declines as climax approaches, then the high mortality may be a normal factor in their successional pattern. More extensive research will be needed to determine this aspect of the relation between production and succession for this forest type.

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