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PRIMARY PRODUCTIVITY OF A YOUNG *Tsuga heterophylla* STAND AND SOME SPECULATIONS ABOUT BIOMASS OF FOREST COMMUNITIES ON THE OREGON COAST

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This research was conducted by Mr. Fujimori when he was working as a research associate at Corvallis, Oregon, in cooperation with Pacific Northwest Forest and Range Experiment Station and Oregon State University.

ABSTRACT

A 26-year-old *Tsuga heterophylla* stand on the Oregon coast had a total biomass and current net annual production of 231.1 and 36.2 metric tons per hectare, respectively.

Keywords: Stand increment estimate, forest appraisal, ecosystem, *Tsuga heterophylla*.

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INTRODUCTION

Studies of primary productivity in forest communities are important not only in themselves but also as essential components of cycling or total ecosystem studies. Many new data on primary productivity have been reported worldwide, some of which have been organized and summarized in general reviews by Kira and Shidei (1967), Tadaki and Hachiya (1968), and Whittaker (1970). At least around the middle latitudinal zone of the northern hemisphere, considerable data on net production have been accumulated. Surprisingly, however, little information has appeared concerning coniferous forest communities in western North America, world famous for high productivity.

In this paper, I report my investigation of net production and production structure of *Tsuga heterophylla* based on analysis of a stand which appeared to be at the peak stage of production in its life cycle. In addition, I have speculated on the factors responsible for the rather large accumulations of biomass in forest communities in this region.

ENVIRONMENT AND FEATURES OF THE EXPERIMENTAL STAND

The experimental stand is located along the Oregon coast in the northwestern United States. Climatic data from a weather station nearby are shown in table 1. Annual temperature differences are minimal, neither excessively hot in summer nor cold in winter. Annual precipitation is high except during the summer; but even during summer months, frequent fog and low clouds compensate for the dry period. Isaac (1946) reported that moisture from fog adds as much as 26 percent to annual precipitation. Soils in the study area are relatively deep, fine textured, and fertile Sols Bruns Acides developed from tuffaceous siltstone (Franklin et al. 1968). The silt loam to silty clay loam A and B horizons are generally 100 to over 150 centimeters in thickness. Although acid (about pH 5.1), the soils are high in organic matter and nitrogen.

The experimental stand lies within the highly productive *Picea sitchensis* Zone (Franklin and Dyrness 1969). Constituent tree species in this Zone are *Picea sitchensis*, *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Thuja plicata* and *Abies grandis*, but only the first three are common in the vicinity of the experimental area. *Alnus rubra* is found on recently disturbed land.

The stand which occupied the experimental area before harvesting was composed of mature *Tsuga heterophylla*, with some *Picea sitchensis*. In 1951 and 1952, it was thinned, eventually resulting in a 1-acre opening. The understory trees then grew rapidly within this opening to form a new stand which was used in the experiment. The area undoubtedly received considerable shade from the sides until the surrounding trees were clearcut in 1962. According to stem analyses, constituent trees are from 19 to 32 years old. The stand is already closed, dense, competitive, and an understory is absent. No management or treatment has been carried out since this new stand formed. Based on figure 1 (Meyer 1937) and stand characteristics, this stand is believed to be at the stage of maximum yearly productivity in the development of *Tsuga heterophylla* forest communities.

Stand characteristics are:

Tree age	19-32 years
Stand density	6,627 trees per hectare
Total basal area	49.4 square meters per hectare
Mean d.b.h. (diameter at breast height)	7.1 centimeters
Mean tree height	10.0 meters
Mean clear stem length	4.2 meters

Table 1.--*Climatic data from near the experimental stand in Oregon and a station in the temperate zone in Japan*

Item	Otis, Oregon	Aomori, Japan
Elevation (meters)	49	4
Latitude	45°02'	40°49'
Temperature (degrees centigrade):		
Average annual	10.3	9.1
January average	5.3	-2.7
January average minimum	2.2	-6.7
July average	15.5	20.4
July average maximum	20.9	24.5
Index of warmth	65.4	73.8
Index of coldness	0	-24.3
Precipitation (millimeters):		
Average annual	2,995	1,305
June to August	196	329
Hours of sunshine:		
April to September	1,511	1,145
October to March	720	575

Remarks: (1) The data from Otis are mean values from 1951-60, and those from Aomori are from 1931-60.

(2) Index of warmth is the summation of the accumulated temperatures over 5° C. in each month for 1 year. Index of coldness is accumulated temperatures below 5° C.

(3) The data concerning hours of sunshine from Otis are from just the experimental area and are the mean value from 1936 to 1952.

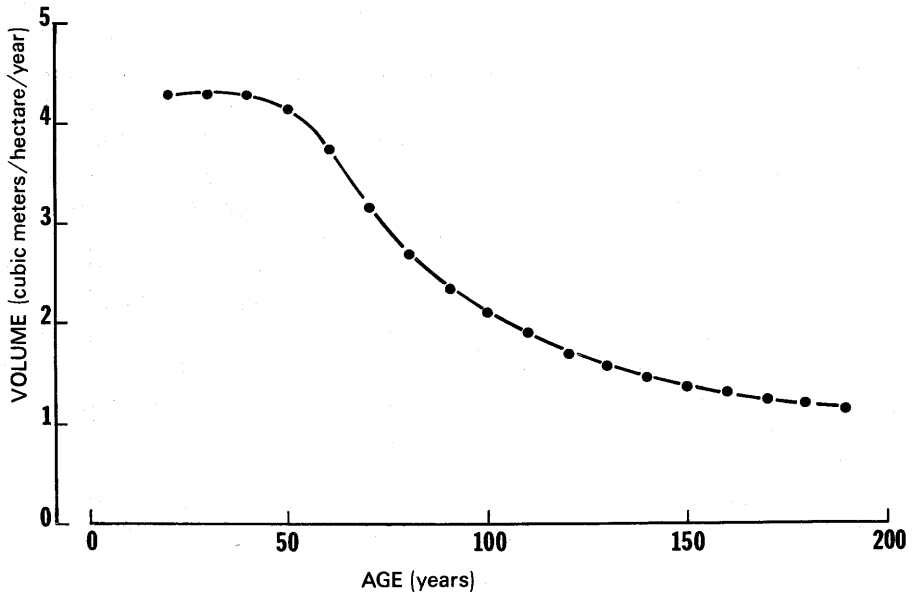

Figure 1.--Periodic annual volume (stem) increment of *Tsuga heterophylla* on highly productive sites in the Pacific Northwest (Meyer 1937).

METHOD

Most fieldwork was carried out between April 20 and May 5, 1970. An 83-square-meter sample plot was selected which included 55 trees. Ten sample trees then were selected in direct proportion to the frequency distribution of d.b.h. and tree height in the stand and were cut down. Each component was measured by the stratified clip method. Since this method was devised by Monsi and Saeki (1953), it has been used mainly by Japanese workers. By use of this method, sample trees are divided into vertical strata of a certain interval (50 cm. in this work) from base to tip. Tree components are measured within each vertical stratum. Adoption of this method makes it easy to describe and illustrate vertical stand structure profiles in experimental stands. As the angles of branches from the stem were regarded as nearly at right angles (90°), a leaf-bearing branch, from base to tip, was placed in the same 50-centimeter stratum, even if the tip was in another stratum.

In general, the net production in 1969 (Pn) is defined as the total amount of the annual biomass increment at the time of investigation (y_N) plus the biomass lost to litterfall and grazing during 1969 (L_N and G_N, respectively) (Kira and Shidei 1967).

$$Pn = y_N + L_N + G_N \tag{1}$$

Since measurements of L_N and G_N are difficult to obtain and are considered relatively small when compared with y_N, they were disregarded, and Pn was defined as follows in this report:

$$Pn = y_{NS} + y_{NB} + y_{NL} + y_{NR} \tag{2}$$

where y_{NS}, y_{NB}, y_{NL}, and y_{NR} indicate the biomass increment produced during 1969 in stems, branches, leaves, and roots.

Stem increment was calculated by the common method of stem analysis. This method was also adapted to the measurement of branch increment (Fujimori 1970). Three to five sample branches were chosen from each stratum in direct proportion to the branch size frequency distribution. Each sample branch was cut into 5- to 30-centimeter segments from bough to twigs in proportion to its length and thickness, and its annual growth rings were examined with a magnifying glass. Total branch increment was determined by multiplying total branch biomass in each stratum by the growth rate of the branch, as determined from the samples, in its respective stratum. Leaf increment was obtained by weighing fresh leaves which had developed during the recent year. Since direct measurement of the root increment is difficult, it was estimated from the product of root biomass and the growth rate of aboveground nonphotosynthetic organs. This calculation is based on the assumption that growth rates of roots are equivalent to those of aboveground nonphotosynthetic organs. This method is probably rough, but more accurate methods for estimation of root increment were not available.

Small samples of tree components were taken to the laboratory for analyses and were ovendried (80° C.). All weight values are expressed as dry in this report.

Area on one side of the leaf was determined by the product of leaf weight and ratio of leaf area per unit of leaf weight in each stratum. Light intensity was measured using Weston Illumination Meters, Model No. 756.[1/]

The allometric method has been developed for estimating biomass values for tree components per unit area from sample trees (Ogawa et al. 1965, Kira and Shidei 1967). Although the allometric method is regarded as the most precise method for estimating values per unit area, the following method provides values regarded as sufficiently accurate and is easier (Ando 1962, Fujimori and Yamamoto 1967). This simpler method assumes that the ratio of the sum of biomass in sample trees to that of whole trees per unit area is in proportion to the ratio of respective basal areas. In effect,

$$y = y' \frac{G}{G'}, \tag{3}$$

where y, y', G, and G' represent the total amount of biomass per unit area, biomass of the sample trees, the total basal area per unit area, and basal area of sample trees, respectively. In this report, biomass values for tree components per unit area were estimated by this method.

RESULTS

Production Structure

The vertical distribution of the total aerial biomass for each tree component in the experimental stand is shown in figure 2. In general, the canopy structure of tolerant tree species is deeper than that of intolerant species. The canopy structure of this stand is that of a typical tolerant species. The vertical distribution of biomass increment is shown in figure 3.

[1/] Use of brand names does not imply endorsement by the U.S. Department of Agriculture.

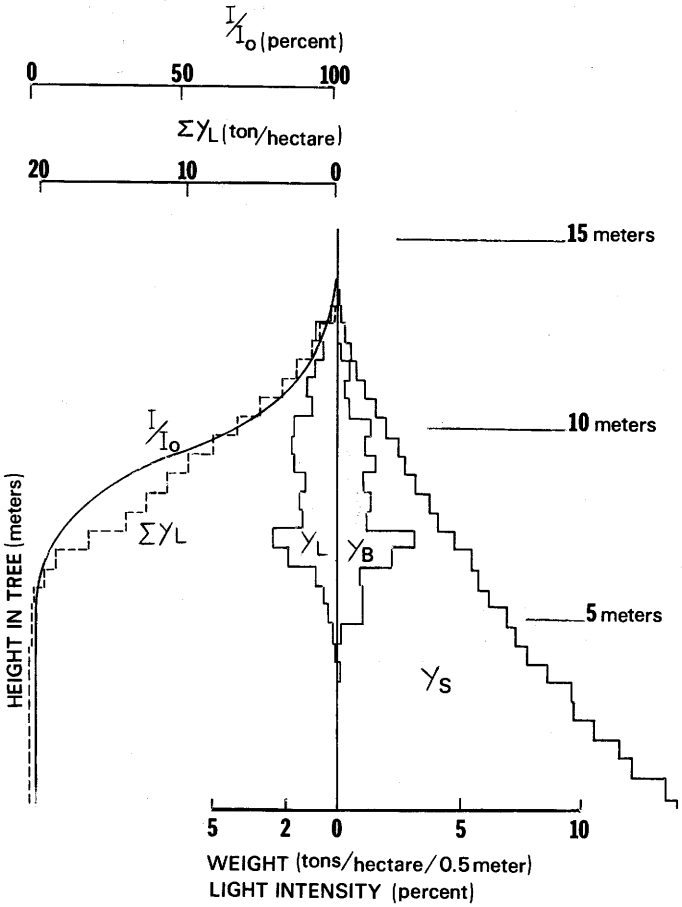

Figure 2.--Vertical distribution of leaf weight (y_L), branch weight (y_B) stem weight (y_S), and relative light intensity ($\frac{I}{I_o}$) in the experimental stand.

The characteristic of light penetration through the forest canopy is a most important factor for determining rates of photosynthesis and the distribution of photosynthetic organs in the forest community. A strong relationship can be observed between the distribution of accumulated leaf weight and relative light intensity (figs. 2 and 3); their distribution and that of stem increment are similar (fig. 3). The characteristics of these relationships have been pointed out by Monsi and Saeki (1953), Tadaki and Shidei (1960), and Shinozaki et al. (1964).

Monsi and Saeki (1953) have shown how the course of light extinction through the plant canopy can be calculated using Beer-Lambert's formula:

$$I = I_o e^{-KF} \tag{4}$$

where I and I_o denote the light intensity under the total leaf area per unit area from the tip to a certain stratum level (F) and the incident light intensity and K denote the extinction

coefficient. The F value at the bottom of canopy is called leaf area index (LAI), i.e., total leaf area within the entire canopy per unit area. Since I, I_o, and LAI were measured, K was calculated using formula 4. The values of I/I_o (percent), LAI (ha./ha.), and K in this stand were 0.79, 7.65, and 0.63. When F is substituted for leaf weight, K becomes 0.23. The I/I_o of this stand is extremely small, demonstrating that *Tsuga heterophylla* is very tolerant.

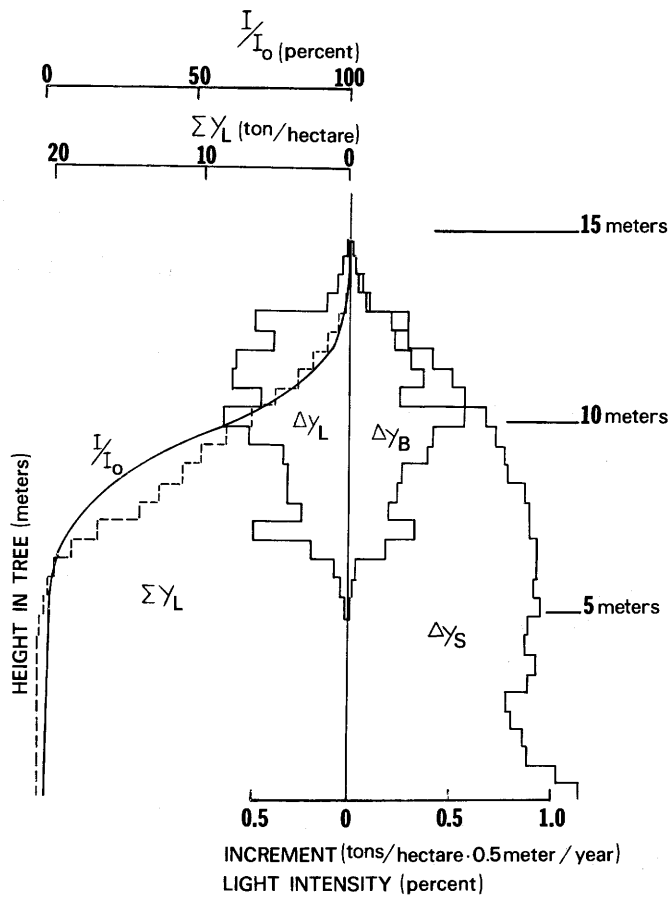

Figure 3.--Vertical distribution of leaf increment (Δy_L), branch increment (Δy_B), stem increment (Δy_S), and relative light intensity ($\frac{I}{I_o}$) in the experimental stand.

Values Per Hectare

Accumulated biomass and net production are 231.1 and 36.2 metric tons per hectare respectively (table 2). The ratio of biomass in the stem to the whole tree (0.65) is quite high for a young stand, which suggests this stand is in a fully stocked, competitive condition.

Table 2.--*Dry weights of forest components (metric ton per hectare) in experimental stand*

Component	Accumulated biomass	Current net annual production
Stem	150.9	20.4
Branch	20.7	4.3
Leaf	21.1	6.0
Root	38.4	5.5
Whole	231.1	36.2

The annual biomass increment (net annual production) is very high, not only for coniferous forests but also for other forests types which have been analyzed in eastern Asia and perhaps even in the world (Tadaki and Hachiya 1968) (fig. 4). Figure 1 shows the periodic annual volume stem increment of *Tsuga heterophylla* in the high site conditions of the study area. When increments of leaf, branch, and root are added to this graph, the peak of the curve will shift to the left to some extent, suggesting that around 20-30 years in this stand might be regarded as the highest stage of production.

Zavitkovski and Stevens[2/] reported that net production of *Alnus rubra* in similar coastal Oregon areas is 26.0 tons per hectare per year in its highest stage of production. Although the method they used seems questionable in part, this value suggests high productivity even in deciduous broadleaf forest communities in this area.

DISCUSSION

Large accumulations of biomass predominate in pure or mixed forest communities of *Pseudotsuga menziesii*, *Picea sitchensis*, and other species, as well as those of *Tsuga heterophylla* in the coastal northwestern America. I would like to speculate briefly on two possible causes for the existence of such large biomasses--high productivity per unit period of time and a comparatively long continuous period at a certain level of productivity during the lifespan of a forest. As for the first cause, the data in this report suggest high yearly productivity of forest communities in this area during early stages of growth.

Relationships between photosynthesis, respiration, and environmental factors, especially climatic conditions, must be the key elements in this situation. Climatic data collected near the experimental stand and, for comparison, from Aomori, Japan, located in a temperate zone of deciduous broadleaf forest but where *Tsuga* and *Abies* forest communities are also common, are shown in table 1.

[2/] J. Zavitkovski and R. D. Stevens. Primary productivity of red alder ecosystems. (Ecology, in press.)

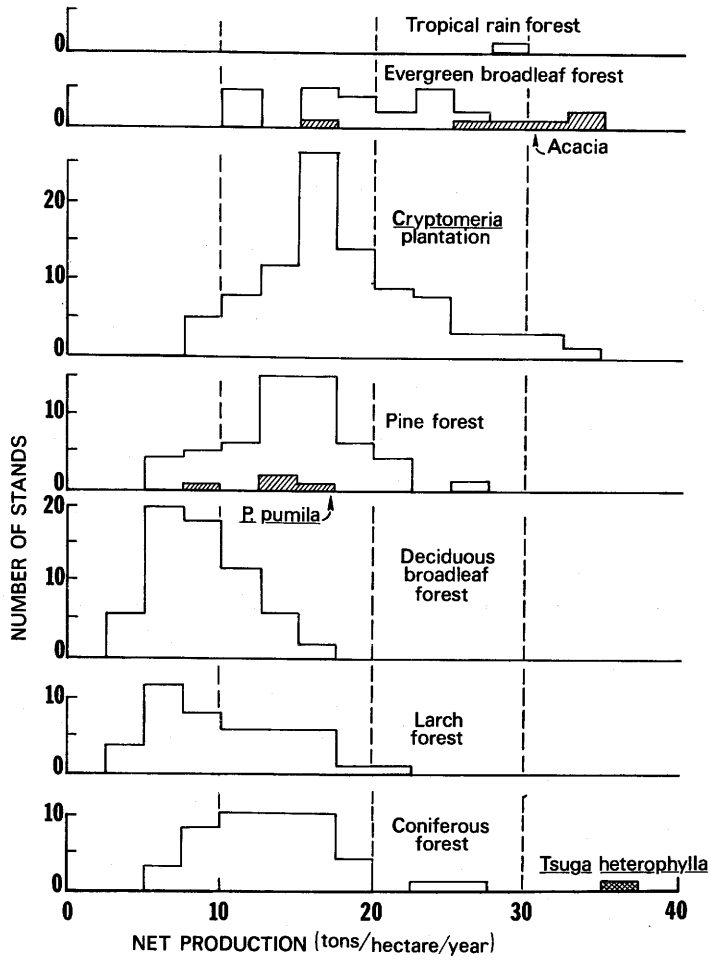

Figure 4.-- Estimates of net production in various forest types (most of these were summarized by Tadaki and Hachiya (1968); these data are limited to forests in Japan except for those for tropical rain and *Tsuga heterophylla* forests)

In the experimental area, accumulated hours of solar radiation during the summer are comparatively high (table 1), because clear weather is common and days are long promoting photosynthesis by forest communities. On the other hand, despite the frequent clear weather, temperatures do not rise so high as to excessively increase respiration rates (table 1). Consequently, the ratio of net production of photosynthate to gross production (net plus respiration loss) is probably comparatively high because temperatures are close to optimum for net production (Negisi 1966).

Mild temperature changes, especially warmth during winter, must be another important factor. The index of coldness in the Oregon coast is zero, which means there is

no month with a mean temperature less than 5° C., whereas the index of coldness in Aomori is -24.3° C. (table 1). In spite of this fact, it is reported that there is no measurable biomass increment in western Washington and Oregon trees during winter (Dimock 1964). This must be an effect of day length, since cessation of growth in fall and winter is usually conditioned by shorter days as well as lower temperatures, and the accumulated hours of sunshine during winter are only half as much as during summer (table 1). However, during winter, even though biomass increment has not been detected, there is a possibility that some photosynthesis is occurring. Appreciable net photosynthesis by *Pseudotsuga menziesii* has been reported during winter in western Washington, and this must contribute significantly to stored food reserves which accumulate prior to the flush of spring growth (Helms 1965). Furthermore, the forest trees on the Oregon coast are less subject to severe coldness, which often weakens the vigor of forest communities, and also drastic temperature changes in spring and autumn, which often prevent normal or rapid growth of trees. All of these environmental influences hasten and prolong productivity.

Concerning the long, continuous period at a certain level of productivity, I would speculate. The climate in this area is mild, and drastic changes of weather, such as might weaken the vigor of forest communities, are infrequent. In particular, strong winds which disturb or weaken forest communities are uncommon in this area compared with many other temperate regions. Root systems of forest communities here are comparatively deep[3/] because of genetic and environmental factors. The latter probably include favorable soil conditions (Franklin et al. 1968) and a summer dry period which encourages deep root penetration. It is proposed that the ratio between above- and below-ground components becomes unbalanced as trees grow; i.e., the root system is too small to support the aerial biomass, thereby limiting size of trees. From this viewpoint, infrequent strong winds and deep root systems may be important factors in permitting large biomass accumulations.

The largest minus factor to the growth of forest trees on the Oregon coast must be the lack of rainfall during summer (table 1), even though the fog and low clouds provide partial compensation. The growth rates of trees decline considerably after mid-July in comparison with those recorded between May and mid-July (Dimock 1964).

Genetic factors are also important in understanding the existence of tree species capable of growth to such large sizes. Reportedly, the potentially large species around this region were able to survive the Glacial Age without major gene pool depletion (Silen 1962). Trees in this region thus escaped the direct effects of glaciers by migrating geographically to the south or north, as the climate varied and glaciers advanced or receded.

Large numbers of advanced ecological data will have to be accumulated in the future to substantiate these speculations and assumptions. Meanwhile, this study provides a profile of biomass accumulation and distribution in a young coniferous forest ecosystem; as such, it provides one set of data which can be combined with further studies of production in other age classes or of processes for fuller understanding of ecosystem function and development.

[3/] Unpublished data on file at Forestry Sciences Laboratory, Pacific Northwest Forest and Range Experiment Station, Corvallis, Oregon.

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