

AN ABSTRACT OF THE THESIS OF

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Title: LIMITS ON ABOVEGROUND NET PRIMARY PRODUCTION, LEAF AREA, AND  
BIOMASS IN VEGETATIONAL ZONES OF THE PACIFIC NORTHWEST.

Signature redacted for privacy.

Abstract approved: \_\_\_\_\_  
Richard H. Waring

Samples of mature vegetation from 8 of 12 major vegetational zones in Oregon and Washington, representing about 80% of the area of the two states, were studied along a latitudinal transect from the Pacific Coast to the east slopes of the Cascade Mountains. Six stands were in forest zones, one in woodland and one in the shrub-steppe. Aboveground net primary production (NPP, estimated as the sum of stem, branch, and foliage production) ranged from 0.3 to 14.7 t ha<sup>-1</sup> yr<sup>-1</sup>, aboveground biomass from 3 to 1500 t ha<sup>-1</sup>, and area of all sides of leaves from 1 to 40 ha ha<sup>-1</sup>, with minimums in the shrub-steppe zone and maximums in the coastal forest zone. Average day air temperatures were less than -2°C only 2% of the winter at the coast, contrasted to 87% in the shrub-steppe. Although annual precipitation ranged from 20 cm in the shrub-steppe to 260 cm at the coast, it was a relatively poor predictor of stand structure and production.

Maximum leaf areas were closely related to a simple growing season water balance in seven vegetational zones. In the subalpine conifer

zone, leaf area appeared limited by temperature. Of the water balance components, evaporative demand alone accounted for 95% of the variance in leaf area. Biomass and NPP increased linearly with leaf area up to a leaf area of 20 ha ha<sup>-1</sup>. Biomass continued to increase with increasing leaf areas. NPP was also linearly related to minimum January temperatures. Except in the coastal forest zones, NPP for any given leaf area was less than maximum values reported for other mature systems elsewhere in the world.

Limits on Aboveground Net Primary Production,  
Leaf Area, and Biomass in Vegetational  
Zones of the Pacific Northwest

by

Henry Lewis Gholz

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LIMITS ON ABOVEGROUND NET PRIMARY PRODUCTION, LEAF AREA, AND BIOMASS  
IN VEGETATIONAL ZONES OF THE PACIFIC NORTHWEST

Henry L. Gholz

Forest Science Department

School of Forestry, Oregon State University

Corvallis, Oregon 97331

Abstract. Samples of mature vegetation from 8 of 12 major vegetational zones in Oregon and Washington, representing about 80% of the area of the two states, were studied along a latitudinal transect from the Pacific Coast to the east slopes of the Cascade Mountains. Six stands were in forest zones, one in woodland and one in the shrub-steppe. Aboveground net primary production (NPP, estimated as the sum of stem, branch, and foliage production) ranged from 0.3 to 14.7 t ha<sup>-1</sup> yr<sup>-1</sup>, aboveground biomass from 3 to 1500 t ha<sup>-1</sup>, and area of all sides of leaves from 1 to 40 ha ha<sup>-1</sup>, with minimums in the shrub-steppe zone and maximums in the coastal forest zone. Average day air temperatures were less than -2°C only 2% of the winter at the coast, contrasted to 87% in the shrub-steppe. Although annual precipitation ranged from 20 cm in the shrub-steppe to 260 cm at the coast, it was a relatively poor predictor of stand structure and production.

Maximum leaf areas were closely related to a simple growing season water balance in seven vegetational zones. In the subalpine conifer zone, leaf area appeared limited by temperature. Of the water balance components, evaporative demand alone accounted for 95% of the variance in leaf area. Biomass and NPP increased linearly

with leaf area up to a leaf area of 20 ha ha<sup>-1</sup>. Biomass continued to increase with increasing leaf areas. NPP was also linearly related to minimum January temperatures. Except in the coastal forest zones, NPP for any given leaf area was less than maximum values reported for other mature systems elsewhere in the world.

Keywords: Net primary production, biomass, leaf area, precipitation, evaporation, temperature, forest, shrub-steppe, Oregon, vegetation zone.

Running title: Limits on structure and production

## INTRODUCTION

The volume of literature dealing with biomass and net primary production (NPP) is growing steadily. But past sampling of these parameters has often not represented major vegetational zones. This is particularly true of tropical ecosystems but also holds for temperate coniferous forests of the Pacific Northwest. The deficiency in sampling large coniferous forests is understandable, for large trees may exceed 2 m in diameter and may require over 100 man-days of field labor to analyze fully. In the Pacific Northwest, productivity research has focused on the economically important natural forests of Pseudotsuga menziesii and Tsuga heterophylla west of the Cascade range (Franklin et al. 1972). Other forests are often less accessible or have less value.

Grier and Logan (1977) recently furnished the first estimates of NPP and biomass for old-growth Pseudotsuga forests in the western Cascade Mountains. Fujimori et al. (1976) reported data for three stands around 100 years old in Oregon: a coastal Picea sitchensis (Bong.) Carr./ Tsuga heterophylla stand, a western Cascades Pseudotsuga stand, and an Abies procera Rehd. stand. Several studies have been done in younger stands of Pseudotsuga in Washington (Turner 1975, Cole et al. 1969, Reikerk 1957, Heilman 1961). Few reports are available from forests located near the Cascade summit and eastern slope, although Gholz (1979) has described the production relations of a Juniperus occidentalis Hook. var. occidentalis stand in central Oregon. Only two studies have generalized about structural characteristics throughout the Pacific Northwest and none have addressed regional production patterns. Grier and Running (1978) found leaf areas for five



vegetation types ranging from coastal forests to desert shrub to be highly correlated with a simple water balance. Waring et al. (1977) found that leaf areas for 40 conifer stands in the western Cascade Mountains and the Siskiyou Mountains in southwest Oregon were related to physiologically defined indices of moisture stress and growing season temperature, with leaf areas decreasing at high or low values of the latter index and at low values of the former index. At a global scale, production and biomass from other regions have been correlated with such variables as annual precipitation and mean annual temperatures, a measure of evapotranspiration, or length of growing season (Leith 1975), and results used to estimate these values for the Pacific Northwest.

This study tests the hypothesis that NPP by mature natural vegetation is in direct proportion to the leaf area supported. This relationship has been reported for plantations of several coniferous tree species (Albrektson et al. 1977, Miller and Miller 1976), and, up to a certain level of leaf area, for a variety of crop species (Watson 1958, Kallis and Tooming 1974, Fukai and Loomis 1976). The production relations of immature forests should be similar to plantations, while old-growth forests have increased mortality and may represent lower levels of production. A wide range of vegetation types was selected to test the hypothesis. In addition, the total aboveground biomass for each stand was calculated and compared with its leaf area. A secondary objective was to evaluate the major climatic restraints upon the development of leaf area and forest productivity.

## STUDY AREAS

Eight of the major vegetation zones in the Pacific Northwest, as described by Franklin and Dyrness (1973), were selected for study along a transect between 44° and 45° N Lat. from the Oregon Coast (124° W Long.) 350 km east to the high desert in central Oregon (121° W Long.). The location of sampled areas are shown in Figure 1. Although this transect was established along one latitude, the general pattern of vegetation and environment should apply equally well along west to east transects from southern British Columbia to northern California. Site descriptions are summarized in Table 1.

The Picea sitchensis zone forms a narrow coastal band highly influenced by the adjacent Pacific Ocean. Picea sitchensis and Tsuga heterophylla are the dominant tree species. Two areas were sampled in this zone, located 0.4 km apart, in the Cascade Head Experimental Forest near Otis, Oregon. A third stand located 3 km away was included for comparative purposes, but was not used as a main site for this study because the canopy has been much reduced by wind damage (Grier 1978). The first (Ia) was dominated by Picea sitchensis and the second (Ib) by Tsuga heterophylla (Table 1, Fig. 2). The understory of the two stands was dominated by 1.5- to 2.5-m tall Tsuga heterophylla. Shrubs were Menziesia ferruginea (nomenclature follows Hitchcock and Cronquist 1973), Vaccinium parvifolium, and Oplopanax horridum. There were several fern species present, especially Polystichum munitum, Blechnum spicant, and Athyrium filix-femina, while Oxalis oregana was the most common herb. Soils were essentially stone free and were residual silt loams to silty

clay loams derived from fine-grained marine sedimentary rocks of the Tyee formation (Grier 1978).

The Coast Range rises to maximum elevations of around 1200 m, and contains rich forests of Pseudotsuga menziesii and Tsuga heterophylla. The second study area (II) was situated on the east side of the Coast Range, overlooking the Willamette Valley in a moderately developed rain shadow (Tables 1 and 2). This area is the dry margin of the Tsuga heterophylla zone and is not representative of much of the Coast Range to the west. The plot was located in a Pseudotsuga/Abies grandis forest in the McDonald Forest of Oregon State University, 8 km northwest of Corvallis. Acer macrophyllum was a minor overstory component occurring in gaps caused by mortality of the Pseudotsuga or Abies. There were a few Pseudotsuga on the plot 300+ years old, but most of the dominants were smaller and averaged 150 years in age. Corylus cornuta var. californica was the most common understory shrub along with some Abies seedlings, Rosa spp., Holodiscus discolor, Vaccinium parvifolium, Symphoricarpos albus, and Berberis nervosa. Common herbs were Adenocaulon bicolor, Achlys triphylla, and Vancouveria hexandra. Soils were derived from colluvium and residuum from basalt. A heavy brown-red clay was encountered at 50 cm and observed to restrict rooting. Stones occupied < 2% of the solum.

The next three study areas were located from the base to the summit of the western slope of the Cascade Mountains. Stand III was in the Willamette National Forest in the Tsuga heterophylla zone 32 km east of Sweet Home, Oregon. This site was dominated by Pseudotsuga menziesii and was a Site Class III Douglas-fir stand (McArdle et

al. 1961). Acer macrophyllum composed about 4% of the basal area. Only 2 shrub species were of major importance, Gaultheria shallon, present at 95% cover, and Acer circinatum. Berberis nervosa was also present as were Rhododendron macrophyllum and Vaccinium parvifolium. The herb layer was generally absent or present in trace amounts and consisted of Galium oreganum and grasses. Surface soils were dark brown gravelly loams with 60% rounded and subangular stones by volume to a depth of 30 cm. Subsoil layers were dark yellowish brown gravelly or cobbly loams, massive with angular gravels increasing to 80% of the volume at 90 cm. Bedrock, encountered at 90 cm, was moderately competent andesites and basalts.

Area IV (Table 1) was located in the Willamette National Forest in the Abies amabilis zone where both Tsuga heterophylla and Abies amabilis occur in the understory. This area was near the summit of the geologically old (Oligocene and Miocene) western Cascades (Franklin and Dyrness 1973). The plot had 5 species of dominant and codominant conifers: Pseudotsuga menziesii, Tsuga heterophylla, Abies amabilis, Abies procera, and Pinus monticola (1 tree on the 0.25 ha plot). Pseudotsuga and Tsuga were the most numerous and averaged 150 years old, although there were a few residual Pseudotsuga 400+ years old. The shrub layer was dominated by Tsuga and Abies amabilis seedlings along with some Acer circinatum, Pachistima myrsinites, Vaccinium membranaceum, and Rosa gymnocarpa. The rich herb layer averaged 50% cover and included mainly Cornus canadensis, Chimaphila umbellata, Asarum caudatum, Clintonia uniflora, and various Pyrola species. Soils were sandy loams with stone volume increasing from 0% at 10 cm to 75% at 90 cm. At 90 cm a bouldery C layer was encountered in

which there were few roots with common 4 to 10 cm chunks of very fine soil in friable matrix.

The third area in the western Cascades (V, Table 1, Fig. 3) was at the summit of Santiam Pass and the crest of the "newer" (Pliocene and Pleistocene) high Cascade Mountains in the Tsuga mertensiana zone. Tsuga mertensiana represented 98% of the basal area with Abies amabilis and A. lasiocarpa sharing the other 2%. No tall shrubs were present, although Tsuga and Abies seedlings abounded. Xerophyllum tenax, Vaccinium membranaceum, and V. deliciosum were the common low shrubs and herbs. Soils were underlain by a gray porphyritic flow bedrock at 50 cm. Stones and boulders were common on the surface, although stone contents in the surface mineral soil were only 15%, increasing to 20% at 50 cm.

The last three areas were located in the increasingly arid rain shadow of the Cascades east of the crest. Study area VI (Table 1, Fig. 4) was in the Pinus ponderosa zone on the Metolius Research Natural Area (Franklin et al. 1972), Deschutes National Forest. Uneven aged Pinus ponderosa was the only tree species. Again, there were a few large (> 1 m DBH) trees, although most of the basal area was in trees 20 to 50 cm dbh. The understory was dominated by Artemisia tridentata var. tridentata, and Purshia tridentata and even-aged groups of young Pinus ponderosa. The sparse herb layer included mainly grasses and sedges. Soils had an Al, AC1, AC2, C1, C2, horizon sequence to 1.5 m where a buried soil was encountered. Surface soils were loamy coarse sands with weak, medium, granular structure. The C1 was hard packed, pale brown-yellow, coarse textured pumice, with strong, single grained structure. The C2 was somewhat finer unmixed pumice that

dacite pumice and andesitic lava (Franklin et al. 1972).

Area VII (Table 1, Fig. 5) was at the Horse Ridge Research Natural Area (Franklin et al. 1972) 30 km southeast of Bend in the Juniperus occidentalis woodland zone; this is the driest evergreen tree habitat in the Pacific Northwest. Gholz (1979) reported on the biomass, leaf area, NPP, and site descriptions of the Juniperus stand in another paper. Juniperus was the only tree, ranging in age from 30 to 350+ years old. Artemisia tridentata var. tridentata was the only large shrub present. The sparse herb layer was mainly grasses and sedges. Soils were derived from aurally deposited pumice, with an A11, A12, AC, C, Cr horizon sequence. Boulders were common on the surface, although soils were essentially stone and rock free to 30 cm, and had only 15% rock from 30 to 60 cm. At 60 cm a Cr layer was encountered which consisted of fractured basalt bedrock with single-grained sandy loam soil in the interstices. The actual rooting depth is unknown, but some coarse roots penetrated this layer.

Area VIII (Table 1) was in the shrub-steppe (with Artemisia tridentata) zone in a basin south and east of Horse Ridge. The vegetation consisted of roughly equal coverage of Artemisia and Chrysothamnus viscidiflorus. The grassy herb layer was very sparse. Soils consisted only of an A11 and A12 horizon to a depth over 1 m. The soil was stone free to 30 cm and averaged 20% stones from 30 to 100 cm.

Generally, weather patterns across the transect are governed by a stable low pressure system located off Vancouver Island in the Pacific all winter and a corresponding high pressure system in the

same area during the summer. The prevailing westerlies carry moisture over the land in winter, resulting in cool, wet conditions, while summers are dry, generally with 2 to 3 months of no measurable precipitation (Table 2). The climate becomes more continental east of the Cascade Mountains.

## METHODS

In each area, a vegetated plot at least 0.25 ha in area was laid out with a buffer zone at least 25 m in all directions. Nearby open areas (usually a clearcutting) of the same slope, aspect and elevation were also located.

### Climatic Measurements

Climatic variables selected for measurement were (1) the components of a seasonal water balance (e.g., Grier and Running 1978), including precipitation, evaporation, and some account of soil water, and (2) soil and air temperatures, including a determination of winter minima. Complete sets of climatic data were not available from other sources, although precipitation was measured at a number of stations throughout Oregon (NOAA 1977). Precipitation and evaporation from May to October 1976 and 1977, were monitored in the open plots in each area. Precipitation was measured with accumulating rain gauges emptied at least every three weeks. Oil was used to prevent evaporation from rain gauges. Evaporation was measured with evaporimeters consisting of 45 cm acrylic tubes (2.54 cm diameter) sealed at one end. A recessed disc of Pinus

ponderosa sapwood ca. 0.63 cm thick was locked into the bottom end when the disc was wetted and swelled. Each tube was filled to a height of 35 cm with distilled water through an inlet port sealed by a cork. Three evaporimeters, previously calibrated under laboratory conditions, were hung on a rack in the middle of each open area, so that the pine evaporating surface was 1 m above the ground. Evaporation from each tube was recorded every three weeks. It should be emphasized that evaporation as presented here is a relative measure, affected by windspeed and temperatures as well as humidity. At most sites dew point recorders were installed at the open areas to accurately track changes in humidity deficits of the air.

Soil temperatures at 20 cm depth and air temperatures at 1 m above the ground surface were measured using Partlow 30 day spring-wound thermographs. Thermographs were installed under the canopies of the forested plots and the air temperature probes shielded from direct and reflected solar radiation. Temperatures under the canopies were less extreme than those recorded in open areas, but were comparable with records from 50+ other forested plots throughout Oregon and Washington (see e.g., Cleary and Waring 1967, Zobel et al. 1976, Zobel 1975, Emmingham and Lundburg 1977). Thermographs were installed in late fall 1975, maintained almost all of 1975-1976 and 1976-1977, and removed in early spring 1978.

#### Soil Water Characteristics

The water storage capacity of soils is an important component of site water balances. Actual soil water use is more informative, but



harder to obtain and less often measured. I used procedures detailed by Waring and Major (1964) to obtain storage capacities of the < 2 mm fraction at each site from 4 depths to 1 m (or a depth of < 1 m if an impediment to roots was encountered). Three gravimetric field samples were taken from each depth from a pit in the middle of each vegetated plot just before bud burst and in August 1977, after the typical summer drought period. These were coupled with determinations of 0.1 and 15 atm water contents obtained in the lab from field samples to permit an estimate of storage capacity and the amount of water extracted over the growing season. The August sampling for areas west of Santiam Pass (site V) was interrupted by abnormally heavy rain. In these areas, August moisture contents were assumed to be 60% of spring contents (after Krygier 1971). At several sites, again from Santiam Pass west, water content was greater than that retained at 0.1 atm in the spring, so that total water depletion during the summer exceeded the storage capacity to a depth of 1 m. Storage capacities and the total estimated water extracted from the soils over the growing season for 1977 were used with precipitation and evaporation to derive separate 15 May to 15 October water balances for 1976 and 1977:

$$WB = P - E + SWC \quad \text{or} \quad WB = P - E + SWE,$$

where WB is the water balance (cm), P is 15 May to 15 October precipitation (cm), E is 15 May to 15 October evaporation (cm), SWC is the soil water storage capacity (cm), and SWE is the Spring to August soil water extraction (cm). Again, because of the methods used for measuring evaporation, WB is an artificial index and was not meant to simulate water use patterns.

### Biomass and Leaf Area

Diameters at breast height (1.37 m) were measured on all trees of the study plots during 1976 for Plots I through VI. Basal circumferences were measured on the Juniperus plot (VII) as part of a double sampling procedure discussed elsewhere (Gholz 1979). Maximum canopy lengths, heights and widths (at right angles to the lengths) were measured for each Artemisia and Chrysothamnus bush on five randomly located circular subplots, each 5 m in radius, at the shrub-steppe plot (VIII). Height and the height to the base of the live canopy of a sample of trees spanning the size range present were measured with abney level and tape within each plot (at least 15 trees per stand).

Stem, live branch, and foliage biomass were computed for each species in each plot using a set of regression equations for Pacific Northwest species which have been compiled into a separate report (Gholz et al. 1979). Biomass of Chrysothamnus was estimated using an Artemisia equation from Uresk et al. (1976), and is probably overestimated. Biomass of Abies grandis at plot II and Abies lasiocarpa at plot V was calculated with a composite "Abies" equation, and biomass of Pinus monticola with a composite "Pinus" equation. Picea sitchensis at the coastal plots (Ia and Ib) was the only major tree species other than Abies grandis for which suitable regressions were unavailable. The only Picea trees that had been destructively analyzed previously were from the wind-damaged plot sampled by Fujimori et al. (1976). The stem and branch biomass equations from Fujimori et al. (1976) were used for Picea on both Ia and Ib. The foliage of these trees had been reduced by almost 35% due to episodic wind damage (Grier 1977, 1978). So for Picea, a

foliage biomass equation from Grier (C. C. Grier, Coll. of For. Res., Univ. Washington, Seattle, pers. communication) that represented a pooled data set from 8 conifer species was used to estimate foliage biomass. The equations from Gholz et al. (1979) are based on destructive sampling in a variety of Pacific Northwest sites, and so more correctly describe average plant component sizes for each species. The Pinus ponderosa samples were from northern Arizona (see Gholz et al. 1979 for documentation), and a comparison of diameters and heights of sampled trees from Arizona and those at plot VI of this study, indicate that Pinus stem biomass in this study may be slightly underestimated.

As a means of comparing the distribution of foliage with height aboveground in each area, a simple computer model was written which assumed that foliage biomass was distributed equally through the canopy. Other distributions, such as the normal distribution, could have been used but there are no data from the Pacific Northwest to indicate whether or not this would improve the model. After foliage biomass was computed for a tree from DBH measurements, it was distributed in 1 m segments through the canopy. Biomass of each segment was then accumulated for all trees in the stand. Finally, a computer histogram was drawn showing the amount of foliage biomass in each 1 m segment with height above ground for the entire stand.

Finally, leaf areas were computed from leaf biomass estimates using specific leaf areas ( $\text{cm}^2 \text{g}^{-1}$ ) of foliage samples shot from the midcanopy area with a shotgun. Samples were collected from at least three dominant trees and all major species in each stand in early August 1978. Juniperus was treated similarly (Gholz 1979). Samples were placed in a cooler and returned to the lab in Corvallis within three hours where they were

either processed or frozen until processing. Each sample was measured for planar surface area using a LiCor model Li-3000 portable surface area meter (Lambda Instr. Corp.). A calibration of the meter with strips of paper 1 cm in length and from 2 cm down to 0.05 cm in width was made. From a plot of actual versus measured areas, corrections were applied to some specific areas where particularly small needles or leaves were used. Specific areas of Pinus ponderosa were determined by measuring fascicle lengths and diameters, assuming that the fascicles when compressed together formed a cylinder, and calculating surface areas for all the needle surfaces. All samples were then dried at 70°C and weighed to 0.1 mg. Cross-sectional adjustments from Gholz et al. (1976) were applied so that projected leaf areas could be converted to a total surface basis.

#### Net Primary Production (NPP)

Stem (wood plus bark) and branch dry biomass increments were calculated for the overstory of each of the forested plots (I-VII). Five year wood diameter (DBH) growth was measured on increment borings from a sample of trees (at least 25 trees per plot) spanning the DBH range of each plot. Bark growth was assumed directly proportional to wood growth. Current DBH values were then corrected down to estimate DBH five years previous. The biomass equations were then applied to both sets to estimate stem and branch biomass. The difference between the two sets was average five year biomass increment. These increment values were regressed against the current DBH. Finally, the resulting equations were applied to the complete current DBH inventory for each

stand to obtain five year biomass increments for the entire stand. Average annual wood increment was calculated as one fifth of these five year increments. Branch and stem annual production equations from Fujimori et al. (1976) were used for Picea at the two coastal plots. Plot VII was treated similarly (Gholz 1979). Average annual total (wood plus foliage) aboveground production estimates for Artemisia were obtained from G. Nelson (Oregon State Univ., Corvallis, pers. comm. as compiled from long term records at Squaw Butte Exp. Stn., Burns, Oregon).

Foliage biomass production for plots I to VII was estimated as a fixed percentage of foliage biomass as no litterfall collections were made. This percentage varied from 20% to 30% depending upon literature values of foliage retention time (Grier and Logan 1977, Fujimori et al. 1976). Pinus and Juniperus foliage production was assumed to be 25% of foliage biomass, based on the western Oregon species, because no other data were available. No direct estimates of mortality, nonfoliar litterfall or herbivore grazing losses were made.

Therefore, aboveground NPP for plots I to VII, as defined in this paper, was the sum of annual stem wood and bark production, branch production, and foliage production. Nonfoliar litterfall, grazing losses and mortality were assumed zero (the consequences of these assumptions are discussed under Results).

No estimates of biomass, leaf area, or NPP of the understory were made for this study. Understory contributions to stand biomass in the Pacific Northwest are usually less than 5% (Long and Turner 1975, Fujimori et al. 1976, Gholz et al. 1976, Waring et al. 1978, Gholz 1979). Golley (1975) showed that most other forest types in the world also have less than 5% stand biomass in the understory. Although no detailed

understory production studies have been done in this region, understory NPP was considered negligible. Data from a variety of mature hardwood and conifer forests in the east and southwest United States indicate that understory layers contribute less than 2.5% to total aboveground stand NPP and less than 8% in immature open stands (Whittaker and Marks 1975). Appropriate measurements were made of understory species on many of the plots for this study, but analysis is incomplete and results will be presented in a later paper.

## RESULTS

### Climate

There is a very wide range in climate across this transect as summarized in Table 2. The moderating influence of the Pacific Ocean on the western plots is obvious. Average annual precipitation decreases markedly from the coast to the desert, but fluctuations are large due to orographic influences of both the Coast Range and higher Cascade Mountains. On the other hand, the frequency of winter days with temperatures less than  $-2^{\circ}\text{C}$  for 1976 and 1977, capable of freezing xylem sap (Tranquillini and Machl-Ebner 1971) and causing a zero or negative net photosynthesis for many conifers (see references in Levitt 1972), increases progressively away from the coast. Mean minimum January air temperatures decrease across the transect from around  $3^{\circ}\text{C}$  to  $-12^{\circ}\text{C}$ .

Precipitation from mid-May to mid-October averages from 13% (at VI) to 19% (at several sites) of annual precipitation for the six westerly zones and 36% of annual precipitation in the two desert zones (VII and

VIII). The year 1977 seemed more representative of long-term trends than 1976 (Table 2). In 1976, summer precipitation was lower than average from the coast to the Cascades, while August precipitation in the desert much exceeded normal levels. For one three week period in mid-August four times more precipitation fell on the desert than on the coast. Evaporation as measured by the evaporimeters, however, was uniformly higher for all sites from May to October in 1977 than in 1976. For the three sites east of the mountains (VI, VII, VIII), evaporative demand remained high until rain fell and then recovered immediately when the rain stopped. West of the Cascades the pattern was less clear. From dew point measurements in July 1977, the interior coast range site (II) had vapor pressure deficits (VPD) exceeding 40 mb for several hours on consecutive days. Average VPD's at the desert sites were always somewhat less, owing to very cold nights, but relatively high deficits were sustained throughout more of the summer. Although this record is incomplete, 1977 daily average VPD's were consistently higher than for 1976. This indicates that, even though the summer of 1977 brought more precipitation to areas west of the Cascades than during 1976, evaporative demands were also higher in 1977.

The two years' water balances reflect these variations (Table 2). At the coast the higher precipitation in 1977 was nearly balanced by higher evaporation and the water balances for both years were similar. In contrast, evaporation increases more than offset precipitation increases from 1976 to 1977 for the rest of the transect. Even though soil water usage may have changed from 1976 to 1977, the relative magnitudes compared to evaporation and precipitation would not be sufficient to offset the

differences in the water balances in which only 1977 soil water data were used.

Temperature growth index summarizes average soil and day air temperatures according to their effects on seedling growth of Pseudotsuga. Even through Pseudotsuga was the initial reference species (Cleary and Waring 1967) this index has been useful in interpreting plant communities in west central and southwestern Oregon whether or not Pseudotsuga was part of the community (Waring 1969, Zobel et al. 1976). Leaf area and biomass in these two regions decrease at either high or low values of the index (Waring et al. 1977, Gholz et al. 1976) in part reflecting the fact that when the temperature index reaches high values, water is usually limiting (Waring 1969, Zobel et al. 1976). Other indices could be used that are species independent (e.g., "degree days"), but they generally lack a soil temperature component and were not used.

#### Biomass and Leaf Area

Among the sites, estimates of total aboveground biomass ranged from 3 t ha<sup>-1</sup> in the Artemisia zone (VIII) to 1492 t ha<sup>-1</sup> in one coastal forest (Ib) (Table 3). The percent of aboveground biomass in foliage increased steadily east of the interior coast range site (II), varying from 2% to 4.9% foliage in the forested zones (Fig. 6). In the Juniperus woodland (VII) the ratio increased to 10.5% and in the Artemisia shrub-steppe to nearly 33%. Likewise, live branch biomass ranged from 6.1% to 9.7% of aboveground biomass for the four western forest zones and increased to 14.4% in the subalpine zone (V), 49% in the Juniperus zone (VII), and 67% in the Artemisia zone (VIII) (assuming Artemisia wood



is all "branches" with no "stem" biomass). The corollary of this set of relationships is that the ratio of stem biomass to foliage biomass decreased dramatically from west to east (Fig. 6).

Although the regression of mean minimum January air temperature with biomass had an  $R^2$  of 0.91, the variance was large (Table 5). The site water balance, and consequently growing season evaporation, were not as highly correlated with biomass, excluding plot V (Table 5). Basal area and leaf area were highly correlated with biomass for all sites. Biomass of the mature, upslope redwood stands of Westman and Whittaker (1975) were correlated equally well with leaf area or basal area. However, all these variables were unable to accurately predict the large biomass accumulated in the better alluvial flat redwood stands.

Leaf areas also covered a large range, from 1.0 to 44.0 ha ha<sup>-1</sup> all-sided (0.5 to 20.0 ha ha<sup>-1</sup> projected area) (Table 3). Again, a general decrease occurred from west to east. Standing crop densities (after Kira and Shidei 1967) represent the dry matter concentrations from the ground to the top of the canopy and indicate the degree to which the growing space is filled. Along this transect densities ranged from 2.0 to 2.7 kg m<sup>-3</sup> in the Picea coastal zone, 1.0 to 1.6 kg m<sup>-3</sup> in the Tsuga heterophylla and Abies amabilis zones, 0.8 kg m<sup>-3</sup> in the Tsuga mertensiana zone, and from 0.28 to 0.34 kg m<sup>-3</sup> in the three rain shadow zones.

To highlight functional differences, one may contrast how foliage is displayed. Figure 7 represents foliage distributions with height aboveground for each of the plots (Ia is used as an example for the Picea zone). Again, a basic assumption is that on any single tree, foliage

is distributed equally through the crown. The Pinus ponderosa canopy was the least dense ( $0.016 \text{ kg m}^{-3}$  foliage). The other eight plots ranged from 0.03 to  $0.08 \text{ kg m}^{-3}$  with no consistent patterns.

Of all the climatic variables and indices measured, the growing season water balance (Grier and Running 1977) provided the best correlations with leaf area for both years (Fig. 9, Table 5) for all sites except plot V in the subalpine Tsuga mertensiana zone. The correlations were higher when soil water extraction was used in the water balance rather than storage capacity (Table 5). The years 1976 and 1977 were very different.

Of the components of the water balance (using 1977 as an example), growing season evaporation was most closely correlated with leaf area ( $r = -0.95$ ), while correlations with precipitation and soil water extraction were lower ( $r = 0.88$ ,  $r = -0.89$ , respectively). In addition, evaporation and soil water extraction were correlated ( $r = -0.82$ ), and the relative magnitudes of the latter were much smaller than either evaporation or precipitation (Table 2). Storage capacities had a smaller range than did extraction and were not highly correlated with leaf area ( $r = -0.15$ ), precipitation ( $r = -0.42$ ), or extraction ( $r = 0.23$ ).

Leaf area is not well correlated with most stand measurements, although basal area gives a good estimate for the plots reported here (Table 5). When one estimates leaf area of an alluvial flat redwood stand ( $\sim 35 \text{ ha ha}^{-1}$  all sided), however, with a basal area of  $\sim 250 \text{ m}^2 \text{ ha}^{-1}$  (Westman and Whittaker 1975) from the same regression the estimate is an unreasonably high  $79 \text{ ha ha}^{-1}$  leaf area.

### Overstory Biomass Increment

Species along the transect differ widely in the relationship of biomass increment to DBH (Fig. 8). However, for plots Ia, Ib, II, and III, all the species behaved in a similar manner, although absolute differences could be large (i.e., Ib-Tsuga versus III-Pseudotsuga at 70 cm DBH). The largest plot IV-Pseudotsuga, however, are not growing as much as Pseudotsuga from the two sites at lower elevations. Pinus ponderosa (plot VI) and Tsuga mertensiana (plot V) exhibit almost identical stem increment patterns, while Juniperus (plot VII) has the lowest stem increment. Increments for two 130 cm DBH Pseudotsuga on plot II were no different than those for 110 cm DBH trees, so that a regression was fit for trees < 110 cm DBH, and actual data points used for the two larger trees.

Regression equations relating 5 year average annual stem biomass increment to DBH were highly significant in all cases (whether data were logarithmically transformed or not) (Table 4).  $R^2$  values for stem increment equations ranged from 0.79 to 0.99, with the exceptions of one at 0.45 (Abies lasiocarpa and Abies amabilis pooled at plot V), and one at 0.32 (Tsuga at Ia). In both cases, the species were minor components of the stands. Variances for most equations were surprisingly small. Variances for linear and logarithmically transformed data are not directly comparable. Tsuga at Ib had the largest variance among the linear equations. This species composed 70% of the basal area of the stand and ranged from < 10 to 135 cm DBH, including many individuals < 50 cm that were growing in the shade of the larger trees. Since Tsuga heterophylla is highly shade tolerant, they can exist for many

decades until an opening becomes available from mortality of larger individuals. Pseudotsuga at plot IV also had a large variance. In this case, many trees < 15 cm DBH were suppressed and, as Pseudotsuga is not highly shade tolerant, were beginning to die. Sapwood basal area could be a better predictor of growth than DBH, as suppressed trees would have less leaf area and therefore less sapwood area than would larger dying trees (Grier and Waring 1974). I used sapwood measurements in some cases to confirm trends of increment with DBH, and found that overall, the DBH equations adequately estimated stem increments on a stand basis.  $R^2$  for live branch increment with DBH ranged from 0.71 to 0.98, with exceptions as above (plot V-Abies, plot Ia-Tsuga). Annual stem increments ranged from 0.20 to 6.93 t ha<sup>-1</sup> yr<sup>-1</sup> (at VII and Ia, respectively), and live branch increments from < 0.01 to 2.01 t ha<sup>-1</sup> yr<sup>-1</sup> (at VII and Ia, respectively).

#### Net Primary Production (NPP)

NPP is defined as gross photosynthesis minus respiration, or, in another manner:  $NPP = \Delta B + L + G$ , where  $\Delta B$  is net branch, stem and bark biomass increment (biomass increment less mortality), L is litterfall, including mortality, and G is herbivore grazing (Kira and Shidei 1967). Most NPP figures reported in the literature are annual estimates and contain some estimate of nonfoliar litterfall. However, very few include stem mortality estimates and it is rare to see estimates of G. In this study,  $\Delta B$  was stem and branch biomass increment, G was assumed to be zero, and L was subdivided into foliar and nonfoliar litterfall. The

nonfoliar component (including stem mortality) was assumed zero and the foliar compartment was estimated as a percentage of foliar biomass.

According to Grier (1978) long-term estimates of stem mortality will add up to about 15% to annual NPP for mature stands in western Oregon. No estimates are available for stands east of the Cascades summit. In overmature stands NPP may consist primarily of detrital production rather than biomass increment in standing crop (Grier and Logan 1977), but the magnitudes should still be comparable to estimates reported here. In much younger stands that have not yet fully occupied a site, NPP would consist of essentially all standing crop biomass increment. Herbivore grazing is usually < 4% of NPP (Whittaker and Marks 1975, Petruszewicz and Grodziński 1975). Nonfoliar L (less stem mortality) could add up to about  $1.5 \text{ t ha}^{-1} \text{ yr}^{-1}$  to the NPP of stands in the Tsuga, Picea, and Abies zones reported here (Grier and Logan 1977, Abee and Lavender 1972). Bray and Gorham (1964) reported that nonfoliar litter for a variety of forest types averaged between 27% and 31% of total litterfall. Again no litterfall estimates are available for central Oregon stands, but a qualitative comparison of litter quantities with western Oregon forests suggests that nonfoliar litter would be much less than  $1.5 \text{ t ha}^{-1} \text{ yr}^{-1}$  for these types. Unmeasured fruit production was probably a significant proportion of NPP only at plots VII and VIII. This component of production is generally less than 3% to 4% of total stand NPP (Whittaker and Marks 1975). Assuming G to be 2% of NPP and nonfoliar (nonstem) L to be  $1.0 \text{ t ha}^{-1} \text{ yr}^{-1}$ , the aboveground NPP of the plot IV Abies site would be underestimated by 11%, excluding an estimate of average long-term stem mortality. It seems reasonable to expect, then, that all the estimates in this study are within about 5% to 15% of

actual aboveground NPP, with stem mortality adding a variable amount from 0% to 15% above this.

Stem increment contributed from 18% to 55% of NPP along the transect. Except for Ib, the Picea, Tsuga heterophylla, and Abies zones together had stem increments representing from 47% to 55% of NPP, the Tsuga mertensiana zone 25%, the Pinus zone 33%, and Juniperus zone 18%. Foliage production exceeded stem increment at Ib, V, and the three sites east of the Cascade summit (Table 3).

NPP ranged from  $0.3 \text{ t ha}^{-1} \text{ yr}^{-1}$  at VIII to  $14.7 \text{ t ha}^{-1} \text{ yr}^{-1}$  at Ia, and decreased from west to east across the transect except at plot IV, which was more productive than plot III (Table 3). Biomass:NPP ratios were highest for plots I and II, intermediate and very similar for III through VI, and lowest for VII and VIII, ranging from an average of 97.0 for the first group, 64.5 for the second, and 15.5 for the last. NPP:foliage biomass ratios generally declined to the east ( $0.44 \pm 0.15$  for all sites with Ia and Ib averaged). NPP:leaf area ratios showed no pattern with geography or environment among the sites, with plots Ib, VI, and VIII being low (Table 3).

Patterns of NPP with the climatic variables are similar to those with biomass. For the seven sites, except plot V, the water balance and growing season evaporation were more highly correlated with NPP than growing season or annual precipitation (Table 5). All the plots including V were highly correlated with mean minimum January air temperatures and somewhat less so with the winter temperature index (Table 5). Excluding V, NPP was negatively correlated with the temperature growth index (TGI), indicating additional restrictions on NPP at higher TGI values such as low available summer moisture or low winter temperatures.

## DISCUSSION

Methods Used in Leaf Area Measurements

These estimates of leaf area, biomass, and NPP seem very reasonable in light of work done previously in northwestern ecosystems. Leaf area, however, is often very difficult to estimate, even though it is very important in studies of ecosystem structure and function. Leaf area is generally calculated from leaf biomass by multiplying by a constant ( $\text{cm}^2 \text{ leaf area g}^{-1} \text{ dry wt. leaf}$ ). These constants are site specific and vary with age and exposure (Gholz et al. 1976, Gholz 1978, Tucker and Emmingham 1977, Del Rio and Berg 1979). Morphological differences related to light intensity can cause constants from the same age of foliage on the same species to increase from  $< 100 \text{ cm}^2 \text{ g}^{-1}$  to  $300 \text{ cm}^2 \text{ g}^{-1}$  from the top of the canopy to the bottom (Gholz et al. 1976). In the current study samples for determining these constants (specific leaf areas,  $\text{cm}^2 \text{ g}^{-1}$ ) were removed from the outer midcrown, separated by age, and averaged from two samples from opposite sides of the trees. As new foliage was measured separately, leaf areas in this report are weighted by age. Previous studies from this region (Gholz et al. 1976, Waring et al. 1978) used constants that may have overestimated leaf areas because mean specific areas were often used without age class weighting, samples were taken lower in the crowns of overstory trees, or constants were used from other sites. Overestimates would be most in areas where differences in microenvironment were large in the stand and least in areas where differences were small. For example, specific leaf areas obtained for this study from mid and lower crowns and from

a previous study (Gholz et al. 1976) from the coastal Picea zone were the same. Specific areas for species at higher elevations, however, were lower than expected based on data for the same species at lower elevations. Apparently, where the highest values would be expected, previous leaf area estimates should be valid. Grier and Running's (1977) leaf area estimate for coastal stands is equivalent to an average of the two stands in this report (Table 3). In contrast, several stands previously reported from the western Cascades with leaf areas over 50 ha ha<sup>-1</sup> (Gholz et al. 1976, Waring et al. 1978), have probably been over-estimated by as much as 15%. From Table 3, average weighted specific leaf areas for the stands in this study can be obtained. These should serve as useful comparisons for future studies.

#### Estimating Leaf Area of Northwest Ecosystems from Climatic Analyses

Grier and Running's (1977) regression of leaf area versus the water balance shows no significant difference from my 1977 line (Fig. 9). They used soil water storage capacity and long term climatic averages with average leaf areas from five zones. The agreement of these independent estimates supports a general regional trend of leaf area and water balance, and also indicates that 1977 was a more "normal" year than 1976.

Because of the proportionally small contribution of the soil component to the balance, using soil water storage capacity rather than soil water extraction makes little difference in determining the water balance. The failure of the water balance to predict leaf area at plot



V was thought to result from important temperature effects upon winter time photosynthesis (Emmingham and Waring 1976, Waring et al. 1978). The plot of leaf area versus the temperature ~~the~~ growth index (TGI) (Cleary and Waring 1967) showed a decline at both high and low TGI values with considerable variation as more fully documented by Waring et al. (1978). In the present study, TGI was not very helpful in explaining changes in leaf area, in part, I felt, because it was defined for the growing season. Mean minimum January air temperatures were highly correlated with leaf area (Table 5). The winter temperature index provided a much poorer fit.

Leaf area predictions across ranges in environment should require some assessment of both water availability and temperature. Where data are available, leaf area could first be estimated from the water balance ( $LA_{WB}$ ); second, estimate leaf area from a temperature regression ( $LA_T$ ); and finally, if  $LA_T$  was less than  $LA_{WB}$ ,  $LA_T$  could be used as the best estimator of site leaf area. This is similar to approaches used to map NPP (Leith 1975), where estimates of NPP from annual precipitation were adjusted downward using a mean annual temperature function. On a region-wide basis, precipitation and temperature records are fairly complete, while evaporation, generally open pan, is rarely measured. However, existing precipitation and temperature records could perhaps be used to estimate evaporative demand, as illustrated nicely by Linacre (1977).

In some cases, such as the wind damaged coastal site, moisture or temperature are not limiting leaf area. In this particular case the presumed limitation is damage by high wind as the canopy develops. Substrate quality could be a possible restraint. Waring et al. (1978)

noted that serpentine soils supported less leaf area than expected based on TGI and a plant moisture index and Zobel et al. (1976) indicated that stands in the western Cascades with lowest available nitrogen appeared to have lower than expected leaf areas.

Maximum leaf areas for the Pacific Northwest according to the relationships displayed here are about  $45 \text{ ha ha}^{-1}$ , which compares well with the other studies already cited, especially when the above reassessment of specific leaf areas is considered.

#### Estimating Aboveground Biomass of Northwest Ecosystems

No single climatic factor or index adequately estimated biomass on all the transect plots. Recently, Crow (1978) reported that aboveground biomass of some Wisconsin hardwood forests could be estimated using a relationship with basal area times canopy height. Even though data for over a third the apparent range is not available, a well-defined trend is evident for the transect plots, and other stands reported from the Northwest (Fig. 10). It is unlikely that any stand would have larger amounts of standing biomass than that reported for the alluvial flat redwood stand (RA in Fig. 10). The more interesting questions are those of the variation around the line, exceptional cases, and the shape of the curve in its midsection.

#### Estimating NPP for Northwest Ecosystems

As is apparent from several analyses, NPP plateaus for natural mature Pacific Northwest forested ecosystems. When NPP is plotted as

a function of aboveground biomass, it increases with biomass to  $14 \text{ t ha}^{-1} \text{ yr}^{-1}$  at  $1100 \text{ t ha}^{-1}$  biomass, after which it plateaus (Fig. 11). NPP increases steeply with basal area (Table 5) and the correlation for sites along the transect is high. Over these sites no maximum is indicated, although the alluvial redwood stand at  $14 \text{ t ha}^{-1} \text{ yr}^{-1}$  and  $250 \text{ m}^2 \text{ ha}^{-1}$  basal area again represents a probable maximum. An analysis similar to Crow's (1978) suggests that a similar maximum NPP is reached at a  $\text{BA} \cdot \text{Ht} \cdot 10^{-2}$  value of about 60.

Given the previous correlations of leaf area and NPP to the water balance, it is not surprising to find a good correlation between NPP and leaf area. This relationship is illustrated in Figure 12 for the transect stands and the two redwood plots of Westman and Whittaker (1975). On the same plot three regions are indicated. Region I defines an area in which no tree dominated ecosystems have been reported from 68 examined. Region II includes young plantations and natural stands that do not have closed canopies or are otherwise judged "immature" by the respective authors ( $n = 25$ ). Region III includes most mature systems reported ( $n = 43$ , including montane tropical forests, temperate forests, and boreal forests, but excluding low elevation tropical forests; references are listed in Fig. 12). Low elevation tropical forests seem to have higher NPP than the others (Murphy 1975), although most of those reported were judged "immature". Region III is bounded at the upper end by the curved solid line, and at the lower end by Region I. Region II is bounded at the top by a line that plateaus at a leaf area around  $20 \text{ ha ha}^{-1}$  and at an NPP of roughly  $30 \text{ to } 35 \text{ t ha}^{-1} \text{ yr}^{-1}$ , not shown within the bounds of Figure 12.

Several points are critical to the interpretation of this figure. First, where the all-sided leaf areas are less than  $30 \text{ ha ha}^{-1}$  (projected LAI of about  $13 \text{ ha ha}^{-1}$ ), a similar ratio of NPP:leaf area exists (mean = 0.46, std. dev. = 0.09, for all forested plots  $< 30 \text{ ha ha}^{-1}$ --excluding plots Ib and VIII), so that increased leaf areas are associated with linear increases in NPP over the range of 0 to  $30 \text{ ha ha}^{-1}$ . As leaf area and sapwood area are positively related in a linear manner for many species (Whitehead 1978, Grier and Waring 1975, Waring et al. 1977), and transpiration and sapwood area also seem to be related linearly for a range in forest types (Jordan and Kline 1977, Kline et al. 1976), a plateau in the transpiration:leaf area ratio should also occur at a leaf area of about  $30 \text{ ha ha}^{-1}$ . Second, Pacific Northwest systems are not generally as productive at any given leaf area as many other systems. An exception is the coastal zone (Ia, Ib, redwoods). The coastal site of Fujimori et al. (1976), with its wind-lowered leaf area, exhibits a relatively remarkable efficiency, although NPP still seems somewhat low compared to Ia and Ib. The difference between actual and potential NPP for the other stands may be due, as mentioned above, to inadequate fertility. Data for making such a case are not currently available. Third, the range of potential NPP values for any leaf area is greatest at the point where NPP plateaus.

Fourth, although the lines in Figure 13 appear quite different than those in a literature survey by Whittaker and Marks (1975), this seems to lie in the difference in expressing leaf areas for broadleaves (all- versus one-sided), and the differentiation I have made between "immature" and "mature" communities. Underestimates of NPP based on

the assumptions I made for nonfoliar litterfall, grazing and mortality would cause our results to converge somewhat more.

Fifth, although my original hypothesis excluded overmature forest types, because, presumably, they are in a state of transition, this appears now to be unnecessary. Grier and Logan (1977) reported NPP and biomass values for five forest types on one 11.2 ha watershed in western Oregon, dominated by 400- to 500-year-old Pseudotsuga. If leaf areas are calculated (using a watershed specific area average of  $140 \text{ cm}^2 \text{ g}^{-1}$ ) from foliage biomass, and are plotted with NPP on Figure 12, the points fall very close to the line for my study plots (I-VIII) from a leaf area of  $12 \text{ ha ha}^{-1}$  to one of  $20 \text{ ha ha}^{-1}$ . This indicates that as the stand becomes decadent, and leaf areas temporarily decrease (before the understory, "climax" species can take up the slack), NPP also decreases, maintaining a similar ratio of NPP:leaf area.

Finally, many forests in the Pacific Northwest have leaf areas greater than  $30 \text{ ha ha}^{-1}$ . In all these forests biomass can accumulate to very high levels, individuals are very long-lived, and forest floor and large organic debris can exceed  $100 \text{ t ha}^{-1}$  (Waring and Franklin 1979). Atmospheric nutrient inputs are low (Fredriksen 1972) except at the coast, and conditions often prohibit photosynthesis during large periods of the "growing season" because of the long seasonal drought (Emmingham and Waring 1977). This same climate with a wet, mild winter, on the other hand, often produces conditions very favorable to photosynthesis during the winter "dormant period" (Emmingham and Waring 1977).

Comparison of preliminary data from March and August 1978, indicate that the weight per unit surface area of needles was from 10% to 50%

higher in March than in August. This means that even after accounting for litter production in the fall, a 25% increase in foliage biomass would enable a mature conifer forest to meet its nitrogen requirements for spring growth ( $\sim 35 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , as reported by Cole et al. 1968) simply through the redistribution of nitrogen accumulated through the winter. The areas most optimal for this winter activity are those same areas most optimal for leaf area accumulation (Table 3, Emmingham and Waring 1977). Because NPP reaches a plateau with leaf area, the overall efficiency of the forest (NPP:leaf area) decreases above a leaf area of ca.  $30 \text{ ha ha}^{-1}$  (Table 3). So for some other reason, perhaps the presence of conditions that permit this winter activity, high leaf areas are advantageous in these environments. If so, the close correlation of NPP to January minimum temperatures may reflect a varying inhibition of this winter "dormant season" activity.

#### SUMMARY

Over a broad range of environments and mature vegetation types in the Pacific Northwest, the NPP:leaf area ratios were very similar at all-sided leaf areas  $< 30 \text{ ha ha}^{-1}$ , resulting in a linear relationship between NPP and leaf area, partially confirming the main stated hypothesis. NPP plateaued at about  $14 \text{ t ha}^{-1} \text{ yr}^{-1}$ . Biomass also increased linearly with leaf area, although no maximum was indicated.

Of a variety of climatic factors evaluated, growing season evaporative demand and mean minimum January air temperatures accounted for most of the variation in leaf area, biomass, and NPP. The former apparently

reflects limitations imposed by a seasonal summer drought period, and the latter reflects limitations on winter carbon and nutrient accumulation, a major adaptive feature in many evergreen Pacific Northwest ecosystems.

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TABLE 1. General description of study sites, from west to east along transect. Physiographic provinces are from Franklin and Dyrness (1973). Plot VII is an intensive site for Gholz (1979).

Plot	Ia	Ib	II	III	IV	V	VI	VII	VIII
Vegetation zone	Picea sitchensis	Picea sitchensis	Tsuga heterophylla	Tsuga heterophylla	Abies amabilis	Tsuga mertensiana	Pinus ponderosa	Juniperus occidentalis	Artemisia shrub-steppe
Physiographic Province	Western Coast Range	Western Coast Range	Interior Coast Range	Low elevation West Cascades	Mid elevation West Cascades	High Cascades Summit	Eastern high Cascades	High lava plain	High lava plain
Latitude	45° 05' N	45° 05' N	44° 32' N	44° 24' N	44° 24' N	44° 26' N	44° 35' N	43° 54' N	43° 50' N
Longitude	124° 00' W	124° 00' W	123° 17' W	122° 20' W	122° 09' W	121° 50' W	121° 36' W	121° 02' W	121° 00' W
Elevation (m)	200	200	365	410	1500	1590	870	1356	1200
Slope (%)	0	10	18	54	15	2	0	18	0
Aspect	--	S 10° W	N 40° W	S 6° W	S 2° W	S 25° E	--	N 50° E	--
Plot size (ha)	0.405	0.405	0.25	0.25	0.25	0.25	0.4225	0.3656	0.25
Stem density (#ha <sup>-1</sup> )									
<10 cm DBH	2500	1500	110	12	1250	1700	490	470	NA
10-70 cm DBH	175	445	292	436	997	804	187	199	0
>70 cm DBH	119	54	20	12	8	0	28	0	0

TABLE 1. Continued

	Ia	Ib	II	III	IV	V	VI	VII	VIII
Overstory basal area (m <sup>2</sup> ha <sup>-1</sup> )	118.2	111.2	84.4	54.5	72.4	57.2	26.1	27.8	15.0
Mean codominant ht. (m)	55	55	55	45	40	35	43	8	1
Mean codominant age (yr)	130	130	150	125	150	150	200	200	NA
Rooting depth (cm)	80	80	50	90	90	50	90	>100	>100
Soil water storage capacity (<2 mm fraction, cm)	13.1	13.1	6.1	4.4	8.5	6.2	16.6	10.1	13.5
Soil Subgroup (tentative)	Typic haplohumult		Dystric xerochrept	Lithic xerumbrept	Typic haplohumult	Entic cryandept	Typic vitrandept	Typic torriorthent	Typic torriorthent

TABLE 2. Climatic characteristics of study sites from west to east along transect.

Plot	I	II	III	IV	V	VI	VII	VIII
Physiographic Province	Western Coast Range	Interior Coast Range	Low elevation west Cascades	Mid elevation west Cascades	High Cascades summit	Eastern high Cascades	High lava plains	High lava plains
Average Annual Precip. (cm) <sup>1</sup>	246.0	120.0	157.0	200.0	230.0	40.0	25.0	20.0
Average May-Oct. precip. (cm)	41.8	15.5	30.0	32.1	39.5	7.5	9.1	7.2
1976 May-Oct. precip. (cm) <sup>2</sup>	29.1	14.4	24.6	30.9	25.4	9.6	15.6	14.6
1977 May-Oct. precip. (cm)	46.3	20.2	35.5	45.5	38.3	5.3	7.5	5.4
1976 May-Oct. evap. (cm)	29.	46.	62.	50.	48.	60.	72.	75.
1977 May-Oct. evap. (cm)	48.	76.	104.5	71.	80.	100.	130.	127.
1977 soil water extract. (cm)	23.7	7.2	5.0	7.6	9.2	6.5	3.6	3.5
1976 water balance <sup>3</sup>	+23.8	-24.4	-27.4	-11.5	-13.4	-43.9	-52.8	-56.9
1977 water balance	+22.0	-48.6	-64.0	-17.9	-32.5	-88.2	-118.9	-118.1
1976 water balance <sup>4</sup>	+13.2	-25.5	-33.0	-10.6	-16.4	-33.8	-46.3	-46.9

TABLE 2. Continued.

	I	II	III	IV	V	VI	VII	VIII
1977 water balance	+11.4	-49.7	-64.6	-17.0	-35.5	-78.1	-112.4	-108.1
Winter temp. index <sup>5</sup>	2%	6%	18%	51%	65%	68%	80%	87%
1976 May-Oct. TGI <sup>6</sup>	58	78	80	65	46	82	91	89
1977 May-Oct. TGI	60	74	76	64	53	79	95	96
Mean Minimum January 1977								
air temperature (°C)	2.9	-0.3	NA	-1.8	-6.0	-8.9	-8.0	-11.7
Mean Maximum July 1977								
air temperature (°C)	11.2	18.9	20.0	18.2	19.0	25.3	25.5	24.7

<sup>1</sup>Average precipitation represents at least 10 years of data from NOAA (1977) or other standard meteorological stations nearest to each site.

<sup>2</sup>1976, 1977 precipitation and evaporation (from evaporimeters) data are from measurements at each study site.

<sup>3</sup>These two balances are for the May-October period and equal precipitation plus 1977 soil water extraction minus evaporation, all in cm.

<sup>4</sup>Same as previous two, but with soil water storage capacity substituted for water extraction.

<sup>5</sup>Average percent of day mean air temperatures less than -2°C from February 1 to April 30, 1976 and 1977.

<sup>6</sup>TGI = temperature growth index (Cleary and Waring 1967); includes soil and air temperature effects on Pseudotsuga menziesii seedling growth from growth chamber studies.

TABLE 3. Structure and production relations of study sites, from west to east across transect. Plot VII data are from Gholz (1979).

Plot	Ia	Ib	II	III	IV	V	VI	VII	VIII
Physiographic Province	Western Coast Range	Western Coast Range	Interior Coast Range	Low elevation west Cascades	Mid elevation west Cascades	High Cascades summit	Eastern high Cascades	High lava plain	High lava plain
Leaf area (ha ha <sup>-1</sup> ) <sup>1</sup>	31.1	44.4	17.5	14.5	21.7	10.0	6.6	2.0	1.0
Foliage biomass (t ha <sup>-1</sup> )	23.1	31.8	15.9	12.1	17.9	14.8	7.0	4.6	0.6
Live branch biomass (t ha <sup>-1</sup> )	97.1	144.4	60.1	30.1	42.5	34.9	30.0	8.0	2.4
Stem biomass (t ha <sup>-1</sup> )	960.	1316.	789.	407.	467.	228.	99.	9.	NA
Stem increment (t ha <sup>-1</sup> yr <sup>-1</sup> )	6.93	3.56	5.44	3.22	5.15	1.01	0.70	0.20	0.30
Branch increment (t ha <sup>-1</sup> yr <sup>-1</sup> )	2.01	1.31	0.48	0.23	0.51	0.16	0.22	0.00	
Foliage production (t ha <sup>-1</sup> yr <sup>-1</sup> )	5.78	7.94	4.63	3.18	3.65	2.95	0.92	0.91	



TABLE 3. Continued.

	Ia	Ib	II	III	IV	V	VI	VII	VIII
Net aboveground primary production (NPP, t ha <sup>-1</sup> yr <sup>-1</sup> )	14.7	12.3	10.5	6.6	9.3	4.1	2.1	1.1	0.3
Total biomass:NPP	73.	121.	82.	68.	57.	68.	65.	20.	11.
NPP:leaf area	0.47	0.28	0.60	0.46	0.43	0.41	0.32	0.48	0.28
NPP:foliage biomass	0.64	0.39	0.66	0.55	0.52	0.28	0.30	0.24	0.47
Standing crop density (kg m <sup>-3</sup> )	1.96	2.71	1.57	1.00	1.32	0.79	0.32	0.28	0.30

<sup>1</sup>All-sided.

TABLE 4. Equations for estimating individual tree 5 year stem and branch biomass increments in kg. A and B are linear regression coefficients, C and D are logarithmic regression coefficients, n is sample size and  $S^2_{y \cdot x}$  is variance (in either linear or logarithmic space). Equations are of the form:  $Y = A + B$  (DBH) or  $\ln(Y) = C + D \ln$  (DBH).

Plot	Species	Y	A	B	C	D	n	R <sup>2</sup>	S <sup>2</sup> <sub>y·x</sub>
Ia	Tsuga	stem			-20.599	6.0473	16	0.32	6.4
		branch			-22.101	6.2462	16	0.39	4.9
	Picea <sup>1</sup>								
Ib	Tsuga	stem	-188.45	5.339			16	0.79	1394.2
		branch	-109.42	3.0175			16	0.76	528.7
	Picea <sup>1</sup>								
II	Pseudotsuga	stem			-9.1766	3.2245	15	0.84	0.508
		branch			-10.812	2.9062	15	0.71	0.879
	Abies	stem			-5.266	2.394	11	0.96	0.148
		branch			-6.8519	2.3473	11	0.91	0.309
	Acer	stem	-19.813	1.8574			6	0.97	30.2
		branch	-2.2483	0.2509			6	0.96	0.6
III	Pseudotsuga	stem			-5.907	2.4805	22	0.81	0.6
		branch	-2.1803	0.1336			22	0.83	2.4

TABLE 4. Continued.

Plot	Species	Y	A	B	C	D	n	R <sup>2</sup>	S <sup>2</sup> <sub>y·x</sub>
	Acer	stem	-5.4361	0.6721			5	0.99	0.1
		branch	-0.6883	0.0968			5	0.98	0.01
IV	Pseudotsuga	stem	-17.455	1.6787			12	0.92	275.0
		branch	-0.1359	0.0677			12	0.75	1.8
	Tsuga	stem			-4.7042	2.2198	8	0.98	0.1
		branch			-6.9094	2.6017	8	0.97	0.2
	others <sup>2</sup>								
V	Tsuga	stem			-5.6439	2.178	16	0.82	0.5
		branch			-5.8523	1.717	16	0.76	0.4
	Abies	stem			-3.6056	1.7558	6	0.45	1.0
		branch			-4.6138	1.4625	6	0.28	1.4
VI	Pinus	stem			-3.1267	1.5692	27	0.89	0.2
		branch			-4.625	1.6564	27	0.89	0.3
VII	Juniperus <sup>3</sup>								

<sup>1</sup>From Fujimori et al. (1976).<sup>2</sup>Use actual data points.<sup>3</sup>See Gholz (1979).

TABLE 5. Regressions among stand and climatic variables across the transect in Oregon. Ia and Ib are averaged for these analyses. All equations are of the form:  $Y = A + B(X)$ .  $S^2_{y \cdot x}$  is the residual mean square error (variance). Equations with n (sample size) = 8, include plot V, those with n = 7, do not.

Y	X	A	B	n	R <sup>2</sup>	S <sup>2</sup> <sub>y·x</sub>
Leaf area (ha ha <sup>-1</sup> )	1976 water balance <sup>1</sup> (cm)	27.215	0.4630	7	0.996	0.68
	1977 water balance <sup>1</sup> (cm)	29.652	0.2455	7	0.975	5.0
	1976 water balance <sup>2</sup> (cm)	21.113	0.3540	7	0.63	75.0
	1977 water balance <sup>2</sup> (cm)	31.003	0.2770	7	0.95	9.7
	1977 May-Oct. evap. (cm)	52.544	-0.4063	7	0.91	19.4
	1977 May-Oct. precip. (cm)	-0.0330	0.6115	7	0.77	45.9
	1977 soil water extract. (cm)	1.0785	1.6384	7	0.80	41.0
	Mean annual precip. (cm)	-1.3164	0.1365	7	0.91	18.5
	Mean May-Oct. precip. (cm)	-2.7221	0.8391	7	0.83	34.9
	Soil water storage capacity (cm)	19.064	-0.4474	7	0.02	196.4
	1976-1977 Winter temp. index (%)	27.651	-0.2921	8	0.67	56.4
	1977 Mean Min. January air temp. (°C)	25.101	2.3404	8	0.88	23.9
	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	-5.2579	0.3362	8	0.92	13.8
Aboveground biomass (t ha <sup>-1</sup> )	1977 water balance <sup>1</sup> (cm)	991.25	8.4176	7	0.85	40821.0
	1977 May-Oct. evap. (cm)	1829.1	-14.495	7	0.85	40074.0

TABLE 5. Continued.

Y	X	A	B	n	R <sup>2</sup>	S <sup>2</sup> <sub>y·x</sub>
	Mean annual precip. (cm)	-55.408	4.5493	7	0.75	68675.0
	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	-277.58	12.591	8	0.94	14.9
	Leaf area (ha ha <sup>-1</sup> )	-50.976	35.318	8	0.91	22066.0
	1977 May-Oct. precip. (cm)	13.004	19.294	7	0.57	116822.0
	Mean May-Oct. precip. (cm)	-77.175	26.733	7	0.62	102615.0
	1976-1977 winter temp. index (%)	1009.0	-12.085	8	0.83	39376.0
	1977 Mean min. January air temp (°C)	864.62	88.323	8	0.91	24526.0
Aboveground NPP (t ha <sup>-1</sup> yr <sup>-1</sup> )	1977 water balance <sup>1</sup> (cm)	12.052	0.0945	7	0.91	2.8
	1977 May-Oct. evap. (cm)	21.26	-0.1606	7	0.89	3.5
	Mean annual precip. (cm)	0.1008	0.0528	7	0.86	4.5
	Mean May-Oct. precip. (cm)	-0.1082	0.3084	7	0.71	9.4
	1976-1977 winter temp. index (%)	12.003	-0.1287	8	0.82	5.0
	1977 mean min. January air temp. (°C)	10.569	0.9788	8	0.97	1.0
	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	-1.8344	0.1365	8	0.95	1.4

<sup>1</sup>Actual extraction of soil water is used in these equations.

<sup>2</sup>Soil water storage capacity is used instead of extraction in these equations.

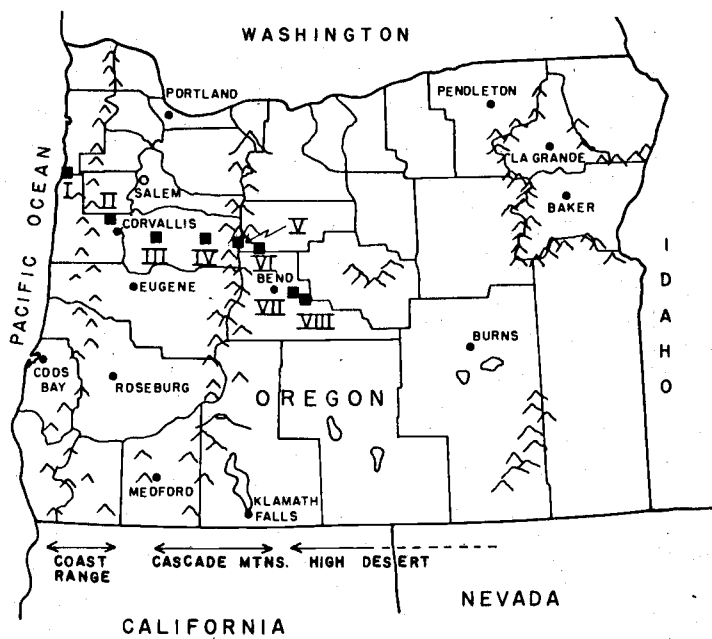


FIG. 1. Location of study sites in Oregon. The stands and their environments are described in Tables 1 and 2.

FIG. 2. Coastal Tsuga heterophylla/Picea sitchensis (plot Ib), in the spring, 1976. Understory is dominated by 2 m Tsuga. Stand is 130 years old. U.S. Forest Service photo by Larry Huditz.





FIG. 3. Subalpine Tsuga mertensiana (plot V), in December, 1976.

Snowpacks 2 m in depth are present much of the winter.



FIG. 4. Pinus ponderosa (plot VI), located on the eastern slope of the Cascade Mountains. Understory shrubs are the nitrogen fixing Pursia tridentata and Artemisia tridentata var. tridentata.



FIG. 5. Juniperus occidentalis (plot VII, and intensive site for Gholz 1979), located at 1356 m on a broad ridge in central Oregon. Largest trees are about 300 years old.



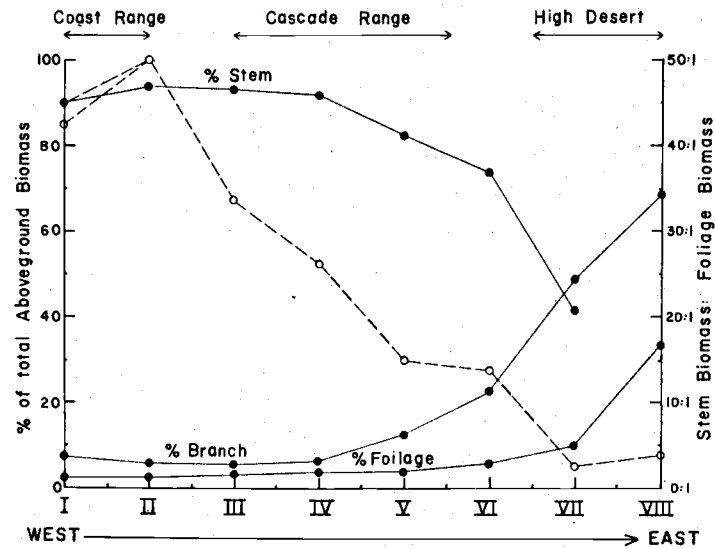


FIG. 6. Distribution of biomass in each stand along the transect. Artemisia wood was considered to be all "branch." Percentages are connected by solid lines and the stem: foliage biomass ratios by a dashed line.

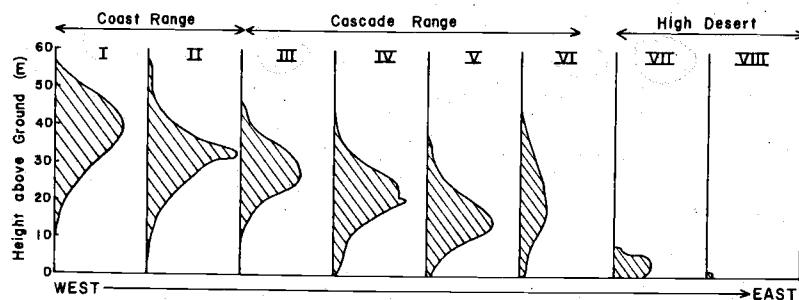


FIG. 7. Patterns of overstory foliage biomass with height for each study site. Foliage was assumed to be evenly distributed throughout the canopy of individual trees. The amount of foliage represented is listed in Table 3.



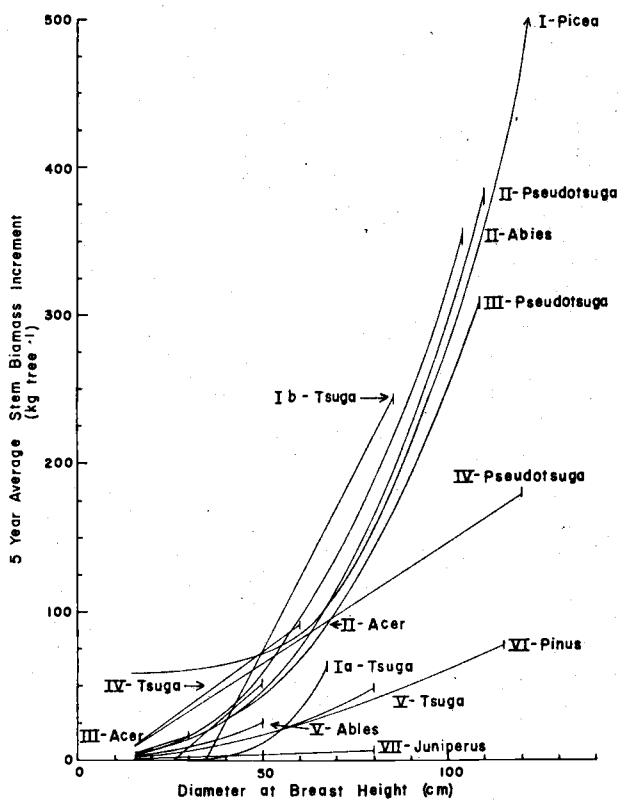
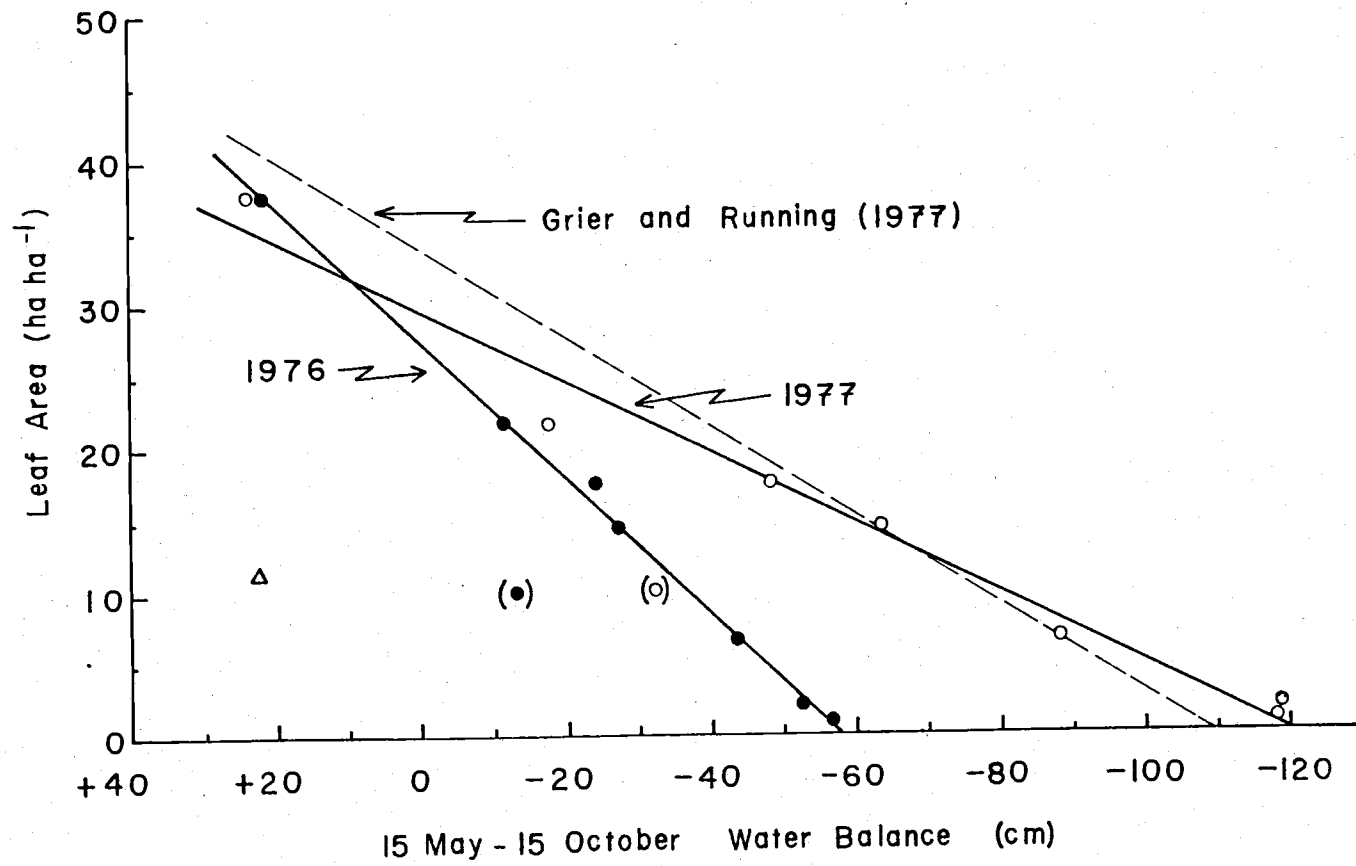


FIG. 8. Five year stem biomass increments as a function of DBH for tree species (> 15 cm DBH) along transect. Line lengths reflect actual DBH ranges for each stand. Equations for stem and branch biomass increments are in Table 4. Picea data are from Fujimori et al. (1976), and Juniperus data from Gholz (1979).

FIG. 9. Relationships between leaf area and a growing season site water balance. Ia and Ib are averaged for this plot. Grier and Running's (1977) regression based on average values for five sites is the dashed line. Open circles are 1977 data, closed circles are 1976 data. Plot V, the subalpine site, is enclosed in parentheses, while a wind-damaged coastal site (Fujimori et al. 1976) is represented by the triangle. Equations and statistics are in Table 5.



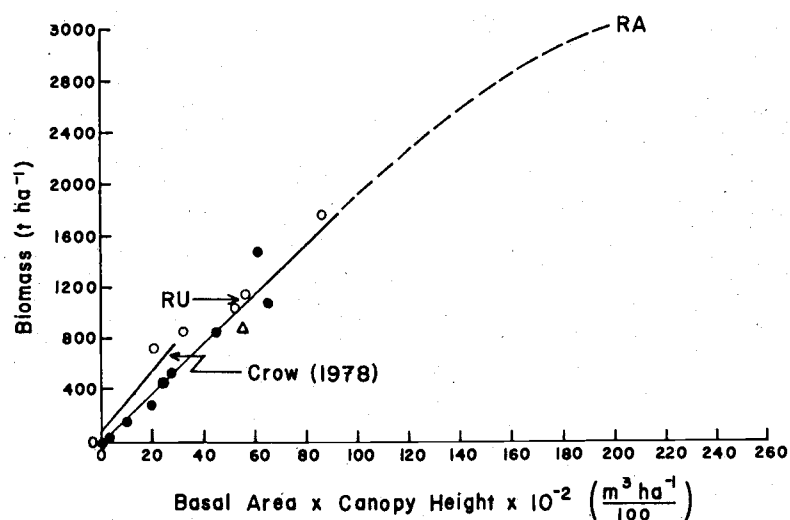


FIG. 10. Relationship between stand basal area times canopy height and aboveground biomass for Pacific northwestern ecosystems. The triangle represents the wind-damaged site (Fujimori et al. 1976), RU and RA are an upslope redwood and an alluvial flat redwood stand from Westman and Whittaker (1975), and open circles are a variety of old-growth conifer forests in western Oregon from Waring et al. (1978).

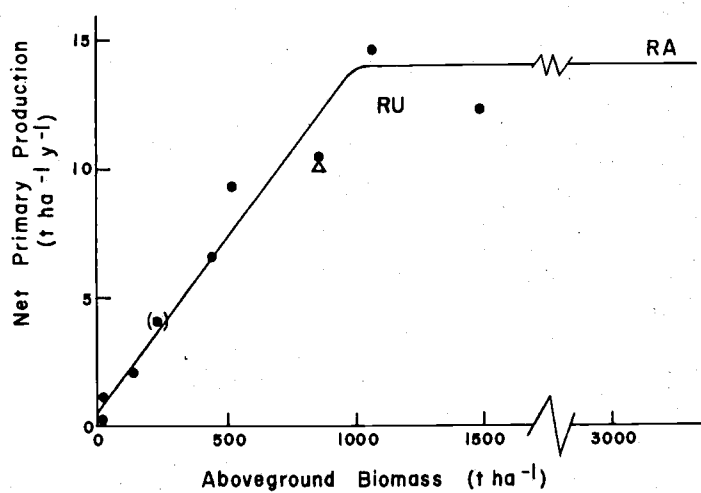


FIG. 11. NPP as a function of total aboveground biomass. Symbols are as in Fig. 10. Line is hand-fit to the points.

FIG. 12. Aboveground NPP of tree dominated ecosystems in relation to leaf area (original data were all standardized to all-sided leaf areas). Region I is unoccupied, Region II includes 25 young stands, not yet fully occupying the site or otherwise "immature", and Region III includes 43 mature stands from montane tropical forests, temperate broadleaf and needle-leaf forests, and boreal forests. Low elevation tropical forests are excluded. Dots are stands from this study, and other symbols are as in Fig. 10. The remaining data are from Whittaker et al. (1974), Whittaker (1966), Grier and Logan (1977), Wells et al. (1975), Fujimori et al. (1976), Kitazawa (1977), Tadaki and Kawasaki (1966), Ovington (1957), Satoo (1964), Reiners (1972), Monk et al. (1970), Fujimori (1971), Grier (pers. comm.), Albrektson et al. (1977), Miller and Miller (1976), Elkington and Jones (1974), Rochow (1974), Crow (1978), Zavitkovski and Stevens (1972), and Zavitkovski et al. (1974). In some cases leaf areas were estimated from foliage biomass using appropriate conversions.

